Interaction between Meloidogyne incognita and Fusarium oxysporum f. sp. phaseoli on Selected Bean Genotypes

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Abstract: Four bean genotypes (IPA-1, A-107, A-211, and Calima), representing all possible combinations of resistance and susceptibility to Fusarium oxysporum f. sp. phaseoli (Fop) and Meloidogyne incognita, were each inoculated with three population densities of these pathogens. Calima and A-107 were resistant to Fop; A-107 and A-211 were resistant to M. incognita; and IPA-1 was susceptible to both pathogens. In Fop-susceptible lines (IPA-1 and A-211), the presence of M. incognita contributed to an earlier onset and increased severity of Fusarium wilt symptoms and plant stunting. However, the Fop-resistant Calima developed symptoms of Fusarium wilt only in the presence of M. incognita. Genotype A-107 (resistant to both M. incognita and Fop) exhibited Fusarium wilt symptoms and a moderately susceptible reaction to Fop only after the breakdown of its M. incognita was generally increased as inoculum density of M. incognita was increased on the M. incognita was generally However, these factors were decreased as the inoculum density of Fop was increased. It was concluded that severe infections of bean roots by M. incognita increase the severity of Fusarium wilt on Fop-susceptible genotypes and may modify the resistant reaction to Fop.

Key words: bean, Fusarium oxysporum f. sp. phaseoli, fusarium wilt, host resistance, interaction, Meloidogyne incognita, nematode, Phaseolus vulgaris, root galling, temperature.

Interactions between *Meloidogyne* spp. and several formae speciales of F. oxysporum have been described on 20 crop species (19,25). These studies demonstrated that the presence of root-knot nematodes enhanced wilt development in Fusariumsusceptible cultivars. A number of these studies also suggested that resistance to Fusarium wilt pathogens was reduced when resistant cultivars were inoculated with Meloidogyne spp. before their inoculation with the wilt pathogen. However, the latter conclusion was not confirmed for several other crops such as cabbage (11), chrysanthemum (18), muskmelon (5), peas (9), summer squash (7), and tomato (2). Thus, the information available suggests that the modification of the resistance reaction to Fusarium wilt by Meloidogyne spp. is not a universal phenomenon and warrants investigation for each crop species.

Both Fusarium oxysporum f. sp. phaseoli (Fop) and Meloidogyne incognita (Mi) are destructive pathogens of beans, and both are widely distributed throughout the major bean production areas of the world (1,3, 24). Thus, the possibility exists that these pathogens when present together in bean fields may interact synergistically, causing more damage and higher wilt severity than either alone. Therefore, this study was conducted to determine the possible role of Mi in modifying the wilt reaction of Fusarium-susceptible and resistant bean genotypes.

MATERIALS AND METHODS

Monosporic cultures of a highly virulent isolate of Fop, originally obtained from Brazil, were established and multiplied on acidified potato dextrose agar at 26 C. Inoculum preparation, plant inoculation, and incubation procedures were as described previously (13). Four bean genotypes (A-107, IPA-1, A-211, and Calima) were selected for this study. The reactions of these genotypes to both Fop and Mi were recently determined (13) and provided all the possible combinations of resistance and susceptible reactions. Genotypes A-107 and IPA-1 are resistant and susceptible, respectively, to both pathogens; A-211 is resistant to Mi and susceptible to Fop, and Calima is resistant to Fop and susceptible to Mi.

