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Ability of Nonpathogenic *Fusarium oxysporum* Fo47 to Protect Tomato against Fusarium Wilt

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The nonpathogenic *Fusarium oxysporum* strain Fo47 is an effective biocontrol agent against Fusarium wilt of tomato caused by *F. oxysporum* f. sp. *lycopersici*. Inoculant delivery protocols in which plants were exposed to Fo47 prior to challenge with the pathogen, so as to promote the strain's ability to induce resistance to Fusarium wilt in tomato, were assessed. In rockwool microcosms, the biocontrol efficacy of Fo47 (inoculated at sowing) against *F. oxysporum* f. sp. *lycopersici* Fol8 (race O) was not improved following a second inoculation of the biocontrol strain at transplanting (i.e., when plants became exposed to the pathogen) or using inoculum levels of Fo47 higher than 10^4 conidia/ml of nutrient solution. In natural soil microcosms (with Fo47 applied into potting mix prior to sowing and to roots at transplanting), effective control of Fusarium wilt required inoculum levels of 10^5 conidia of Fo47/ml. Strain Fo47 was also studied in greenhouse microplots in which soil was artificially infested with the pathogenic strain Fol8. Fo47 delayed the progression of the disease in each of the two years and also improved final plant health in the second year. The protective effect of Fo47 resulted in a significant increase in the yield of first-grade tomatoes in the first year. Treatments did not influence yield in the second year. The results of this investigation illustrate how a biocontrol fungus can be used at a moderate inoculum level to obtain disease control under commercial conditions. It is hypothesized that this was achieved by making use of the ability of the biocontrol agent to induce resistance to Fusarium wilt in tomato. © 1999 Academic Press

Key Words: **nonpathogenic *Fusarium oxysporum*; biocontrol; induced resistance; Fusarium wilt; tomato; *Fusarium oxysporum* f. sp. *lycopersici*.**

INTRODUCTION

Fusarium wilts are economically important soilborne diseases affecting many crops worldwide. Chemical control of Fusarium wilts relies to a large extent on the fumigant methyl bromide. However, the use of methyl bromide will be restricted in the near future due to environmental and food quality considerations. The development of resistant cultivars is an attractive strategy against Fusarium wilts but new virulent races of fusaria can appear within a few years after commercialization of resistant cultivars. Biological control methods, based on the use of beneficial microorganisms isolated from suppressive soils, represent an alternative for protection of plants against Fusarium wilts (Alabouvette *et al.*, 1993).

Certain soils are naturally suppressive to Fusarium wilt, a property due in part to the role of nonpathogenic *Fusarium oxysporum* in the indigenous microbiota of those soils (Alabouvette and Couteaudier, 1992; Rouxel *et al.*, 1979; Smith and Snyder, 1971; Tamietti *et al.*, 1993). One of these nonpathogenic *F. oxysporum* is Fo47, a strain isolated from a suppressive soil that can control Fusarium wilt of several plants such as carnation, cyclamen, flax, and tomato (Alabouvette and Couteaudier, 1992; Alabouvette *et al.*, 1987, 1993; Lemanceau and Alabouvette, 1991; Lemanceau *et al.*, 1992; Postma and Rattink, 1992). This protective effect has been attributed to the ability of Fo47 to compete with pathogenic fusaria for nutrients such as organic carbon and iron, and/or for infection sites at the rhizoplane (Alabouvette and Couteaudier, 1992; Alabouvette *et al.*, 1985; Lemanceau *et al.*, 1988, 1993). Strain Fo47 is currently in the process of becoming registered for commercialization as a biocontrol agent (Alabouvette *et al.*, 1996).

Certain microorganisms can also protect plants by inducing resistance to diseases (Kuć, 1982; Matta, 1989). Several reports have documented the induction of resistance to Fusarium wilt by using either nonpathogenic strains of *F. oxysporum*, as in the case of cucumber (Mandeel and Baker, 1991) and chickpea (Hervás *et*

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al., 1995), or formae speciales of *F. oxysporum*, such as f. sp. *melonis* in cucumber (Gessler and Kuć, 1982) and f. sp. *dianthi* in tomato (Kroon *et al.*, 1991). Recently, nonpathogenic *F. oxysporum* strain Fo47 was shown to induce resistance to Fusarium wilt in tomato (Fuchs *et al.*, 1997).

