Effects of Initial Inoculum and Cultivar Resistance on Incidence of Fusarium Wilt and Population Densities of *Fusarium oxysporum* f. sp. *dianthi* on Carnation and in Soil

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ABSTRACT

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The effects of initial inoculum and cultivar resistance on the incidence of Fusarium wilt and the population densities of *Fusarium oxysporum* f. sp. *dianthi* on carnation and in soil were studied in the field and in large containers filled with naturally infested soil. Five carnation cultivars that ranged in their response to Fusarium wilt from completely resistant ('Scarlette'), highly resistant ('Eveline'), moderately resistant ('Galit'), susceptible ('Lior'), to highly susceptible ('Hermon') were included in all experiments. In the field, Fusarium wilt incidence and counts of CFU of *F. oxysporum* f. sp. *dianthi* recovered from soil or plants increased with time. The magnitude of that increase and the final population density of the pathogen, however, were affected by the degree of cultivar resistance. For example, the number of CFU of the pathogen on stems of cultivar Hermon was 10,000-fold higher than that on cultivar Scarlette. Population densities of the pathogen on plant stems were linearly related to disease incidence; the more severe the disease, the larger the number of CFU of *F. oxysporum* f. sp. *dianthi* recovered. The pathogen also was recovered (about 10^4 CFU/g of plant) from symptomless plants. A similar relationship was observed in soil, sampled from beneath plants, except that the increase in CFU was not linear and pathogen CFU leveled off gradually at high disease incidence. In containers, disease incidence increased significantly ($P < 0.05$) with increasing initial inoculum levels for the susceptible, but not for the resistant, cultivars. The number of *F. oxysporum* f. sp. *dianthi* CFU in soil increased for the cultivars Hermon, Lior, and Galit, but not for 'Eveline' or 'Scarlette'; in the stems, the number of CFU increased for all cultivars.

Carnation (*Dianthus caryophyllus* L.) is one of the main species cultivated by the floricultural industry in Israel. Plants are grown in greenhouses as a monoculture, sometimes consecutively for more than 15 years. Stem-rooted cuttings are planted during mid-June to mid-August. The first crops are harvested about 140 to 160 days after planting and growth continues until late April to early May in the following year, 300 to 330 days after planting. Fusarium wilt, caused by *Fusarium oxysporum* Schlechtend.:Fr. f. sp. *dianthi* (Prill. & Delacr.) W. C. Snyder & H. N. Hans., often causes severe yield losses in susceptible cultivars. The pathogen is present in the soil profile in which carnation roots are distributed and may infect the plants at any time during the season. In the field, the disease is observed only in late summer and autumn (September to December) when the temperatures are favorable for the expression of symptoms.

The most important factor influencing wilt development is cultivar resistance to *F. oxysporum* f. sp. *dianthi*. Currently, eight different races of *F. oxysporum* f. sp. *dianthi* are known (14), with race 2 being the most prevalent (6,17). Partial resistance to *F. oxysporum* f. sp. *dianthi* race 2 exists in carnation (2,4,11,21,25). A wide range of responses is apparent among cultivars with complete wilt occurring in highly susceptible cultivars (e.g., Hermon and Fantasia) 90 to 110 days after planting, whereas for highly resistant cultivars (e.g., Eveline), disease incidence usually does not exceed 3 to 10% by the end of the season (10). Because highly resistant cultivars have lower yield or are commercially undesirable, growers prefer to plant susceptible cultivars whenever possible. In greenhouses that had severe Fusarium wilt during the previous season, growers are advised to fumigate the soil with methyl bromide and replant only those cultivars with high resistance, even though they are less profitable.

Initial inoculum is another important factor affecting Fusarium wilt. In general, increasing amounts of initial inoculum of soilborne wilt pathogens cause earlier disease onset and higher wilt severities (3,5,13,15,16,18,20,22,23,24). Since carnation is grown as a monoculture, methyl bromide (800 kg/ha) has become a common practice to reduce the amount of initial inoculum of *F. oxysporum* f. sp. *dianthi*. This treatment, however, does not completely eradicate the pathogen from fumigated soils, especially in the deeper soil layers (5,8). In a recent study, both the inoculum level in soil at the end of each of four growing seasons and the Fusarium wilt incidence varied in four commercial greenhouses planted with susceptible carnation cultivars, irrespective of the amount of CFU of *F. oxysporum* f. sp. *dianthi* present in the soil after fumigation. In one greenhouse with a moderately resistant cultivar, the number of CFU in soil at the end of each growing season remained undetectable, as it was after fumigation (8).

