Effect of Successive Watermelon Plantings on *Fusarium oxysporum* and Other Microorganisms in Soils Suppressive and Conducive to Fusarium Wilt of Watermelon

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ABSTRACT

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Five successive greenhouse plantings of watermelon cultivars Florida Giant (susceptible to Fusarium wilt) and Crimson Sweet (moderately resistant and associated with soil suppressiveness) had different effects on the populations of *Fusarium oxysporum* f. sp. *niveum*, indigenous *F. oxysporum*, and various microorganism groups in the soil and on watermelon roots within four soils representing different suppressive and conducive conditions to Fusarium wilt. Pathogen populations were not affected by planting either cultivar in an induced suppressive soil developed by monoculture of Crimson Sweet or in a nonsuppressive Florida Giant monoculture soil. In a previously fallow, conducive soil and in a suppressive soil rendered conducive by microwave treatment, successive plantings of Florida Giant, but not Crimson Sweet, resulted in increasing populations of *F. o. niveum*. Indigenous populations of *F. oxysporum* showed no overall change in soil successively planted to Florida Giant, whereas planting Crimson Sweet resulted in increased populations in all field soils. Successive planting of Florida Giant also resulted in an increase in incidence of wilt, whereas planting Crimson Sweet maintained low wilt incidence throughout the study. Colonization of roots by *F. o. niveum* and other *F. oxysporum* was similar in both suppressive and nonsuppressive monoculture soils, indicating that suppression was not directly related to the degree of root colonization. Higher populations of actinomycetes, fluorescent pseudomonads, and overall bacteria occurred with successive plantings of Crimson Sweet than in nonplanted soil or most soils planted to Florida Giant. These results suggest that cultivar differences are responsible for the promotion of differences in rhizosphere microflora populations that are associated with soil suppressiveness.

Additional keywords: biological control, *Citrullus lanatus*, soil microbiology.

Soil suppressiveness to plant disease may occur naturally as an inherent characteristic of the physical, chemical, and/or biological structure of a particular soil, or it may be induced by some practice or activity, such as planting a crop or the addition of organisms or nutritional amendments, which causes a change in the microflora environment (9,20,33,36). Induced suppressive soils are exemplified by the occurrence of take-all decline of wheat, in which suppressiveness to *Gaeumannomyces graminis* (Sacc.) Arx & D. Oliver var. *tritici* J. Walker results after several years of continuous monoculture to wheat (8,13,36,37). A similar induction of suppressiveness has been observed over a much shorter time period with *Rhizoctonia solani* Kühn on radishes, alfalfa, and sugar beets (7,14,15). In these soils, suppressiveness apparently develops as a result of the buildup of antagonists in response to high pathogen populations produced by the successive growing of susceptible cultivars. Suppression of take-all has been associated with certain fluorescent pseudomonads as well as other bacteria (10,42,43), whereas the suppression of *Rhizoctonia solani* is attributed to *Trichoderma* spp. (7,14,15,27).

Most soils known to be suppressive to Fusarium wilt diseases are naturally occurring (1,2,9,28,40). However, a soil suppressive to Fusarium wilt of watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nikai), caused by *Fusarium oxysporum* f. sp. *niveum* (E. F. Sm.) W. C. Snyd. & H. N. Hans., has been described that was induced by monoculture of a particular cultivar of watermelon (Crimson Sweet) (18,24,26). Few other examples of induced Fusarium wilt-suppressive soils have been reported. Sneh et al (38) reported a soil suppressive to *F. o. melonis* that was induced by continuously cropping to resistant melon varieties for several years. Evidence of a similar induction of suppression in the early 1900s was recounted by Kommedahl et al (23), in which long-term monoculture of a cultivar resistant to flax wilt resulted in a marked decline in disease following several years of increases, whereas cropping to susceptible cultivars resulted in complete wilt (100%) every year. Schneider (34), also observed what may have been an induced suppression to Fusarium wilt of celery where "islands" of healthy celery plants were found in fields otherwise uniformly devastated by wilt. In both of these most recent cases, the organisms responsible for suppressiveness were concluded to be isolates of *F. oxysporum* not pathogenic to the crop plant.

Previously, the population dynamics and chlamydospore germination of *F. o. niveum*, as well as root colonization by *F. oxysporum* and other microorganism groups, were studied in the Crimson Sweet suppressive monoculture soil and compared with those of similar conducive soils; some distinct differences were demonstrated among these soils (26). Because the induction of suppression in this monoculture soil is linked with the cultivation of a particular watermelon cultivar, it is valuable to study the effects of such cultivation on different groups of microorganisms. By comparing the changes in populations of soil and rhizosphere microflora directly due to the planting of different cultivars of watermelon, insight may be gained into the microbial interactions related to planting Crimson Sweet and their role in suppression.

Using four soils representing different suppressive and conducive conditions, the objectives of this study were to evaluate the effect of successive plantings of two different watermelon cultivars on the population dynamics of and root colonization by *F. o. niveum*, indigenous *F. oxysporum*, and other general microorganism groups, as well as their relationship to the incidence of Fusarium wilt. Because previous studies with Fusarium wilt-suppressive soils have indicated a potentially important role

for nonpathogenic isolates of *F. oxysporum* and their relationship with the pathogen, special emphasis was placed on changes in the populations of *F. oxysporum* and watermelon root colonization by *F. oxysporum*.

MATERIALS AND METHODS

Soils. The four soils used throughout this study to represent different conditions of suppressiveness and conduciveness to Fusarium wilt of watermelon are from the Central Florida Research and Education Center, Leesburg, and have been described previously (26). All are of the Apopka Fine Sand soil series (loamy, siliceous, hyperthermic Grossarenic Paleudults) and have similar physical and chemical characteristics. They differ primarily in their cropping history and the resulting biology. The soil designations and suppressiveness rankings are as follows: Crimson Sweet monoculture soil (CSS) (suppressive); Florida Giant monoculture soil (FGM) (nonsuppressive); Leesburg fallow soil (LFC) (conducive); and microwave-treated CSS soil (CSMW) (conducive).

Successive plantings of watermelon and assay of Fusarium wilt. An orange-colored mutant isolate of the pathogen (FG-OR3), which was comparable to the wild-type isolate of race 1 in growth, pathogenicity, and root colonization, was used to distinguish the pathogen from indigenous *F. oxysporum* in the field soils (26). Soils were infested with chlamydospore inoculum of the orange mutant (OM) pathogen as was described previously (26).