Disinfested seeds of the four cultivars were planted in 10-cm-d pots filled with pasteurized (70 C for 30 minutes) sand-soil

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(coarse sandy loam) mix (1:1, v:v), inoculated with freshly hatched eggs of Mi race 3. Eggs of Mi were harvested from infected tomato roots (6 to 12 weeks) using sodium hypochlorite (17). Inoculation of plants by Mi was accomplished by pipetting 1 ml of the appropriate concentration of the egg suspension onto each bean seed and immediately covering the seeds with pasteurized sand-soil mixture. The pots were maintained for 2 weeks in a growth chamber at a temperature of 18–20 C in a 12-hour photoperiod (light intensity = 235 μ E/m²/sec). The plants were then removed and inoculated with Fop, utilizing the dip inoculation technique (25). Inoculated plants were replanted in the original pots and transferred to the greenhouse (26 C temperature) for an additional 4 weeks. Pots were watered twice a day and fertilized weekly with 50 ml solution of NPK (16-32-16). Control of insects and foliar diseases was provided as needed.

Three inoculum densities were included for each pathogen. The densities for Fop were 0, 10^4 , and 10^6 spores/ml suspension, whereas those for Mi were 0, 1,500, and 3,000 eggs/500 ml of soil (pot). Thus, each line evaluated was inoculated with nine combinations of inocula, which were abbreviated as given in Table 1.

The statistical design of the tests was a $3 \times 3 \times 4$ factorial, for each genotype, in a randomized complete block design with five replications. Individual plots consisted of one pot with two plants. Wilt incidence and severity were recorded weekly for each plant in the pot and the results were pooled, whereas severity of root galling and nematode reproduction were deter-

TABLE 1. Combination of *Meloidogyne incognita* (Mi) and *Fusarium oxysporum* f. sp. *phaseoli* (Fop) inocula used in the experiment.

Inoculum density of Mi (eggs/pot)	Inoculum density of Fop (spores/ml)				
	0	10 ⁴	10 ⁶		
0	M1 F1	M1 F2	M1 F3		
1,500	M2 F1	M2 F2	M2 F3		
3,000	M3 F1	M3 F2	M3 F3		

mined at harvest. Wilting severity was evaluated using a scale from 1 (no visible disease symptoms) to 9 (96-100% of the tissues affected). Ratings of 2-8 indicate that 1-5, 6-10, 11-25, 26-50, 51-75, 76-90, and 91-95% of tissue affected with typical symptoms of wilting. The experiment was repeated once and the data of each trial were subjected to analysis by a two-way ANOVA, with similar results for each. The data obtained from the uninoculated check treatments for Fusarium (F1) were not included in the analysis of variance for wilt severity evaluation, whereas those of Meloidogyne (M1) were not included in the analysis of variance for the data on root galling and nematode reproduction. The data on reproduction of Mi were transformed to natural log scale before performing the ANOVA.

Effect of incubation temperature: Two sets of the same four bean genotypes used in the previous experiments were similarly prepared. Seeds were surface disinfected, planted in 10-cm-d clay pots (2 seeds/pot), inoculated with 3,000 fresh eggs of Mi race 3 per pot, and incubated in growth chambers at 19 ± 1 or 27 ± 1 C for 2 weeks. All the plants were removed from the pots, their roots cleaned in running tap water and inoculated with 10⁶ spores/ml suspension of Fop, as previously described. The inoculated seedlings were incubated for an additional 4 weeks in the greenhouse at a fluctuating temperature of 20 to 28 C. The individual pots with two plants were arranged in a randomized complete block design with five replications. The incidence and severity of Fusarium-wilt symptoms were determined weekly; whereas root galling severity, nematode reproduction, and plant dry weight were recorded at harvest (6 weeks after planting). The experiment was repeated once and the data were evaluated separately by ANOVA, followed by Duncan's multiple-range test to compare means.

RESULTS

Effect of Fop and Mi on severity of Fusarium wilt: Wilt symptoms progressed rapidly in

the inoculated Fusarium-susceptible genotypes IPA-1 and line A-211. Initial symptoms (chlorotic and wilted areas at the margins of the primary leaves) of Fusarium wilt were observed as early as 5 days after inoculation. At 21 to 28 days after inoculation most of the Fusariumsusceptible plants were necrotic and defoliated with pink-orange spore masses visible on the surface of the stem tissues. Increasing the inoculum density of Fop resulted in a corresponding increase in the severity of Fusarium wilt symptom development and restriction of plant size on susceptible genotypes IPA-1 and A-211.