Presumably, the amount of *F. oxysporum* f. sp. *dianthi* inoculum that recolonizes the soil after a carnation crop is dependent on initial inoculum, cultivar susceptibility, and soil environment. In the *F. oxysporum* f. sp. *lycopersici*-tomato system following artificial inoculation, the amount of new inoculum produced in completely resistant cultivars was smaller than that in susceptible cultivars (1,12). Little is known about these relationships for the *F. oxysporum* f. sp. *dianthi*-carnation pathosystem. The purpose of

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this work was to study the relationship between effects of initial inoculum and degree of cultivar resistance on the incidence of Fusarium wilt and the population densities of *F. oxysporum* f. sp. *dianthi* on plants and in soil.

MATERIALS AND METHODS

The effects of initial inoculum levels and degree of cultivar resistance on the incidence of Fusarium wilt and the population densities of *F. oxysporum* f. sp. *dianthi* on plants and in soil were studied in experiments conducted in concrete containers (1993 to 1994 and 1994 to 1995) and in the field (1991 to 1992, 1992 to 1993, and 1993 to 1994). Five carnation cultivars with known degrees of resistance were included in all experiments: 'Scarlette,' completely resistant; 'Eveline,' highly resistant; 'Galit,' moderately resistant; 'Lior,' susceptible; and 'Hermon,' highly susceptible (7,10). These cultivars are currently used to compare the response of new carnation cultivars with *F. oxysporum* f. sp. *dianthi* and will be referred to hereafter as the "reference cultivars."

Container experiments. Experiments were conducted in containers to determine the influence of initial inoculum on the Fusarium wilt incidence and the population densities of *F. oxysporum* f. sp. *dianthi* on plants and in soil for cultivars with different degrees of resistance to the pathogen. Concrete containers (100 cm in height by 60 cm in diameter) were filled with pathogen-free soil to a depth of 70 cm. The soil was light sandy soil, similar to that used in commercial carnation greenhouses in Israel. On top of this uninfested soil, a 20-cm layer of soil uniformly infested with *F. oxysporum* f. sp. *dianthi* was added. Naturally infested light sandy soil was used as the source of *F. oxysporum* f. sp. *dianthi* inoculum. The infested soil was diluted with noninfested soil (of the same type) to reach the desired inoculum concentration, and the inoculum concentration was determined before planting as described below. There were four amounts of initial inoculum levels (0, 10, 100, and 1,000 *F. oxysporum* f. sp. *dianthi* CFU/g of soil) in 1993 to 1994 and five (0, 40, 200, 1,000, and 5,000 CFU/g of soil) in 1994 to 1995. At the end of the 1993 to 1994 season, the soil in the containers was fumigated with methyl bromide and metham-sodium to eliminate viable *F. oxysporum* f. sp. *dianthi* CFU before starting the next growing cycle, as described recently (5). Briefly, soil was fumigated by successive application of methyl bromide (1.25 g/kg of soil) and metham-sodium (1.5 ml/kg of soil; Vapam = Edigan, Agan Ltd., Ashdod, Israel). These rates were 19 times higher for methyl bromide and five times higher for metham-sodium than those recommended for commercial growers. Such high rates were used to ensure maximal reduction of fungal CFU before starting the new growing cycle. Each container was covered with a 0.1-mm thick polyethylene cover. Methyl bromide was then injected into the soil at the center of each container by inserting a metal tube with pores at 10-cm intervals to a depth of 60 cm. Four days later, metham-sodium was applied through the irrigation system, with the water volume adjusted to ensure penetration of the fumigant throughout the soil column.