Infested soil was placed in 10-cm plastic pots (0.5 kg per pot) in the greenhouse and allowed to equilibrate for approximately 3 wk. Watermelon seeds of Florida Giant, a cultivar susceptible to Fusarium wilt, or Crimson Sweet, a moderately resistant cultivar associated with soil suppressiveness, were planted in the infested soil (10 seeds per pot, four to six replicate pots per treatment). Plants were maintained for 4 wk at 20–30 C. Fusarium wilt was assessed by visual inspection of the plants for wilt symptoms several times a week and verified periodically by plating surface-disinfested stem pieces on Komada's (22) selective medium for *F. oxysporum*. Wilt was expressed as the percentage of diseased plants over the 4-wk period. After the final wilt assessment, plants were harvested, soil and root samples were collected, the soil was mixed thoroughly within the pot, and the pots were replanted with the same cultivar in the same manner. This was continued for four to five successive plantings over a 6-mo period. All tests were conducted at least twice.

Population dynamics of and root colonization by *Fusarium oxysporum*. Soil samples of 5 g each were taken from each pot at the time of initial infestation and immediately before each successive planting. Populations of *F. o. niveum*, as represented by the OM pathogen, and of indigenous *F. oxysporum*, were determined by serial dilution plating on Komada's (22) selective medium as described previously (26).

Whole root samples of the watermelon plants were gently removed from the pots and rinsed under running water. Surface colonization was determined by embedding the roots in molten Komada's (22) selective medium as previously described (26). Internal colonization was determined by surface-sterilizing roots in 0.5% sodium hypochlorite for 1 min, rinsing in sterile water, then plating in molten Komada's (22) selective medium as with the others.

Colonies of the OM pathogen, other *F. oxysporum*, and other fungi were differentiated by color and morphology. In addition, the spatial arrangement of the pathogen in relation to indigenous *F. oxysporum* and other fungi was observed. Lengths of plated root systems were estimated by a line intersect method (41), and colonization was expressed as colonies per 100 cm of root. All experiments used four replications of four to six root systems each and were conducted twice.

Soil microorganism populations. Estimates of populations of general soil microorganisms were made using standard serial dilution plating procedures as described previously (26). Overall populations of aerobic, heterotrophic bacteria were estimated using nutrient agar, and actinomycete populations were estimated on alkaline water agar, pH 10.5 (16). Fluorescent pseudomonad populations were estimated using selective King's medium B with cycloheximide, penicillin, and novobiocin added (32). General fungal populations were estimated on potato dextrose agar with 1 ml of tergitol NP-10 and 50 mg of chlortetracycline added per liter. All plates were incubated at 26 C. Nutrient agar and King's medium B plates were incubated 3–4 days, and King's medium B plates were examined under ultraviolet light for colonies producing diffusible fluorescent pigments. Alkaline water agar plates were incubated 7–10 days, and total colonies were counted. Fungal plates were incubated 5–6 days. Populations were expressed as log colony-forming units (log cfu) per gram of soil, and four replications of four plates per treatment were used.

Statistical analyses. Statistical analyses were conducted using the general linear models procedures of Statistical Analysis Systems version 6.04 (SAS Institute, Inc. Cary, NC). Experimental design for most tests were variations on a randomized complete block, generally with four to six replications and a factorial treatment structure. Experiments were analyzed using standard 1- to 3-factor analysis of variance (ANOVA) with interactions. The effect of successive plantings was analyzed by repeated measures ANOVA using a split-plot design. Significance was evaluated at $P < 0.05$ for all tests. Factor and interaction sums of squares were partitioned into single degree of freedom planned orthogonal contrasts, as class comparisons for qualitative factors and poly-

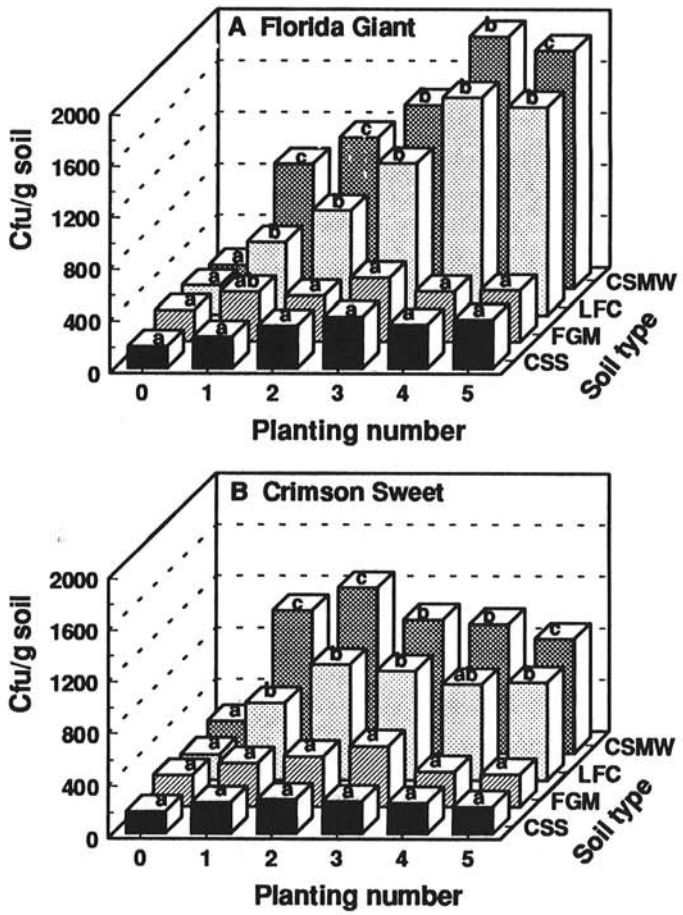

Fig. 1. Population dynamics of *Fusarium oxysporum* f. sp. *niveum* (as represented by an orange-colored mutant pathogen) in four soils with successive plantings of two different watermelon cultivars (CSS = suppressive, monoculture soil; FGM = nonsuppressive, monoculture soil; LFC = fallow, conducive soil; CSMW = suppressive soil rendered conducive by microwave treatment). **A,** Cultivar Florida Giant (susceptible to Fusarium wilt); **B,** cultivar Crimson Sweet (moderately resistant to Fusarium wilt and inducer of soil suppressiveness). Population estimates were made at the time of planting for each planting number. Values within each planting for each cultivar topped by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test. All results are from a single representative experiment.

nomial trend contrasts for quantitative factors. Mean separation for some experiments with qualitative treatments was accomplished using Duncan's multiple range test. Correlation or regression analyses were conducted where appropriate. Residual error terms were plotted and tested for normality. All data expressed as percentages were arcsine-transformed ($\sin^{-1}\sqrt{x}$) before analysis.