Wilt symptoms were observed throughout a period of 4 weeks after inoculation with the maximum doses of Fop and Mi; lower doses produced intermediate results. The presence of Mi contributed to an earlier onset of Fusarium wilt symptoms and plant stunting on IPA-1 (Fig. 1A). Genotype A-211 had the greatest susceptibility to Fop among the bean lines tested, especially at the highest inoculum density. Plants of A-211 inoculated with both Fop and Mi showed visible increased stunting, as well as exhibiting similar wilting severity ratings throughout the duration of the experiment (Fig. 1B).

The genotype Calima (resistant to Fusarium wilt) did not show visible Fusarium wilt symptoms at 28 days after inoculation with different densities of Fop. However, moderate wilt developed in the presence of Mi (Fig. 1C). The combined effects of high densities of Fop and Mi in this genotype were expressed as wilting, stunting, and chlorosis of the lower leaves. Thus, a significant (P = 0.05) interaction was observed at the end of the experiment among the different inocula combinations of Fop and Mi on Calima (Fig. 2C). No interaction between these two pathogens was observed, as the presence of Mi at different densities did not affect the incidence and severity of wilting in the other three genotypes (Fig. 2A,B,D). The geno-

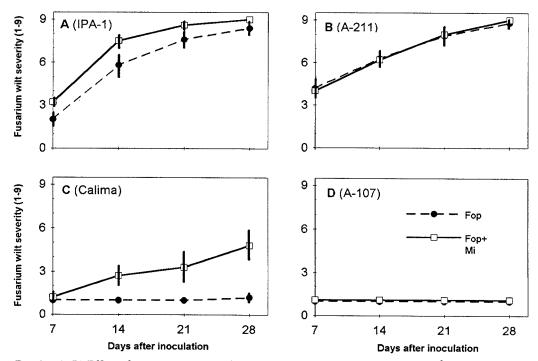


FIG. 1. A–D) Effect of Fusarium oxysporum f. sp. phaseoli alone (Fop [broken line] at 10^6 spores/ml suspension) and in combination with *Meloidogyne incognita* (Mi [solid line] at 3,000 eggs/pot) on the development and severity of wilting on four bean genotypes. Fusarium wilt severity rated on a scale of 1 = no visible symptoms to 9 = >95% of tissues affected. Bars indicate SE.

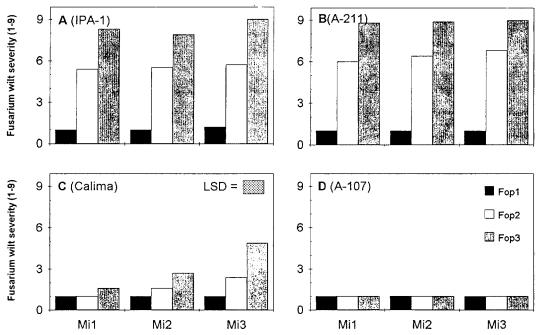


FIG. 2. A–D) Results of different combinations of inocula of *Meloidogyne incognita* (Mi) and *Fusarium oxy-sporum* f. sp. *phaseoli* (Fop) on the severity of Fusarium wilt symptoms on four bean genotypes at 4 weeks postinoculation with Fop. Mi 1, Mi 2, and Mi 3 refers to inoculum density of 0, 1,500, and 3,000 eggs/pot, respectively; whereas Fop 1, Fop 2, and Fop 3 refers to 0, 10⁴, and 10⁶ spores/ml suspension, respectively. Fusarium wilt severity rated on a scale of 1 = no visible symptoms to 9 = >95% of tissues affected. Least significant difference (LSD) is only shown in the genotype with significant treatment interactions (P = 0.05).

type A-107 was resistant to Fop and did not exhibit any Fusarium wilt symptoms during the experiment (Fig. 1D and 2D).