Twenty stem-rooted cuttings of each cultivar were planted into separate containers in mid-June 1993 and 1994. The experiments included the five reference cultivars, each planted in the four (1993 to 1994) or five (1994 to 1995) levels of initial inoculum. There were four replicates (containers) for each combination (cultivar × initial inoculum) that were laid out in a complete randomized design. A control treatment was included in the experiments to determine changes in the *F. oxysporum* f. sp. *dianthi* population in soil over time. For that purpose, for each inoculum concentration, four containers filled with infested soil were left unplanted. The plants were irrigated and fertilized as necessary and maintained according to recommendations for carnation growers in Israel (10). Prior to planting, stem segments from 20 cuttings of each of the cultivars to be planted were examined for possible contamination by *F. oxysporum* f. sp. *dianthi*. Segments were surface sterilized and plated in petri dishes on potato-dextrose agar supplemented with 250 mg of dihydrostreptomycin (PDAS) (Sigma Chemical Co., St. Louis). Cultures resembling *F. oxysporum* were evaluated for pathogenicity by inoculating carnation plants ('Hermon'). When wilt was observed, it was concluded that the *F. oxysporum* culture was *F. oxysporum* f. sp. *dianthi*. Contamination by *F. oxysporum* f. sp. *dianthi* was not detected in any sample.

Disease incidence and the number of CFU of *F. oxysporum* f. sp. *dianthi* on plants and in soil beneath the plants were determined 180 and 260 days after planting, respectively. Disease incidence was assessed visually (10), and population densities of *F. oxysporum* f. sp. *dianthi* were determined as described below.

The data were analyzed by means of a general linear model (GLM) procedure of SAS (release 6.03; SAS Institute, Cary, NC). The dependent variables in the analyses were disease incidence, the number of *F. oxysporum* f. sp. *dianthi* CFU in plants, and the number of *F. oxysporum* f. sp. *dianthi* CFU in soil beneath the plants. Disease incidence (y; the proportion of plants showing wilt symptoms) was expressed in term of $\ln(1/(1 - y))$; the number of *F. oxysporum* f. sp. *dianthi* CFU was expressed in log units. The GLM included two independent variables: one discrete (cultivar resistance) and one continuous (amount of initial inoculum, expressed in log units). The significance of these variables on the dependent variables, as well as the covariance among them, was estimated at $P < 0.05$.

Field experiments. Experiments in the field were conducted to study the dynamics of wilt development and to quantify changes in the number of *F. oxysporum* f. sp. *dianthi* CFU in plants and in soil beneath the plants over time. A 0.1-ha field with light sandy soil was infested with *F. oxysporum* f. sp. *dianthi* by amending the soil with wilted carnation plants. Carnation plants infected with Fusarium wilt were collected during March 1988 from commercial greenhouses in various parts of the country to ensure a wide-ranging collection of isolates and pathotypes existing in Israel. The wilted plants were ground to a powder, spread on the soil surface, and the soil was then disked to a depth of 15 to 20 cm. In subsequent growing seasons, soil in the experimental site was not subjected to further infestation, since examination of the soil each season before planting revealed a high level of inoculum (8,800 to 10,000 CFU/g of soil). The five reference cultivars were planted in the field in late-June 1991, 1992, and 1993 for the 1991 to 1992, 1992 to 1993, and 1993 to 1994 seasons, respectively. Each experimental plot consisted of a bed 1 m wide and 1 m long, with 32 stem-rooted cuttings planted in four rows. There were eight replicates for each cultivar and the treatments were laid out in a randomized complete blocks design. The carnation plants were maintained and treated as described previously (10) and, by the end of the season, they were removed from the field. The cultivar Scarlette was introduced for the first time in 1992; thus, it was not included in the 1991 to 1992 experiment. In addition to the reference cultivars, the experiments included two additional cultivars, Candy (resistant) and Raggio-di Sole (highly susceptible). In 1993 to 1994, 26 additional carnation cultivars with undefined resistance to *F. oxysporum* f. sp. *dianthi* were examined as well. These cultivars were supplied by breeders in Israel and Europe for determination of their response to the pathogen. Prior to planting, possible contamination in stem-rooted cuttings by *F. oxysporum* f. sp. *dianthi* was determined as described above. Contamination by *F. oxysporum* f. sp. *dianthi* was not detected in any sample.