RESULTS

Population dynamics of *Fusarium oxysporum* and Fusarium wilt. Five successive plantings of watermelon cultivars Florida Giant and Crimson Sweet resulted in distinct differences in the populations of *F. o. niveum* among the four soils (Fig. 1). After the equilibration period (3 wk) and at the time of the first planting, pathogen populations in the suppressive soil (CSS) were lower than in the two conducive soils (LFC and CSMW) for both cultivars, but were not different from those in nonsuppressive monoculture soil (FGM). This increase in the pathogen populations of the conducive soils before planting was similar to that observed previously in nonplanted soils (26). Significant differences were noted in pathogen populations between the conducive soils and the monoculture soils beginning with the second planting of Florida Giant and at each subsequent planting. With Crimson Sweet, pathogen populations in the two monoculture soils were also lower than in the conducive soils at all plantings except at the fourth, when pathogen populations in LFC soil were similar to those in the monoculture soils.

Analysis over all factors (soil type, cultivar, and planting) demonstrated that there were differences in the effect of successive plantings on the population of *F. o. niveum* among the soils and between cultivars (planting × soil, planting × cultivar, and planting × soil × cultivar interaction terms significant) (Table 1). Further partitioning of the interaction sums of squares indicated no difference in pathogen populations between the CSS and FGM soils or between LFC and CSMW soils in their response to planting. There was, however, a significant difference between the monoculture soils and the conducive soils, with the monoculture soils maintaining low pathogen populations throughout the plantings (averaging 227 and 322 cfu/g of soil for CSS and FGM soil planted to Crimson Sweet and 307 and 374 cfu/g of soil when planted to Florida Giant). Populations of *F. o. niveum* increased to the greatest extent when conducive soils were successively planted to Florida Giant (populations reaching 1,956 and 1,688 cfu/g of soil for CSMW and LFC, respectively). Comparisons within each soil determined that successive plantings of either cultivar Florida Giant or Crimson Sweet had no effect on pathogen populations in either monoculture (CSS or FGM) soil throughout the study period. In the conducive soils, plantings of Florida Giant resulted in increasing pathogen populations with successive plantings (linear regression analysis, $b = 3.31 \pm 0.41$ and 3.05 ± 0.29 for CSMW and LFC soil, respectively). With planting to Crimson Sweet, however, pathogen populations leveled off after the initial population increases in the raw soils and stabilized, showing no further increases throughout the remaining successive plantings in the conducive soils.

Estimates of soil populations of indigenous *F. oxysporum* (all *F. oxysporum* other than the OM pathogen) also indicated differences among soils and between cultivars in response to successive plantings (planting × soil, planting × cultivar, and planting × soil × cultivar interaction terms significant) (Table 1 and Fig. 2). When planted to Florida Giant, populations of *F. oxysporum* fluctuated widely in each field soil, but showed no consistent change with successive plantings and stayed within the range normally observed with each soil. Soil populations of *F. oxy-*

TABLE 1. Repeated measures analysis of variance for five successive plantings of four soils to two watermelon cultivars and their effects on the incidence of Fusarium wilt and the population dynamics of introduced *Fusarium oxysporum* f. sp. *niveum* and indigenous *Fusarium oxysporum* in the soil (data shown in Fig. 1–3)

		Sums of squares			
Source of variation[y]	df	*F. o. niveum*	*F. oxysporum*	df	Fusarium wilt
Soil	3	2,229.8**[z]	10,388.0**	3	38,133.9**
CSS vs. FGM	1	15.8	159.4*	1	3,618.1**
LFC vs. CSMW	1	152.2**	1,353.0**	1	2,565.1**
Monoculture vs. conducive	1	2,061.8**	8,875.6**	1	31,950.7**
Cultivar	1	200.4**	936.2**	1	47,300.0**
Soil × cultivar	3	92.2**	716.7**	3	3,835.3*
CSS vs. FGM × cultivar	1	0.5	311.2**	1	12.8
LFC vs. CSMW × cultivar	1	0.1	86.8	1	1,683.6
Monoculture vs. conducive × cultivar	1	91.7**	318.7**	1	2,138.9*
Error (Soil)	24	107.2	532.8	24	9,992.3
Planting	5	858.7**	2,560.3**	4	6,721.5**
Linear	1	665.6**	1,274.1**	1	4,241.3**
Quadratic	1	177.3**	297.6**	1	981.1
Cubic	1	8.7	245.8**	1	781.2
Quartic	1	7.1	548.2**	1	717.8
Residual	1	0.0	194.5*	...	...
Planting × soil	15	609.6**	1,482.6**	12	3,356.8
CSS vs. FGM × planting	5	0.9	263.4*	4	1,334.7
LFC vs. CSMW × planting	5	51.6	509.4**	4	489.9
Monoculture vs. conducive × planting	5	553.4**	709.8**	4	1,532.2
Planting × cultivar	5	301.6**	659.7**	4	1,777.1
Planting × soil × cultivar	15	194.0**	1,167.3**	12	2,875.2
CSS vs. FGM × cult × planting	5	2.1	667.9**	4	1,191.2
LFC vs. CSMW × cult × planting	5	3.6	43.4	4	488.2
Monoculture vs. conducive × cult × planting	5	188.2**	455.9**	4	1,195.8
Error (planting)	120	563.6	2,723.0	96	30,892.9

[y] Repeated measures ANOVA was conducted as a split-plot design with soil type and cultivar as the main factors and planting number as the subfactor. Factor and interaction sums of squares were partitioned into single degree of freedom orthogonal contrasts. Soil type was divided into CSS (suppressive) vs. FGM (nonsuppressive) monoculture soils, LFC (conducive) vs. CSMW (microwave-treated suppressive) soils, and monoculture (CSS, FGM) vs. conducive (LFC, CSMW) soil comparisons. Cultivars used were Florida Giant (susceptible) and Crimson Sweet (moderately resistant and associated with soil suppressiveness). Planting was partitioned into linear, quadratic, cubic, quartic, and residual polynomial trend contrasts. Interaction sums of squares were further partitioned into their individual polynomial trend contrast (results not shown).