Effect of Fop and Mi on root galling severity and reproduction of Mi: Differences (P = 0.05) in root galling were observed on the Meloidogyne-susceptible IPA-1 and Calima (Fig. 3A,C). In contrast, the Mi-resistant A-211 and A-107 exhibited a resistant reaction with low incidence of visible rootgalling symptoms (Fig. 3B,D). Root galling severity was generally increased as inoculum density of Mi was increased on IPA-1 and Calima. However, in IPA-1 the severity of root galling diminished as the inoculum density of Fop was increased due to rotting of roots (Fig. 3A).

Reproduction of Mi on the same bean genotypes followed a similar pattern to that of the root galling (data not shown). Genotype A-107 supported limited reproduction of Mi, and there was a significant difference of the number of eggs produced on plants inoculated with the low and high initial density of Mi. Genotype A-211 supported a low reproduction of Mi regardless of the initial density of Mi used. Reproduction of Mi on the two Mi-susceptible genotypes increased as the initial density of Mi was increased. Generally, reproduction of Mi decreased as the density of Fop inoculum was increased.

Effect of incubation temperature on Mi susceptibility and Fusarium-wilt severity: Significant modifications in the incidence and severity of Fusarium-wilt development were observed when the temperature of incubation was varied during the first 2 weeks after Mi inoculation. Symptoms of Fusarium wilt were detected earlier and the rate of disease development was higher in Miinfected plants incubated at 27 C than those incubated at 19 C (Fig. 4). Additionally, the Fop- and Mi-resistant genotype (A-107) exhibited a moderately susceptible reaction to Fusarium at 27 C.

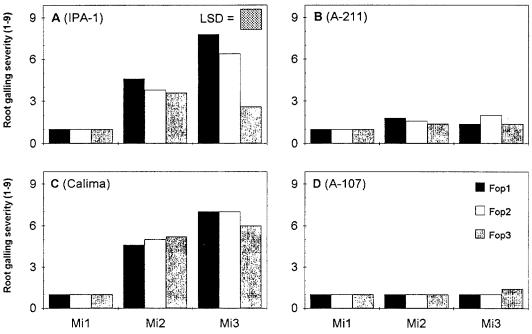


FIG. 3. A–D) Influence of different combinations of inocula of *Meloidogyne incognita* (Mi) and *Fusarium oxysporum* f. sp. *phaseoli* (Fop) on the severity of root galling on four bean genotypes at 6 weeks postinoculation with Mi. Mi 1, Mi 2, and Mi 3 refers to inoculum density of 0, 1,500, and 3,000 eggs/pot, respectively; whereas Fop 1, Fop 2, and Fop 3 refers to 0, 10^4 , and 10^6 spores/ml suspension, respectively. Root galling severity rated on a scale of 1 = no visible symptoms to 9 = 95% of root system galled. Least significant difference (LSD) is only shown in the genotype with significant treatment interactions (P = 0.05).

Four weeks after inoculation with Fop, an interaction was observed between the initial incubation temperature and reaction of bean genotypes to Fop and Mi as measured by wilt symptom severity, root galling severity, dry plant weight, and nematode reproduction. The Fusariumresistant A-107 and Calima exhibited increased susceptibility to Fop (P = 0.05) as a result of inoculation with Mi and incubation at 27 C for 2 weeks (Table 2). In contrast, the Fusarium-susceptible IPA-1 and A-211 behaved similarly to Fop when initial temperatures were 19 or 27 C.