Several times during the season (three in 1991 to 1992, five in 1992 to 1993, and four in 1993 to 1994), the number of *F. oxysporum* f. sp. *dianthi* CFU in soil beneath the plants was determined for the reference cultivars, and it was determined once for all cultivars by the end of the season. In the 1993 to 1994 season, the number of *F. oxysporum* f. sp. *dianthi* CFU in the plant stems was determined three times for the reference cultivars and once for all cultivars. Procedures for these tests are described below. Disease incidence was assessed visually at biweekly intervals. A

plant was considered diseased if wilt was observed on at least one stem. Assessments were performed from mid-September to mid-December (85 to 180 days after planting). No further increase in disease incidence was observed after that time.

Differences among the reference cultivars for disease incidence and the population of *F. oxysporum* f. sp. *dianthi* on plants or in soil were determined for each sampling date, using the analysis of variance procedure. When differences among cultivars were significant, a least significant difference (LSD) test ($P < 0.05$) was used to compare means. In some cases, regression analysis was conducted. The independent variable was disease incidence; the dependent variables were *F. oxysporum* f. sp. *dianthi* populations on plants and in soil. Linear and quadratic equations with the higher coefficient of determination (r^2), and the lower P value and mean square error were chosen.

Determination of population densities of *F. oxysporum* f. sp. *dianthi* in soil. The number of *F. oxysporum* f. sp. *dianthi* CFU in soil was determined in container and field experiments. In the field experiments, one plant from each of the four rows was removed from each experimental plot. Soil subsamples were taken from the upper 10-cm layer in the vicinity of the removed plants. The four soil subsamples were combined and mixed to form one composite sample (about 2 kg). For the container experiments, five soil subsamples were taken from each container, as described above, and mixed to form one composite sample. Soil samples were dried in an air-conditioned greenhouse (23 to 27°C) for 4 days. Subsequently, they were passed through a 710-µm sieve and returned to the greenhouse for another 10 to 15 days to dry, so that only *F. oxysporum* f. sp. *dianthi* chlamydospores would be counted. Five grams of air-dried soil was diluted in 45 ml of sterile, diluted water-agar (0.1%), and 1 ml of this suspension was pipetted onto each of five plates containing pentachloronitrobezene (PCNB)-agar medium (19). *Fusarium*-like colonies, randomly selected from the five plates, were transferred to PDAS medium for identification of *F. oxysporum*. *F. oxysporum* f. sp. *dianthi* was identified by a pathogenicity test on the susceptible cultivar Hermon. About 1,000 pathogenicity tests were conducted each year on samples taken from soil. Of these tests, 100 were before planting, 500 were on samples taken from the field (five carnation cultivars × 20 colonies × five dates of sampling), and 400 were on samples taken from containers (five carnation cultivars × four inoculum concentrations × 20 colonies).

The number of *F. oxysporum* CFU was estimated by multiplying the *F. oxysporum* proportion (the fraction of *F. oxysporum* CFU from the total number of colonies plated on PDAS) by the total number of colonies recovered on PCNB media. The number of *F. oxysporum* f. sp. *dianthi* CFU was calculated by multiplying the *F. oxysporum* f. sp. *dianthi* proportion (the fraction of plants wilted from the total number of plants inoculated) by the total number of *F. oxysporum* CFU/g of soil. For data analyses, the number of CFU in nonplanted plots was subtracted from the number estimated for plots with carnations, to account for changes in the population density of the pathogen.

Determination of population densities of *F. oxysporum* f. sp. *dianthi* in plants. This was tested in the 1993 to 1994 field experiment and in the 1993 to 1994 and 1994 to 1995 container experiments. For the field experiment, four plants were sampled from each experimental plot of the reference cultivars 120 and 170 days after planting, and eight plants were sampled from all cultivars included in the test 260 days after planting. For the container experiments, 10 plants from each container were sampled 260 days after planting. Plants were removed from the soil with part of their upper rooting system attached. However, the majority of the roots were detached and left in the soil. Plants were left to dry outside for 3 weeks, washed in water to remove soil particles, inserted into paper bags, and left to dry for another 9 weeks (minimum and maximum temperatures were 14 and 29°C in April and 18 and 31°C in May). After drying, the lower 10 cm of the above-ground part of the stem was ground into a fine powder with a Wiley mill (model 2, Arthur H. Thomasco, Philadelphia), and a 5-g sample of that powder was passed through a 500-µm sieve. Three 200-mg subsamples were dispersed in sterile, diluted water-agar (0.1%), and 1 ml of this suspension was pipetted onto each of five plates containing PCNB-agar medium (19). The number of *F. oxysporum* f. sp. *dianthi* CFU was then determined as described above for soil. In total, 500 pathogenicity tests were conducted on samples taken from plants. Ninety-five to 100% of the *F. oxysporum* colonies sampled from soil or plants were confirmed to be *F. oxysporum* f. sp. *dianthi*.