[z] Sums of squares followed by * or ** denotes a significant effect due to the source of variation with F significant at $P < 0.05$ and $P < 0.01$, respectively.

sporum also fluctuated when planted to Crimson Sweet, but showed a significant trend of increase with successive plantings in LFC, FGM, and CSS soils (linear regression analysis, b = 3.18 ± 0.48, 2.23 ± 0.67, and 3.88 ± 1.67, for LFC, FGM, and CSS soils, respectively). Populations of *F. oxysporum* increased to the greatest extent in CSS soil planted to Crimson Sweet, and this response was different from that observed in any other soil/cultivar combination (Table 1). There was virtually no detectable population of indigenous *F. oxysporum* in CSMW soil throughout most of the experiment due to the microwave treatment this soil received. The low levels of *F. oxysporum* observed in CSMW soil at plantings four and five represent limited recolonization.

Incidence of Fusarium wilt in soils planted to Florida Giant was high (82–100%) throughout all plantings in conducive soils and tended to increase with the first few successive plantings in the monoculture soils (Fig. 3). Suppression of Fusarium wilt in CSS soil, which was evident at the first planting (significantly lower wilt than all other soils), was no longer present by the third planting or thereafter. In contrast, Fusarium wilt remained low (20–27% wilt) throughout the five successive plantings of Crimson Sweet in CSS soil and also did not increase in FGM soil, although initial incidence levels were higher (34–42%) than those in CSS soil (Fig. 3). In LFC and CSMW soils, wilt incidence was high in the first planting, but did not change dramatically with successive plantings (46–66 and 65–83% for LFC and CSMW soils, respectively). Differences in wilt suppression among the soils were evident through each successive planting, with CSS soil maintaining a lower disease incidence than that in LFC or CSMW soils.

Analysis of Fusarium wilt incidence over all factors did not indicate any differences in the response of the soils or cultivars to successive planting (planting × soil, planting × cultivar, and planting × soil × cultivar interaction terms were not significant) (Table 1). The monoculture soils planted to Crimson Sweet maintained lower wilt incidence than those planted to Florida Giant (soil × cultivar interaction significant). There also was a slight linear effect of increasing wilt with successive plantings.

A repeat of this experiment as well as a similar additional experiment showed similar results regarding *F. o. niveum*, indigenous *F. oxysporum*, and wilt levels, with the exceptions that disease incidence in FGM soil continued to increase through the fourth and fifth planting of Florida Giant and that declining wilt incidence was observed in LFC soil successively planted to Crimson Sweet.

Root colonization by *Fusarium oxysporum*. Root surface colonization measured after four successive plantings of Crimson Sweet and Florida Giant revealed differences among the soils and between cultivars (soil × cultivar interaction term not significant for any variable) (Table 2). Colonization of Crimson Sweet by *F. o. niveum* was lowest in the two monoculture soils, but was not different between CSS and FGM soil. Root col-

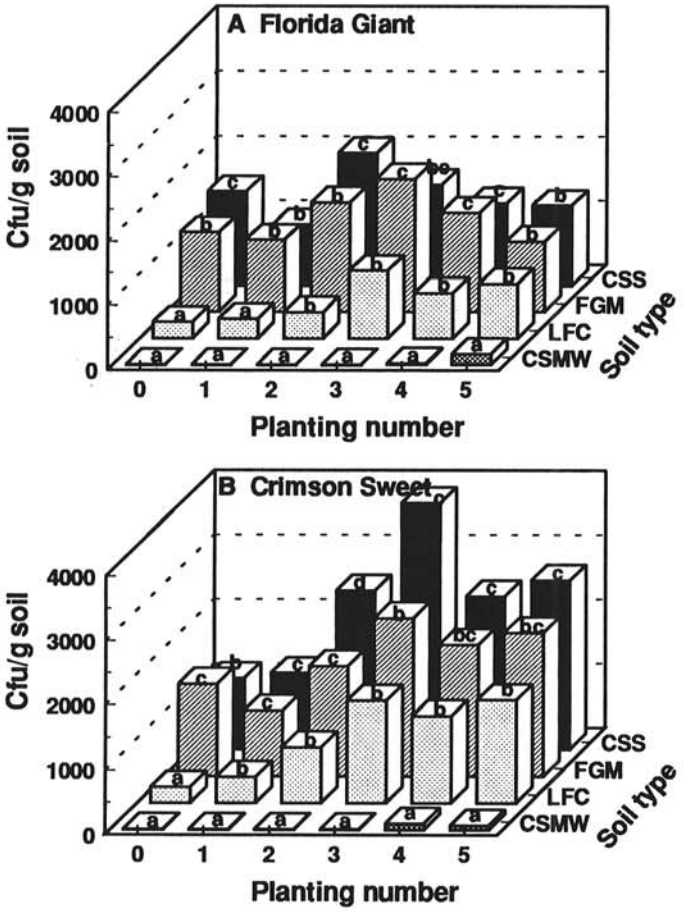

Fig. 2. Population dynamics of indigenous *Fusarium oxysporum* in four soils with successive plantings of two different watermelon cultivars (CSS = suppressive, monoculture soil; FGM = nonsuppressive, monoculture soil; LFC = fallow, conducive soil; CSMW = suppressive soil rendered conducive by microwave treatment). **A,** Cultivar Florida Giant (susceptible to Fusarium wilt); **B,** cultivar Crimson Sweet (moderately resistant to Fusarium wilt and inducer of soil suppressiveness). Population estimates were made at the time of planting for each planting number. Values within each planting for each cultivar topped by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test. All results are from a single representative experiment.