A good understanding of the mechanisms responsible for crop protection is a preliminary condition for the effective use of biocontrol methods under commercial situations. Induced resistance requires that the plant be exposed to the inducing agent prior to the attack by the pathogen. The time needed for development of induced resistance is in the range of one to a few days in the case of Fusarium wilt diseases (Matta, 1989). The objective of the current work was to evaluate, in microcosms and in greenhouse microplots, the biocontrol ability of *F. oxysporum* Fo47 against Fusarium wilt. Inoculation procedures were chosen to make use of the strain's ability to induce resistance, which is one of the biocontrol mechanisms by which Fo47 was previously shown to protect tomato from Fusarium wilt (Fuchs *et al.*, 1997).

MATERIALS AND METHODS

Organisms and culture conditions. Fo47, a nonpathogenic strain of *F. oxysporum* originating from a soil suppressive to Fusarium wilts located at Châteaurenard in France (Alabouvette *et al.*, 1987) and *F. oxysporum* Schlecht f. sp. *lycopersici* Snyder & Hansen strain Fol8 (race O), which causes Fusarium wilt disease in tomato (*Lycopersicon esculentum* Mill.), were used. Both fungi were maintained on 1.5% malt agar (Keel *et al.*, 1989) at 3°C. In all experiments, they were introduced as conidia (essentially microconidia) obtained by filtration of 3-day-old liquid 2% malt cultures (24°C, shaking). The conidia were rinsed with sterile double-distilled water prior to use.

Seeds of Fol8-susceptible tomato 'Bonny Best' (Peptoseed Co., Saticoy, CA) were surface-disinfected in 1% hydrochloric acid for 30 min and rinsed several times in sterile double-distilled water prior to sowing in rockwool (Type AO 36/40-10/10, Grodan, Hedehusene, Denmark) soaking in sterile OTCMG1 nutrient solution, or in autoclaved Potgrond BF4 4C potting mix (M. de Baat B.V., Coevorden, The Netherlands). The OTCMG nutrient solutions (A. Wigger, OTCMG, Geneva, Switzerland) are routinely used to grow soilless tomatoes in Switzerland. All contain 3.1 mg $MnSO_4 \cdot H_2O$, 3.2 mg $Na_2B_4O_7 \cdot 10H_2O$, 0.6 mg $CuSO_4 \cdot 5H_2O$, 1.3 mg $ZnSO_4 \cdot 7H_2O$, 0.12 mg $Na_2MoO_4 \cdot 2H_2O$, 1 µl 62% HNO_3, 25 mg Fe-EDDHA (Sequestrene 138 Fe, Novartis), and 4 mg EDDHA (Sigma) per liter. The OTCMG1 solution (used until 5 days after sowing) contained also 0.96 g $Ca(NO_3)_2 \cdot 4H_2O$, 0.36 g $MgSO_4 \cdot 7H_2O$, 0.17 g K_2SO_4, 78 mg KH_2PO_4, 0.45 g KNO_3, and 66 mg $NH_4H_2PO_4$ per liter. The OTCMG2 solution (used from day 6 to day 28 after sowing) contained also 1.1 g $Ca(NO_3)_2 \cdot 4H_2O$, 0.45 g $MgSO_4 \cdot 7H_2O$, 0.22 g K_2SO_4, 98 mg KH_2PO_4, 0.56 g KNO_3 and 83 mg $NH_4H_2PO_4$ per liter. The OTCMG3 solution (used from day 29 after sowing) contained also 1.40 g $Ca(NO_3)_2 \cdot 4H_2O$, 0.54 g $MgSO_4 \cdot 7H_2O$, 0.26 g K_2SO_4, 120 mg KH_2PO_4, 0.68 g KNO_3, and 99 mg $NH_4H_2PO_4$ per liter. Tomato seedlings were grown in a greenhouse at 50% relative humidity with 16 h of light (25°C) and 8 h of dark (20°C) prior to transplanting. All microcosm experiments were carried out in this greenhouse.