RESULTS

Container experiments. In 1994 to 1995, the highly resistant (Scarlette and Eveline) and the moderately resistant (Galit) cultivars remained symptomless for all amounts of initial inoculum. For the susceptible (Lior) and highly susceptible (Hermon) cultivars, however, the disease incidence increased significantly ($P < 0.05$) with increasing amounts of initial inoculum (Table 1 and

TABLE 1. General linear model analyses of the relationship between the amount of initial inoculum and cultivar resistance and the incidence of Fusarium wilt and the population of *Fusarium oxysporum* f. sp. *dianthi* on carnation plant stems and in soil[a]

	Independent variable						
Dependent variable	Main effects	Covariance	*F*	*P*	Coefficient	*t*	*P*
Disease incidence	Initial inoculum		2.48	0.05			
	Cultivar resistance		18.50	0.001			
		'Scarlette'			0.0	0.0	1.0
		'Eveline'			0.0	0.0	1.0
		'Galit'			0.036	0.35	0.726
		'Lior'			0.266	2.06	0.01
		'Hermon'			0.948	9.25	0.001
Population on plants	Initial inoculum		19.25	0.001			
	Cultivar resistance		24.00	0.001			
		'Scarlette'			1.109	3.18	0.001
		'Eveline'			1.589	5.27	0.001
		'Galit'			2.380	7.91	0.001
		'Lior'			0.300	1.03	0.03
		'Hermon'			1.160	3.87	0.001
Population in soil	Initial inoculum		58.66	0.001			
	Cultivar resistance		53.20	0.001			
		'Galit'			0.962	11.15	0.001
		'Lior'			0.332	3.85	0.001
		'Hermon'			0.18	2.09	0.001

[a] The experiment was conducted in large containers in 1994 to 1995. Data are presented in Figure 1.

Fig. 1A). Cultivar resistance and the amount of initial inoculum significantly affected the population densities of *F. oxysporum* f. sp. *dianthi* on plants and in soil (Table 1). Increasing the amount of initial inoculum by 125-fold (from 40 to 5,000 CFU/g of soil) had a greater effect on the final population densities of the pathogen in the resistant cultivars than in the susceptible ones. For example, this increase resulted in about a 3,000-fold difference in the number of *F. oxysporum* f. sp. *dianthi* CFU on stems of 'Galit,' but only a 140-fold difference on 'Hermon' (Fig. 1B). The lower increase observed in the more susceptible cultivars was a result of the high population densities in these cultivars, even with the low amounts of initial inoculum. 'Eveline' and 'Scarlette' were not included in Figure 1C because the number of CFU per gram of soil was similar to that observed in the control (nonplanted containers). Results of the 1993 to 1994 container experiment showed similar trends and the GLM analyses of the data yielded similar effects to those presented in Figure 1 and Table 1. Consequently, results of the 1993 to 1994 experiments are not shown in this report.