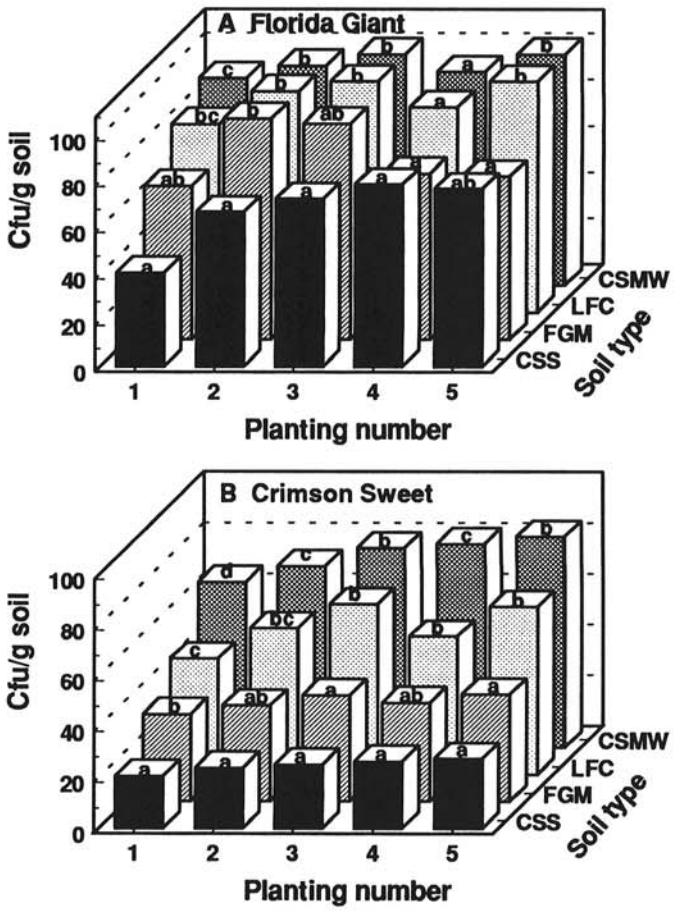

Fig. 3. Fusarium wilt in four soils with successive plantings of two different watermelon cultivars (CSS = suppressive, monoculture soil; FGM = nonsuppressive, monoculture soil; LFC = fallow, conducive soil; CSMW = suppressive soil rendered conducive by microwave treatment). **A,** Watermelon cultivar Florida Giant (susceptible to Fusarium wilt); **B,** watermelon cultivar Crimson Sweet (moderately resistant to Fusarium wilt and inducer of soil suppressiveness). Values within each planting topped by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test. All results are from a single representative experiment.

TABLE 2. Surface colonization of roots of two watermelon cultivars by *Fusarium oxysporum* in relation to soil populations and disease incidence in four soils after four successive watermelon plantings

Cultivar and soil type[v]	Colonies per 100 cm root[w]		Colonization ratio[x]	% Wilt	Soil populations[y] (cfu/g)	
	OM pathogen	*F. oxysporum*			OM pathogen	*F. oxysporum*
Crimson Sweet						
CSS	10.6 a[z]	79.8 a	0.14 a	26.3 a	240 a	2,375 a
FGM	18.2 a	78.7 a	0.23 a	38.7 ab	270 a	2,038 ab
LFC	29.0 b	50.3 b	0.78 b	53.7 bc	730 b	1,338 b
CSMW	67.6 c	30.8 c	2.66 c	80.0 c	990 b	133 c
Florida Giant						
CSS	21.8 a	97.5 a	0.24 a	78.8 a	340 a	1,294 a
FGM	38.4 ab	68.3 a	0.53 a	72.0 a	387 a	1,550 a
LFC	49.6 b	36.2 b	1.67 b	62.0 a	1,690 b	700 b
CSMW	71.8 c	19.8 c	3.63 c	92.5 a	1,960 b	25 c

[v] Soil type represents differences in the ability of a soil to suppress Fusarium wilt of watermelon. CSS = Crimson Sweet suppressive, monoculture soil; FGM = Florida Giant monoculture soil (nonsuppressive); LFC = Leesburg fallow conducive soil; CSMW = microwave-treated, Crimson Sweet soil (conducive).

[w] Colonization of roots by the orange mutant (OM) strain of *F. o. niveum* and all *F. oxysporum* other than the OM pathogen was determined by washing the roots of 3-wk-old plants and embedding them intact in Komada's (22) medium. Four replications of four to six roots each were used. Root length was estimated by the line-intersect method (41).

[x] The colonization ratio represents the mean of the colonization by the OM pathogen divided by the colonization by other *F. oxysporum* calculated for each sample.

[y] Soil populations of the OM pathogen and other *F. oxysporum* were determined by dilution-plating at the time of root colonization measurements. Initial inoculum of OM pathogen was approximately 200 cfu/g soil.

[z] Means within columns for each cultivar followed by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test. Results of two-way ANOVA indicated significant effects due to soil type for all variables and significant cultivar effects for all variables except colonization by *F. oxysporum*. Soil type × cultivar interaction was not significant for any variable. All data are from a single representative experiment.

onization by the pathogen was greater in LFC and CSMW soils than in both monoculture soils, and was greater in CSMW soil than in the other three soils. Colonization by indigenous *F. oxysporum* was several times that by *F. o. niveum* in both CSS and FGM soils, both of which had greater levels of colonization by *F. oxysporum* than those in LFC and CSMW soils. Colonization by *F. oxysporum* was lowest in CSMW soil, but did show substantial root colonization due to recolonization of the soil over time after microwave treatment. Ratio of colonization by the pathogen to colonization by indigenous *F. oxysporum* also was similar in CSS and FGM soils and was less than in the two conducive soils. Root surface colonization of Crimson Sweet by the pathogen was correlated ($r = 0.71$) to soil population levels of the pathogen at the time of root sampling. Colonization by *F. oxysporum* also was correlated ($r = 0.69$) with its respective soil populations. Colonization by the pathogen was negatively correlated ($r = -0.79$) with colonization by *F. oxysporum*. Wilt was lower in CSS than in LFC and CSMW soils with cultivar Crimson Sweet. Wilt incidence also was correlated ($r = 0.68$) with soil populations of the pathogen.