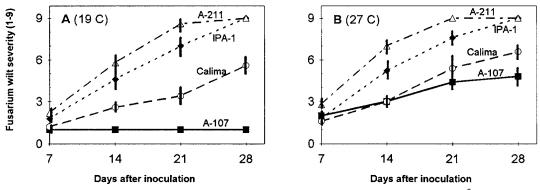


FIG. 4. A–B) Development of Fusarium-wilt in four bean genotypes inoculated with 10^6 spores/ml of *Fusarium oxysporum* f. sp. *phaseoli* and 3,000 eggs/pot of *Meloidogyne incognita* as affected by incubation temperatures of 19 C (A) and 27 C (B) during the first 2 weeks. Fusarium wilt severity rated on a scale of 1 = no visible symptoms to 9 = >95% of tissues affected. Bars indicate SE.

Bean germplasm	Wilt severity (1-9)†		Root-galling severity (1-9)†		Plant-dry weight (g/plant)‡		Eggs/g dry root (in 1,000's)§	
	19 c	27 C	19 C	27 C	19 C	27 C	19 C	27 C
IPA-1	9.0 a	9.0 a	4.0 b	3.4 b	1.2 c	1.0 b	5 c	4 c
A-107	1.0 c	4.8 c	1.0 с	3.8 b	8.8 a	5.2 a	10 b	29 Ь
A-211	9.0 a	9.0 a	1.6 c	1.4 c [¶]	1.0 с	0.7 b	3 d	1 d¶
Calima	5.6 b	6.6 b	6.0 a	5.6 a	5.8 b	4.8 a	209 a	156 a

TABLE 2. Severity of Fusarium-wilt and root galling, plant dry weight, and reproduction of *Meloidogyne* incognita in four bean genotypes as influenced by incubation temperatures.

 \dagger Fusarium wilt and root galling severity were evaluated on a scale from 1 (= no visible symptoms) to 9 (>95% of tissues affected).

‡ Plant dry weight was determined at termination of the test (6 weeks after planting).

§ Data were transformed to natural log before analysis of variance.

^{\parallel} The expected breakdown of resistance due to the high incubation temperatures was not observed due to the extensive decay of the root system caused by F. axysporum f. sp. phaseoli.

[¶] In each column, mean values followed by a common letter are not different according to the Duncan multiple-range test (P = 0.05).

Root galling by Mi was also affected by incubation temperature during the first 2 weeks. Root-gall ratings were increased (P = 0.05) on A-107 incubated at 27 C, but not for the other genotypes (Table 2).

Plant dry weight of all the cultivars inoculated with Mi and incubated at 27 C was decreased as compared to corresponding plants incubated at 19 C (Table 2). However, statistical differences in the suppression of plant growth as a result of incubation at the higher temperature were observed only in lines A-107 and the cultivar Calima, as they were suppressed by 41 and 17%, respectively.

Nematode reproduction on IPA-1 and A-211 plants initially incubated at 19 or 27 C were not different (Table 2). Higher reproduction of Mi was observed on A-107 incubated at 27 C than those incubated at 19 C during the first 2 weeks, whereas reproduction on Calima was decreased by incubation at 27 C.

DISCUSSION

The incidence and severity of Fusariumwilt symptoms caused by Fop were found to be the most reliable parameters in this study for assessing the susceptibility of bean cultivars to this pathogen and its interaction with Mi. The genotype A-107 and Calima were resistant to Fusarium wilt; whereas IPA-1 and A-211 were susceptible. These results are in agreement with those reported previously (13,25). However, the amount of wilting on Fopsusceptible genotypes was modified with prior inoculation with Mi, with the susceptibility of IPA-1 to Fop increasing in the presence of Mi. Similar interactions have been described for *F. oxysporum* and *M. incognita* on several crop species (2,5,11,15,16,18,26,27). Fusarium-susceptible cultivars parasitized by *Meloidogyne* spp. often are colonized faster by the wilt pathogen as compared to those that are not infected by Mi (2,15,16).