Biocontrol experiment in rockwool microcosms. The objective of the first experiment was to assess whether the number of inoculations with Fo47 and inoculum levels had an influence on biocontrol of Fusarium wilt of tomato in rockwool microcosms. Rockwool is an artificial inorganic substrate widely used for commercial production of vegetables and flowers under soilless conditions. Soilborne fungi are not present in rockwool but may be introduced by irrigation water and/or airborne deposition and can cause considerable damage (Alabouvette *et al.*, 1996). Tomato seeds were sown in rockwool cubes previously soaked in OTCMG1 nutrient solution and 18 days later the tomato seedlings were transplanted into rockwool blocks previously soaked in OTCMG2 nutrient solution. Each plant was watered with a drip-irrigation system. The pathogen *F. oxysporum* f. sp. *lycopersici* Fol8 was added to the rockwool blocks immediately after transplanting (10^6 conidia/ml of nutrient solution). Strain Fo47 was inoculated once, by soaking the rockwool cubes at sowing, or twice by soaking the rockwool cubes at sowing and the rockwool blocks at transplanting (inoculation levels of 10^4, 10^5, or 10^6 conidia/ml of nutrient solution). The experiment included an uninoculated control, as well as a treatment in which only Fol8 was present. Severity of Fusarium wilt was assessed when the progression of wilt symptoms stopped in the treatment with Fol8 alone (Lemanceau *et al.*, 1992), i.e., about 50 days after transplanting. The percentage of leaf yellowing/wilting was determined using a five-class scale adapted from that used by Maurhofer *et al.* (1995) and Fuchs *et al.* (1997): 0 = 0% foliar wilting, 12.5 = ($0 < x \leq 25\%$), 50 = ($25 < x \leq 75\%$), 87.5 = ($75 < x < 100\%$), and 100 = 100% (dead plant).

Biocontrol experiment in natural soil microcosms. A soil microcosm experiment was carried out to evaluate whether inoculum level of Fo47 affected the efficacy of Fusarium wilt control under conditions where the biocontrol inoculum had to compete with the resident soil microbiota. The soil used was from a fallow located at Eschikon in County Zürich in Switzerland (Wüthrich and Défago, 1991). Each microcosm (in a 450-cm^3 pot) contained 350 cm^3 of soil (i.e., 420 g of soil; soil sieved at 5 mm) above a layer of 100 cm^3 of coarse quartz sand.

Tomato seeds were sown in autoclaved potting mix and seedlings were transplanted in the soil 17 days later. The pathogen *F. oxysporum* f. sp. *lycopersici* Fol8 was added to the soil three days prior to transplanting, as a conidial suspension (10^6 conidia/cm^3 of soil). Fo47 was inoculated into the potting mix prior to sowing (10^4, 10^5, or 10^6 conidia/cm^3 of potting mix) and by soaking the roots at transplanting in suspensions containing 10^4, 10^5, or 10^6 conidia/ml, respectively. The experiment was comprised also of an uninoculated control, as well as a treatment in which only Fol8 was present. Disease severity was determined 50 days after transplanting.

Biocontrol experiments in greenhouse microplots. After having investigated Fo47 in microcosm experiments, the strain was evaluated for biocontrol of Fusarium wilt of tomato in greenhouse microplots (under natural daylight conditions). The greenhouse used was located at the ETH center in Eschikon. Tomato seeds were sown in autoclaved potting mix, grown for 21 days, transplanted in autoclaved potting mix, and grown for another 28 days. The 49-day-old plants were then transplanted in the greenhouse soil, which had been steam-treated *in situ* 21 days before. *F. oxysporum* f. sp. *lycopersici* was naturally present in the greenhouse soil, but Fol8 was added to the soil in certain treatments to increase the disease levels and to ensure a uniform presence of *F. oxysporum* f. sp. *lycopersici* in soil. The pathogen was introduced into soil 21 days after transplanting the tomatoes in the greenhouse, by spraying a conidial suspension (5×10^{10} conidia/m^2 of soil). Fo47 was added four times: to the greenhouse soil immediately after the steam treatment *in situ* (5×10^{10} conidia sprayed per m^2 of soil), into potting mix at sowing and at the first transplanting (5×10^6 conidia/cm^3 of potting mix), and at the second transplanting by soaking roots for 5 min in a suspension containing 10^6 conidia/ml prior to their introduction into soil. Three treatments were compared: no inoculation, inoculation with Fol8, and inoculation of Fol8 and Fo47. Individual plots (2.5 m $\times$ 2.5 m; 12 plants each) were surrounded by a vertical plastic liner. The experiment was started in the spring and was repeated the following year at the same location (after steaming of the soil). Disease severity was monitored as described above. Yield of first-class tomatoes (with diameter >55 mm) was recorded.