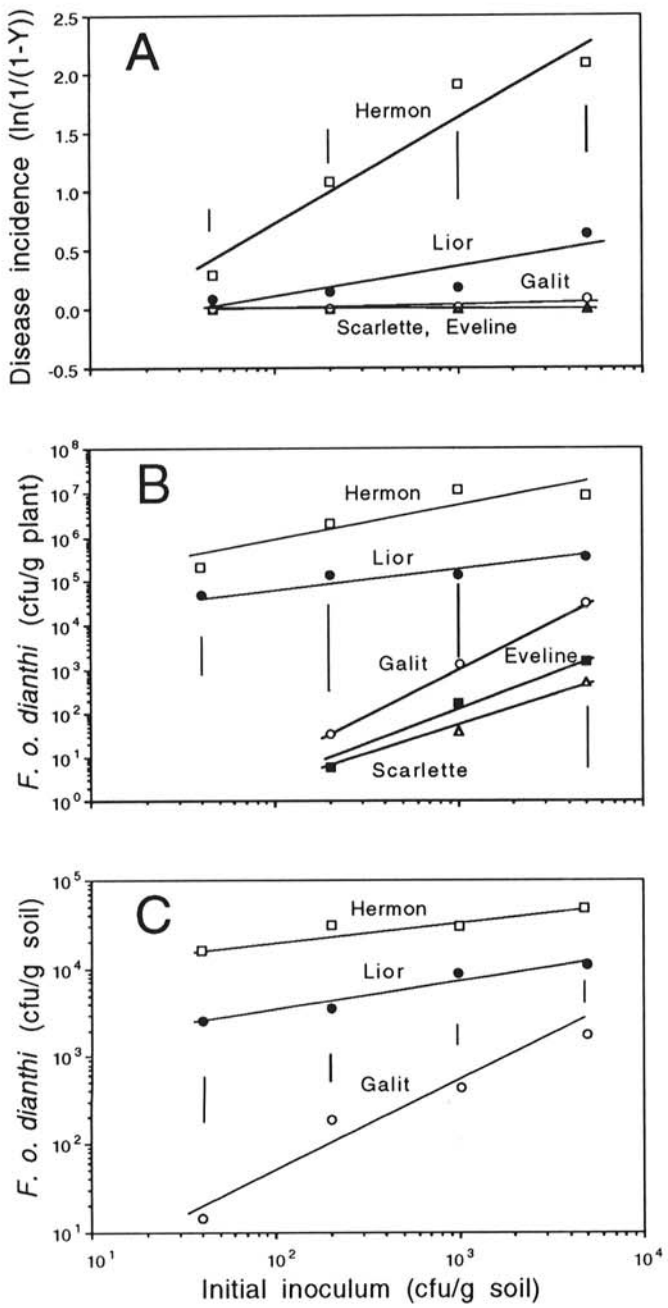

Fig. 1. The relationship between the amount of initial inoculum and **A,** the incidence of Fusarium wilt; and **B,** the population of *Fusarium oxysporum* f. sp. *dianthi* on plant stems; and **C,** in soil beneath the plants for carnation cultivars with diverse levels of resistance to the pathogen. Experiments were conducted in large containers in 1994 to 1995. The disease incidence was assessed 180 days after planting. CFU of *F. oxysporum* f. sp. *dianthi* on stems and in soil were determined 260 days after planting. Bars indicate the least significant difference (in log units) at $P < 0.05$. Statistics for the general linear model analyses of the data are presented in Table 1.

Field experiments. Changes in the disease incidence and the population densities of *F. oxysporum* f. sp. *dianthi* throughout the season were determined in the 1991 to 1992, 1992 to 1993, and 1993 to 1994 field experiments. Results are presented in Figure 2. As expected, the disease incidence in the five reference carnation cultivars developed in accordance with their level of resistance to the pathogen. Disease on 'Hermon' appeared early and, by 100 to 110 days after planting, the disease incidence reached 100%. Disease on 'Lior' and 'Galit' appeared later and, by the end of the season, it reached 75 to 90% and 35 to 40%, respectively. For 'Eveline,' the disease incidence was low (<10%) till the end of the season; no symptoms were apparent on 'Scarlette' (Fig. 2).

Changes over time in the population density of *F. oxysporum* f. sp. *dianthi* on plants was examined only in 1993 to 1994. In general, the number of *F. oxysporum* f. sp. *dianthi* CFU recovered from plant stems increased with time (Fig. 2). The magnitude of that increase and the final number of CFU were related to the degree of resistance in cultivars to *F. oxysporum* f. sp. *dianthi*; the highest population densities developed on the highly susceptible cultivar Hermon and the lowest on the highly resistant cultivar Scarlette. In soil, changes over time in the population densities of *F. oxysporum* f. sp. *dianthi* followed similar trends for 'Hermon,' 'Lior,' and 'Galit.' However, for 'Eveline' and 'Scarlette,' the number of *F. oxysporum* f. sp. *dianthi* CFU in stems did not change over time (Fig. 2). Differences among cultivars in the count of *F. oxysporum* f. sp. *dianthi* CFU were greater on plants than those in soil. For example, in 1993 to 1994, about 10,000 more *F. oxysporum* f. sp. *dianthi* CFU were recovered from the lower stems of 'Hermon' than from the lower stems of 'Scarlette.' However, the differences in the number of CFU in soil beneath these two cultivars was only 50-fold (Fig. 2).