Although Calima was resistant to Fop, it showed an increased susceptibility to Fop with co-infection by Mi. Thus, the presence of *M. incognita* lowered the resistance to the Fusarium-wilt pathogen in Calima. Similar results were obtained with the bean cultivar Dark Red Kidney (France and Abawi, unpubl.). Breakdown of the resistance to Fop by prior infection with M. incognita has been reported for several crops, including alfalfa (15), chickpea (27), cotton (29), cowpeas (16), cucumber (14), soybean (22), tobacco (26), and tomato (28). The extensive physiological and anatomical changes produced by infections of Mi and other species in the root system result in modification of the normal functions and possibly the defense mechanisms against soilborne pathogens. Giant cells induced by Meloidogyne spp. are found often with

higher infection sites of major and minor fungal soilborne pathogens and saprophytes (19,20). Bean plants infected by M. incognita contain significantly lower quantities of chlorophyll, carbohydrates, and nitrogen compounds, and show reduced water and nutrient uptake. Consequently, such infected plants are weaker and support fewer flowers, pods, and seeds as compared to healthy plants (3,21,30). Overall, plants infected with root-knot nematodes show an increased vulnerability to any stress condition. However, the breakdown of resistance to the Fusariumwilt pathogen (F. oxysporum f. sp. lycopersici) in tomato cultivars by infections with M. incognita is likely under genetic control (2). Apparently, the reaction of Fusarium-wilt resistant cultivars that did not harbor the dominant monogenic resistance gene against F. oxysporum f. sp. lycopersici was modified by prior infections with Mi (19).

In this study, the Fop and Mi-resistant A-107 exhibited visible Fusarium wilt symptoms when inoculated with both pathogens and incubated at high temperature (27 C) during the first 2 weeks. Apparently, the resistance to Mi was lost or altered at high temperature, and the nematode then modified resistance to Fusarium wilt. Nevertheless, the root damage and wilting severity caused by Fop on A-107 was still lower than those occurring in other cultivars. These results suggest that for tropical or hot climatic production areas where both of these pathogens are endemic, the use of temperature-insensitive resistance to M. incognita in beans should be given important consideration.

Breakdown of resistance to *M. incognita* by high temperatures has been described in beans (23) and other plant species (6,10). However, the combined effect of elevated temperatures and *M. incognita* on Fusarium wilt incidence and severity has been less studied. The combined effects of these two pathogens and temperatures of incubation were studied by Griffin and Thyr (15) in alfalfa, but they did not test a resistant cultivar to both pathogens. Abawi and Barker (2), working on the interaction between M. incognita and F. oxysporum f. sp. lycopersici in tomato, included in their study the cultivar 'Nematex', which is resistant to both pathogens. However, they concluded that although this cultivar lost its resistance to Mi at high temperature, it retained its resistance to F. oxysporum f. sp. lycopersici.

Resistance to F. oxysporum in crop plants can be either monogenic or polygenic (4). The monogenic type of resistance has been suggested to be more stable and not likely to be modified by temperature or infections by plant-pathogenic nematodes as the polygenic sources of resistance. For example, prior infections of tomato by Mi modified the polygenic resistance sources to F. oxysporum f. sp. lycopersici, but not the resistance sources controlled by the dominant single I- genes (2). The inheritance of resistance to Fop in line A-107 is not known, but these results suggest that it might be under the control of polygenic factors.

Infection of Fusarium-susceptible cultivars by Fop was detrimental to the reproduction of Mi and the development of root galling. The extensive root damage caused by Fop probably decreased the sites for MI penetration and sedentary feeding. Moreover, giant cells induced by Meloidogyne spp. are known to increase susceptibility to the wilt pathogen and soil microorganisms (20). This damage may also explain the restricted root-knot nematode reproduction potential and the development of rootgalling symptoms. Similar results have been published for alfalfa (15), soybean (22), and tobacco (26). In addition, translocatable toxic metabolites produced by plant-pathogenic fungi may cause deterioration of giant cells, reduce hatching, and immobilize the second-stage juveniles (8,12). All these processes may have contributed to the observed suppression in reproduction of Mi in this investigation.

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