Statistical analyses. Each microcosm experiment was studied in triplicate and was performed on three independent occasions. Data were pooled since (1) repeated experiments displayed the same disease levels in the Fol8 treatment and (2) variances were homogeneous (Mandeel and Baker, 1991). A total of 8 (rockwool microcosms) or 18 plants (6 pots with 3 plants/pot; soil microcosms) were studied per treatment in each replication of repeated experiments. The greenhouse experiments were performed in duplicate, with 12 plants per replicate per treatment. Disease severity data were arcsine-transformed. Data were analyzed by analysis of variance followed, when appropriate, by Fisher's LSD tests ($P = 0.05$).

RESULTS

Influence of inoculum delivery on biocontrol of Fusarium wilt of tomato by nonpathogenic F. oxysporum Fo47 in rockwool and soil microcosms. All treatments were comprised of at least an inoculation performed at sowing (i.e., prior to exposure of the plant to the pathogen), to make use of the ability of Fo47 to induce disease resistance in tomato. In rockwool microcosms, inoculation of rockwool cubes at sowing with Fo47 at 10^4 conidia/ml of nutrient solution decreased disease severity from 55 to 41% (Fig. 1). The biocontrol efficacy of Fo47 was not improved following a second inoculation of the biocontrol fungus when tomatoes were transplanted in rockwool blocks. Similarly, increasing inoculum levels from 10^4 to 10^5 or 10^6 conidia of Fo47/ml of nutrient solution had no effect on the extent of protection, regardless of whether Fo47 was applied once or twice (Fig. 1).

The nonpathogenic *F. oxysporum* strain Fo47 was applied twice in the experiment performed in natural soil microcosms. Fo47 proved ineffective at protecting tomatoes when it was added at 10^4 conidia/cm^3 of potting mix (prior to sowing), followed by inoculation of tomato roots in a suspension containing 10^4 conidia of Fo47/ml at transplanting (Fig. 2). However, the extent of Fusarium wilt was reduced from 39 to 22% when

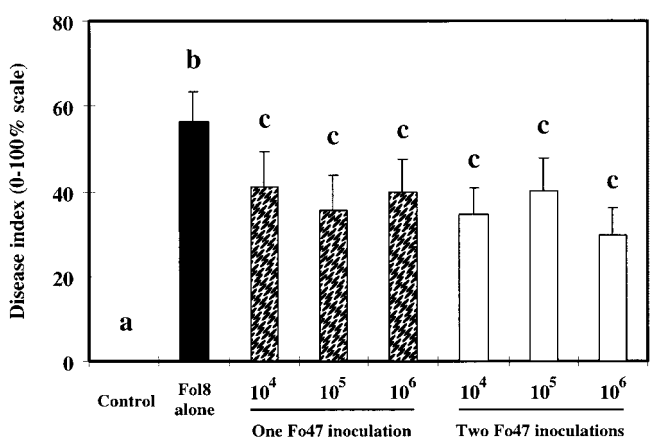

FIG. 1. Disease index of tomato plants in rockwool microcosms. The nonpathogenic *F. oxysporum* strain Fo47 was inoculated at sowing (with 10^4, 10^5, or 10^6 conidia/ml of nutrient solution) or both at sowing and at transplanting (both with 10^4, 10^5, or 10^6 conidia/ml of nutrient solution). The pathogen *F. oxysporum* f. sp. *lycopersici* Fol8 was added immediately after transplanting (10^6 conidia/ml of nutrient solution). The experiment included also an uninoculated control, as well as a treatment in which only Fol8 was present. Error bars represent standard errors. Disease index values denoted with different letters are statistically different ($P = 0.05$).