Overall higher levels of root colonization by *F. o. niveum* were observed in all soils planted to cultivar Florida Giant than in those planted to Crimson Sweet, and differences between the monoculture soils (CSS and FGM) and the conducive soils were similar to those observed with cultivar Crimson Sweet (Table 2). Colonization of Florida Giant by indigenous *F. oxysporum* as well as the difference in colonization among soil types was similar to that observed for Crimson Sweet. Colonization ratios of *F. o. niveum* to *F. oxysporum* were higher for Florida Giant due to higher colonization by the pathogen and reflected differences among soils as previously observed. However, wilt was high in all soils with no significant differences among them. Wilt, then, was not directly related to the level of colonization by the pathogen or indigenous *F. oxysporum*. With Florida Giant, correlations among colonization, soil populations, and wilt incidence were not significant. Soil populations of the pathogen at the time of sampling were lower in the monoculture soils than in conducive soils, and populations of *F. oxysporum* were highest in monoculture soils planted to Crimson Sweet. Similar results for all factors were observed in a repeat of this experiment.

Internal root colonization by *F. o. niveum*, measured using surface-disinfested roots, was not different between CSS and FGM soils, although both monoculture soils resulted in lower colonization by the pathogen than that observed in LFC soil (Table 3). Colonization by indigenous *F. oxysporum* was similar among all three soils. Ratio of colonization by the pathogen to *F. oxysporum* was similar in the two monoculture soils, but lower in both than in LFC soil. Wilt incidence was again significantly different among the three soils; wilt was low in CSS soil, moderate in FGM soil, and severe in LFC soil.

TABLE 3. Internal colonization of Crimson Sweet watermelon roots by *Fusarium oxysporum* in soils suppressive and conducive to Fusarium wilt following four successive plantings

Soil type[w]	Colonies per 100 cm root[x]		Colonization ratio[y]	Wilt (%)
	OM pathogen	*F. oxysporum*		
CSS	1.17 a[z]	1.59 a	1.31 a	9.9 a
FGM	4.68 a	2.37 a	1.44 a	35.1 b
LFC	15.70 b	2.55 a	9.13 b	61.4 c

[w] Soil type represents differences in the ability of a soil to suppress Fusarium wilt of watermelon. CSS = Crimson Sweet suppressive, monoculture soil; FGM = Florida Giant monoculture soil (nonsuppressive); LFC = Leesburg fallow soil (conducive); CSMW = microwave-treated, Crimson Sweet soil (conducive).

[x] Colonization of roots by the orange mutant (OM) isolate of *F. o. niveum* and all *F. oxysporum* other than the OM pathogen was determined on the roots of 3-wk-old plants that had been washed, surface-sterilized in 0.5% sodium hypochlorite for 1 min, rinsed, and embedded intact in Komada's (22) medium. Four replications of four to six roots each were used. Root length was estimated by the line-intersect method (41).

[y] The colonization ratio represents the mean of the colonization by the OM pathogen divided by the colonization by other *F. oxysporum* calculated for each sample.

[z] Means in columns followed by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test. Means are from a single representative experiment.

Soil microorganism populations. Successive plantings of watermelon had different effects on microorganism populations depending on the soil type and cultivar used (soil × planting interaction term significant) (Fig. 4). Planting to watermelon had differing effects among soil types on the populations of bacteria, fluorescent pseudomonads, and fungi, with lower prokaryote populations observed in LFC soil planted to watermelon than with other soils, and higher fungal populations in LFC nonplanted soil than other soils. Successive plantings of Crimson Sweet in CSS, FGM, and CSMW soil resulted in increases in populations of bacteria, actino-

mycetes, fluorescent pseudomonads, and other pseudomonads compared to nonplanted soil. Increases in populations were observed in LFC soil for actinomycetes, fluorescent pseudomonads, and other pseudomonads, but not for overall bacteria. In FGM soil, population increases following planting to Crimson Sweet also were greater than after planting to Florida Giant for all microorganism groups except fungi. Populations of actinomycetes and fluorescent pseudomonads also were greater in CSS and CSMW soils when planted to Crimson Sweet than to Florida Giant. Overall, in all soils, planting watermelon (Florida Giant or Crimson Sweet) caused increases in the general prokaryotic microorganism populations as measured in this study. Planting watermelon had no effect on overall fungal populations in any soil, except LFC, in which overall fungal populations decreased when successively planted to Crimson Sweet or Florida Giant. Fungal populations also were lower when planted to Crimson Sweet than to Florida Giant in this soil. LFC soil had the highest overall fungal populations and lowest bacterial populations initially.

DISCUSSION

In this study, cultivation of watermelon, as well as the particular cultivar planted, had significant effects on the populations of *F. oxysporum* pathogenic and not pathogenic to watermelon. When conducive soils were planted to the susceptible cultivar Florida Giant, pathogen populations tended to increase with successive planting, while populations of indigenous *F. oxysporum* did not change significantly. When planted to Crimson Sweet, pathogen populations in all soils did not differ substantially from those observed in nonplanted soils (26), regardless of the number of plantings. Populations of indigenous *F. oxysporum*, however, tended to increase with successive planting to Crimson Sweet. Thus, Crimson Sweet appeared to selectively favor the growth of nonpathogens over pathogens, whereas Florida Giant tended to promote pathogen development over nonpathogens. Several studies have demonstrated that susceptible crops increase pathogen populations, whereas nonhost or resistant hosts, even when colonized by the pathogen, do not result in pathogen population increases (4,21,31,44). A similar response may be occurring in this suppressive soil to maintain low pathogen populations. The low pathogen to nonpathogen balance may be maintained by a preferential selection for certain organisms. Hopkins et al (19) also demonstrated that monoculture of race 1-resistant cultivars selectively increased the proportion of race 2 isolates in the soil. The relationship between race and cultivar resistance has been previously described (25).

Planting watermelon also had significant effects on other microorganism populations, with overall populations of bacteria, actinomycetes, and pseudomonads increasing after a number of successive plantings. This general increase due to planting is not surprising, however, because plant roots provide nutrients in the form of exudates, which serve as substrate for large numbers of a wide variety of soil microorganisms (12). There also were differences between cultivars, with planting to Crimson Sweet resulting in overall greater populations for most prokaryote groups than planting to Florida Giant. These differences substantiate the generally higher prokaryote populations observed in CSS soil in the field (26). Although only general numbers of microorganisms were assayed in this study and no information on the possible changes in the composition or diversity of species is available, changes in population numbers were evidence of some direct effects on the microflora.