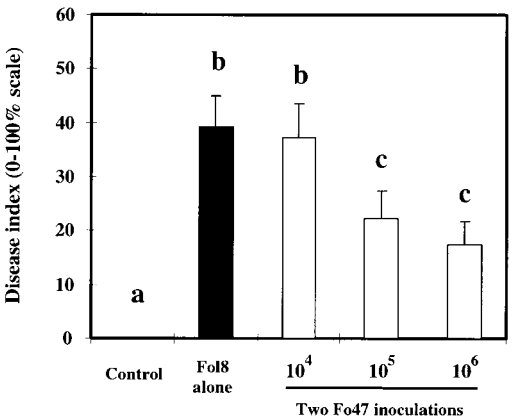

FIG. 2. Disease index of tomato plants in soil microcosms. The nonpathogenic *F. oxysporum* strain Fo47 was inoculated into the potting mix prior to sowing (10^4, 10^5, or 10^6 conidia/cm^3 of potting mix) and by soaking the roots at transplanting in suspensions containing 10^4, 10^5, or 10^6 conidia/ml, respectively. The pathogen *F. oxysporum* f. sp. *lycopersici* Fol8 was added to soil 3 days prior to transplanting (10^6 conidia/cm^3 of soil). The experiment included also an uninoculated control, as well as a treatment in which only Fol8 was present. Error bars represent standard errors. Disease index values denoted with different letters are statistically different ($P = 0.05$).

inoculation was carried out with 10^5 conidia of Fo47 per cm^3 of potting mix (prior to sowing), followed by dipping of tomato roots in a suspension containing 10^5 conidia of Fo47/ml (at transplanting). Increasing further the inoculum levels of Fo47 did not provide any improvement in protection.

Biocontrol of Fusarium wilt of tomato by nonpathogenic F. oxysporum Fo47 in greenhouse microplots. The nonpathogenic *F. oxysporum* Fo47 was assessed for biocontrol of Fusarium wilt of tomato in greenhouse microplots in which the soil was artificially infested with *F. oxysporum* f. sp. *lycopersici* Fol8. Strain Fo47, applied four times as described under Materials and Methods, delayed the progression of the disease in the first year, but the final disease index was similar to that in the treatment where only the pathogen Fol8 had been added (Fig. 3A). However, the presence of Fo47 resulted in a significant increase in the yield of first-grade tomatoes compared with the Fol8 treatment (Fig. 3B).

The experiment was repeated the following year, in the same microplots. Disease development in the Fol8 treatment was not as rapid as during the previous year, but final disease indices were similar in both experiments (Figs. 3A and 3C). Addition of Fo47 delayed the progression of Fusarium wilt and resulted in a significantly lower disease index at the end of the 146-day experiment (Fig. 3C). Tomato yields were higher than in the previous year (Figs. 3B and 3D) but they were influenced little by the treatments (Fig. 3D).

DISCUSSION

In this work, the biocontrol efficacy of nonpathogenic *F. oxysporum* Fo47 against Fusarium wilt of tomato was assessed both in microcosms and in greenhouse microplots. Results obtained in microcosm experiments showed that inoculant delivery influenced the biocontrol efficacy of Fo47 in natural soil microcosms but not in rockwool microcosms, a difference probably due to the indigenous microbiota present in the soil. Rockwool is a substrate that is initially sterile or that displays very low counts of indigenous microorganisms (Lemanceau *et al.* 1992; Alabouvette *et al.*, 1996), which we have confirmed (data not shown). Unlike in the rockwool microcosms, Fo47 needs to compete successfully with the indigenous microbiota in soil to be able to implement its biocontrol potential.