These alterations in the populations of *F. oxysporum* and

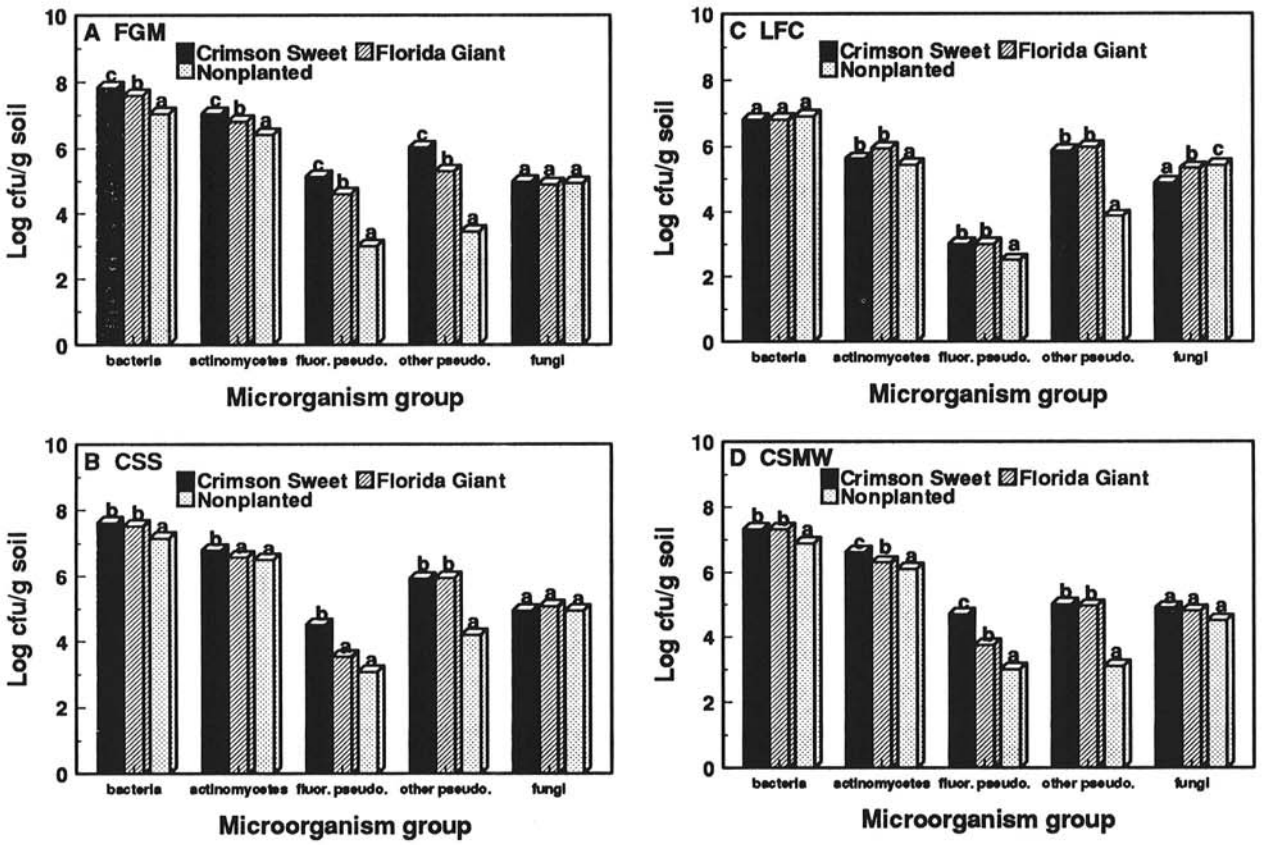

Fig. 4. Populations of bacteria, actinomycetes, fluorescent pseudomonads, other pseudomonads, and fungi in four soils after four successive plantings of watermelon cultivars Florida Giant and Crimson Sweet and in nonplanted soil. **A,** FGM (nonsuppressive, monoculture) soil; **B,** CSS (suppressive, monoculture) soil; **C,** LFC (fallow, conducive) soil; **D,** CSMW soil (suppressive soil rendered conducive by microwave treatment). Values within each microorganism group topped by the same letter are not significantly different ($P < 0.05$) according to Duncan's multiple range test. Two-way analysis of variance indicated a significant interaction between soil type and planting to watermelon for populations of bacteria, fluorescent pseudomonads, and fungi. Orthogonal contrasts determined specific differences among soil types and planting factors and interactions. All results are from a single representative experiment.

bacteria suggest the promotion of differences in rhizosphere microflora populations caused by cultivar differences. Although it is readily acknowledged that rhizosphere microflora are influenced by the host, there is very little known regarding the degree and level of control plant genotype has on the composition of rhizosphere microflora. Work done by Atkinson and co-workers (3,30) demonstrated that host genotype of spring wheat had significant and specific effects on the composition of its rhizosphere microflora. More recently, Bourbos and Skoudridakis (5) found that a resistant tomato cultivar specifically promoted the growth of various fungi antagonistic to plant pathogens in the rhizosphere, whereas a susceptible cultivar did not. There also have been other reports on various effects of varietal differences on rhizosphere microflora (6,29,39). The situation observed in this study may be another case where cultivar differences are sufficient to substantially change the rhizosphere microflora, either by enhancing microorganism populations in general or by selectively favoring certain groups or strains of organisms. The mechanism by which this stimulation takes place is not known, but presumably results from differences in the quantity and composition of root exudates.

Additional tests with successive plantings of other watermelon cultivars, Calhoun Gray, a highly resistant cultivar, and Charleston Gray, a moderately resistant cultivar, also suggested that the level of cultivar resistance affects microflora populations (24). Calhoun Gray and Crimson Sweet generally showed somewhat higher total populations of bacteria, actinomycetes, and pseudomonads than the less resistant cultivars Charleston Gray and Florida Giant. The population levels observed corresponded roughly with levels of resistance in the field. Neither of these two additional cultivars promoted detectable soil suppressiveness, however. Several other cultivars classified as having equal or greater levels of resistance than Crimson Sweet also did not induce suppression in the field (17,18). Thus, there is evidently more to this suppression than cultivar resistance and a general stimulation of microorganism activity.

Although most bacterial groups were affected by planting to watermelon, there was no noticeable effect on total fungal populations in all but the LFC soil. The decrease in fungal populations in LFC soil is presumably a result of the increase in bacterial numbers. It may be that through the planting of watermelon this conducive soil is slowly converting to the microbiology that characterizes suppressive soil. In some of the wilt assays, this possible conversion toward suppression could be seen as a reduction in wilt in LFC soil after a number of successive plantings of Crimson Sweet (24). Although overall fungal populations decreased in this soil, the reduction of wilt may have been related to changes within the population structure of *F. oxysporum*; indigenous populations of *F. oxysporum* increased, while the OM pathogen population did not change with successive plantings of Crimson Sweet. The significant effect of planting on populations of *F. oxysporum* in these soils suggests a specific relationship between *F. oxysporum* and planting to watermelon that was not reflected in total fungal populations.

Differences in incidence of disease also were observed between planting to the two cultivars and among soils. Wilt, in general, was highest in conducive soils planted to Florida Giant. However, although the effect of successive planting on populations of *F. o. niveum* and other *F. oxysporum* was different among the soils and between cultivars (significant planting × factor interactions), these interactions were not observed for incidence of wilt. This may have been due to the initially high wilt incidence in the soils planted to Florida Giant. Because of this already high wilt, incidence could not increase much with successive planting to Florida Giant, particularly in the conducive soils. As a result, the overall effects of planting were not significantly different between cultivars or among soils, even though there were some indications of different responses due to planting (regression analysis). An increase in wilt was observed in CSS soil and in FGM soil in some experiments when planted to Florida Giant.

Although direct comparison between these two cultivars is complicated by their difference in resistance level (Crimson Sweet is classified as moderately resistant and Florida Giant is considered susceptible [11,17,25]), this difference in resistance does not totally explain the differences in suppressiveness observed. Although Florida Giant does show greater levels of wilt than Crimson Sweet in the same soils, initial differences in suppressiveness between soils were apparent with both cultivars. However, after just two plantings of Florida Giant, all indications of differences in disease suppression among the soils were removed. This was not due merely to an increase in pathogen populations, because an increase in disease was noted in CSS and FGM soils even when OM pathogen populations did not substantially increase. Suppressiveness was maintained with Crimson Sweet and eliminated with Florida Giant. Sneh et al (38) also found that planting to susceptible cultivars would nullify a similarly induced suppression after as little as two plantings.

Root colonization of Crimson Sweet by *F. o. niveum* did not change in CSS, FGM, and LFC soil after successive plantings, but did substantially increase in CSMW soil compared to initial levels observed previously (26). Root colonization by indigenous *F. oxysporum* was greater in all soils after successive plantings than that observed in initial plantings (26), and colonization in the monoculture soils was significantly greater than in the conducive soils. Colonization by *F. o. niveum* was negatively correlated with colonization by *F. oxysporum* when planted to Crimson Sweet, but not when planted to Florida Giant. Even after a number of successive watermelon plantings, however, there was no difference observed in colonization by *F. o. niveum* or indigenous *F. oxysporum* between the two monoculture soils (CSS and FGM), although large differences were often observed between the monoculture soils and LFC soil. Thus, despite differences in population dynamics of *F. o. niveum* and indigenous *F. oxysporum* due to planting to watermelon, root colonization by the OM pathogen and indigenous *F. oxysporum* (whether surface or internal) was similar in both suppressive and nonsuppressive monoculture soils and was not consistently related to wilt. This suggests that general population levels of *F. oxysporum* not pathogenic to watermelon are not directly related to suppressiveness in these soils. Thus, if nonpathogenic *F. oxysporum* is involved in the suppressive response, specific isolates rather than general population levels must be responsible. These specific antagonistic isolates may be more abundant in CSS than FGM soil, but cannot be distinguished by colonization data alone. It does not appear that the ability to colonize effectively is a distinguishing trait; nonpathogens in FGM soil were able to colonize as well as those in CSS soil, but did not suppress disease. Previous tests have indicated populations of *F. o. niveum* tend to average slightly higher, though generally not significantly higher, in FGM soil than CSS soil in the field (18,19, D. L. Hopkins and R. P. Larkin, *unpublished data*). However, the problem associated with indigenous pathogens being included in indigenous *F. oxysporum* counts in this study has been recognized and does limit the conclusions that can be made regarding nonpathogenic populations of *F. oxysporum* (26).

Differences in microorganism populations were previously observed between suppressive and conducive soils (26). In this study, changes in the populations of *F. oxysporum* and various bacteria were directly related to plantings of watermelon, and particularly cultivar Crimson Sweet. From the observed changes in pathogenic and nonpathogenic populations of *F. oxysporum*, it is evident that planting watermelon has a profound effect on populations of *F. oxysporum*, their development, and the distribution of pathogens versus nonpathogens. Because these specific changes in the dynamics of *F. oxysporum* are due to the cultivar that promotes suppressiveness and because *F. oxysporum* has often been implicated in the suppression of Fusarium wilt in other soils, it suggests that the relationship between pathogenic and nonpathogenic *F. oxysporum* is involved in this suppressive response. However, it is also quite likely that other organisms, such as fluorescent pseudomonads or other bacteria, may be involved, because these organisms also showed significant population changes due to planting.

The effect of monoculture on soilborne plant pathogens and disease varies considerably with different pathosystems and the

conditions within them (9,36). In this system, while cultivation of susceptible and many resistant cultivars results in an irreversible increase in disease, cultivation of at least one particular partially resistant cultivar has resulted in disease decline and soil suppressiveness. This response apparently differs from other pathosystems involving induced suppression, such as seen with take-all decline (8,35,37) and *Rhizoctonia solani* (7,14,15), in which susceptible cultivars are involved and there is no apparent interaction with host resistance. Although the successive planting experiments in this study are not directly comparable to the conditions of monoculture in the field, these tests indicated possible effects as a result of monoculture. Cultivar Crimson Sweet, which is responsible for the induction of suppression, also caused many changes in the soil and root microbiology of these soils, presumably through the effect of differences in host genotype on the rhizosphere microflora. A resistance mechanism such as this host enhancement of the growth and establishment of organisms antagonistic to plant pathogens may indicate another direction for biological control. Development of the biological control potential of both the antagonists and host genotype through isolation, identification, and utilization of specific effective antagonistic organisms as well as the incorporation of the inherent genetic ability of the plant to enhance the development of such organisms may enable an integrated biological control that may be effective in overcoming difficulties often encountered with the introduction of antagonist organisms.

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