Although the experimental procedures followed in this work were not fully comparable to those used elsewhere to study Fo47, it is interesting to note that the ratio between inoculum levels of Fo47 and Fol8 needed here to protect tomato against Fusarium wilt in natural soil microcosms was significantly lower than those required for biocontrol of Fusarium wilt of carnation in rockwool (Lemanceau *et al.*, 1992) or flax in natural soil (Alabouvette and Couteaudier, 1992) by the same strain. In the last two studies, the number of conidia of Fo47 needed for effective protection was ten times higher than that of pathogenic conidia. Those results were in line with the fact that the ratio of nonpathogenic fusaria to *F. oxysporum* f. sp. *dianthi* influence their antagonism *in vitro* (Lemanceau *et al.*, 1993). In the current work, biocontrol of Fusarium wilt was achieved with an inoculum of Fo47 ten times lower than the number of conidia of *F. oxysporum* f. sp. *lycopersici* Fol8.

Mechanisms of wilt biocontrol documented for Fo47 include induced resistance (Fuchs *et al.*, 1997) and microbial competition (Lemanceau *et al.*, 1993). The fact that successful biocontrol was obtained with an inoculum of Fo47 lower than that of the pathogen suggests that induced resistance took place. One important factor with induced resistance is the need for the inducing organism to be in contact with the plant prior to exposure to the pathogen, a condition fulfilled in this work. In contrast, plants became exposed simultaneously to nonpathogenic and pathogenic strains in the work from Alabouvette and Couteaudier (1992). Advance inoculation of Fo47 was performed with carnations grown in steamed soil (Postma and Rattink, 1992) or rockwool (Lemanceau *et al.*, 1992). In the latter study, the reduction in the extent of Fusarium wilt became statistically significant only when Fo47 and pathogenic fusaria were used in a 10:1 ratio (Lemanceau *et al.*, 1992). However, in the work of Postma and Rattink (1992), which was performed with steamed

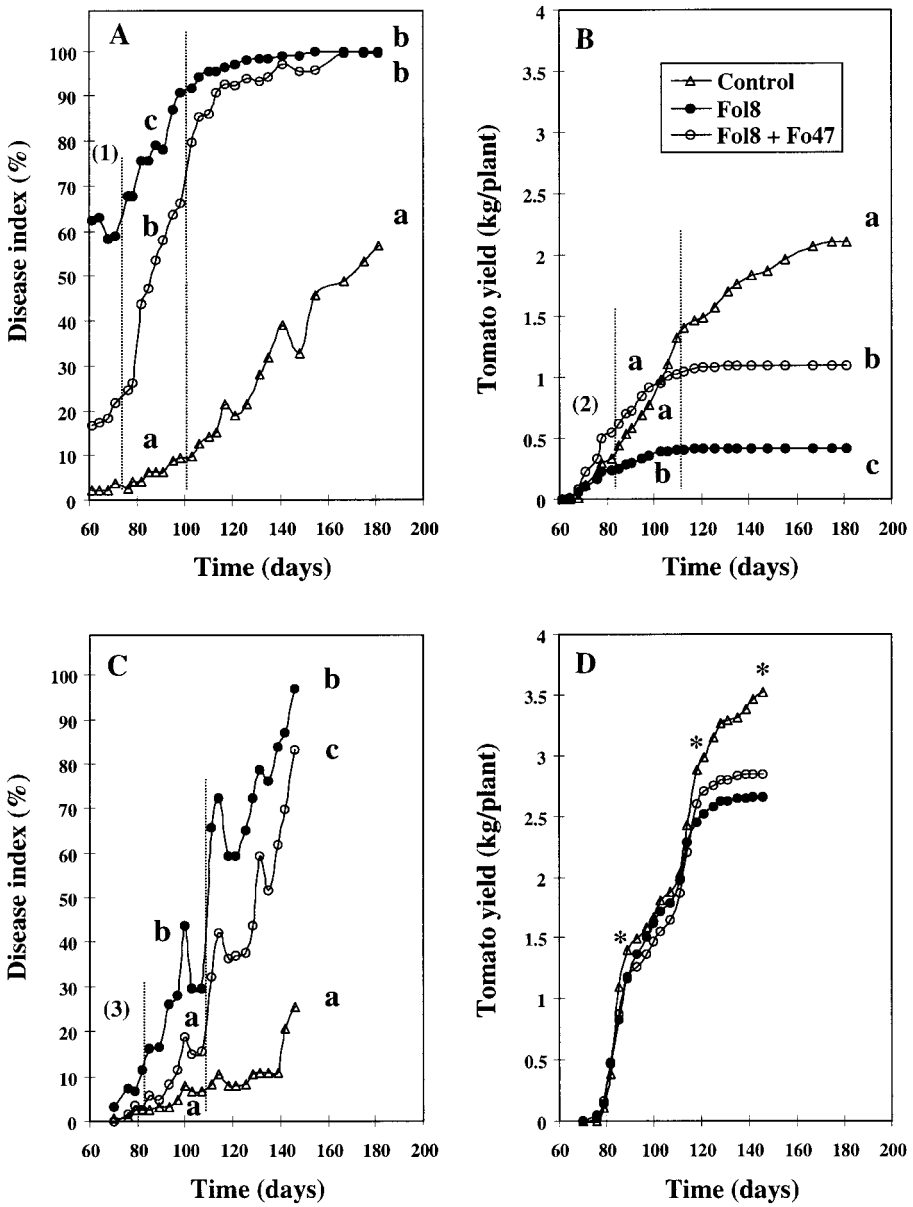

FIG. 3. Disease index (A,C) and cumulative yield (B,D) of tomato plants in greenhouse microplots. The experiment (A,B) was repeated the following year (C,D). Inoculations were performed with *F. oxysporum* f. sp. *lycopersici* Fol8 alone or with Fol8 and the nonpathogenic *F. oxysporum* strain Fo47. An uninoculated control was also studied. Statistical analyses were done at each sampling time and values that are statistically different are indicated with different letters ($P = 0.05$). (1) = The disease index was higher in the Fol8 treatment than in the other two treatments; for the latter, disease indices were statistically identical at three of the four samplings due to substantial fluctuation of data. (2) = Yield was statistically higher in the Fol8 + Fo47 treatment than in the Fol8 treatment at four of the seven samplings. (3) = There was no difference between treatments at three of the four samplings. * = Yield was statistically higher in the control than in the other two treatments at the three samplings indicated with an asterisk, and yields from the different treatments were statistically identical at the other samplings.

soil, Fo47 and *F. oxysporum* f. sp. *dianthi* were added at somewhat similar levels and the nonpathogenic strain successfully protected carnations from Fusarium wilt. Arguably, the fact that Fo47 was introduced in advance of Fol8 in the current work was likely to have also favored the strain in its competition with the pathogen (Alabouvette *et al.*, 1993). Combining different modes of action is a strategy advocated for improved biocontrol of Fusarium wilts (Alabouvette *et al.*, 1996).

Further evaluation of the biocontrol ability of *F. oxysporum* Fo47 was undertaken in greenhouse microplots, which represented experimental conditions closer to those prevailing in commercial greenhouses. Previous work has shown the difficulty in documenting the

protective effect of Fo47 in greenhouse soil naturally infested with *F. oxysporum* f. sp. *lycopersici*, due to the spatial heterogeneity of Fusarium wilt pressure (Alabouvette *et al.*, 1987). Recently, Fuchs *et al.* (1997) showed evidence that direct interactions between Fo47 and Fo18 could increase the level of protection achieved by induced resistance alone. Similarly, a nonpathogenic strain of *F. oxysporum* protected cucumber against Fusarium wilt through a combination of competition for infection sites and induced resistance (Mandeel and Baker, 1991). Therefore, several inoculation procedures were combined to deliver Fo47 in the current work. Results showed that Fo47 delayed the evolution of Fusarium wilt in both years and increased the yield of first-grade tomatoes in one year where treatments had a statistical influence on yield (Fig. 3), confirming the results of Alabouvette *et al.* (1987, 1996) on the usefulness of Fo47 as a wilt biocontrol agent.

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