The relationships among the disease incidence 180 days after planting and the number of *F. oxysporum* f. sp. *dianthi* CFU on plants and in soil at 260 days after planting are presented in Figures 3 and 4. The counts of *F. oxysporum* f. sp. *dianthi* CFU on plants were determined in 1993 to 1994 for 33 different cultivars with diverse resistances to *F. oxysporum* f. sp. *dianthi*. In general, results observed in the container experiments (Fig. 1) were corroborated in the field. The population densities of the pathogen on plants were related to their resistance to the pathogen; larger numbers of CFU were recovered from susceptible cultivars (which were severely diseased) than from resistant cultivars. The relationship between disease incidence and the number of *F. oxysporum* f. sp. *dianthi* CFU was linear (Fig. 3). It should be noted that the pathogen was recovered also from symptomless plants at relatively high numbers (10^4 CFU/g of plant). A similar relationship was observed between the disease incidence and the population density of *F. oxysporum* f. sp. *dianthi* in soil, except that the increase in population density was not linear and the number of pathogen CFU leveled off gradually at high disease incidence (Fig. 4).

DISCUSSION

This study demonstrated that the Fusarium wilt incidence and the population density of *F. oxysporum* f. sp. *dianthi* on carnation plants and in soil beneath the plants were affected by the degree of cultivar resistance and the amount of inoculum in the soil before planting. The relationship between the amount of initial inoculum and the severity of the resulting epidemic in susceptible crops by

wilt pathogens has been demonstrated for several *F. oxysporum* pathosystems (5,13,16,18,24) and other pathogens (e.g., *Verticillium dahliae* [3,15,20,22,23]). Little is known, however, about the effects of durable resistance, as present in carnation, on wilt and on the population densities of the pathogen on plants and in soil. Alon et al. (1) and Elgersma et al. (12) compared the reproduction of *F. oxysporum* f. sp. *lycopersici* in stems of susceptible and completely resistant tomato cultivars following artificial inoculation. They found that the number of CFU of the pathogen on stems increased more in the susceptible than in the resistant cultivar. In our study, carnation plants were grown in infested soil in large containers and in the field. The number of *F. oxysporum* f. sp. *dianthi* CFU increased for all cultivars with time and with increasing amounts of initial inoculum. The magnitude of these increases was related to the degree of resistance of the cultivar. For example, the number of *F. oxysporum* f. sp. *dianthi* CFU recovered from stems of the highly susceptible cultivar Hermon was about 1,000 to 100,000 times larger than the number recovered from the resistant cultivar Scarlette. Increases in the population densities of *F. oxysporum* f. sp. *dianthi* in soil, in relation to the amount of initial inoculum, occurred for the highly susceptible (Hermon), susceptible (Lior), and the moderately resistant (Galit) cultivars, but not for the highly resistant cultivars (Eveline and Scarlette) (Figs. 1C and 2). The actual number of CFU recovered from soil by the end of the season was related to the resistance of the cultivar to *F. oxysporum* f. sp. *dianthi*. This implied that the choice of cultivar not only affected the severity of the epidemic in the current season, but may also have governed the buildup of inoculum in the following seasons.

Not all infected plants showed disease symptoms (Fig. 3). The reason for the lack of symptoms in infected plants is not fully understood, but it may be related to a presymptom incubation period or environmental influences. Under controlled conditions, the most severe epidemics developed at low radiation intensities (200 to 300 μE m^{-2} s^{-1}) and at temperatures close to 25 to 26°C. However, at solar radiation intensities above 1,000 μE m^{-2} s^{-1} and temperatures below 18 or above 34°C, plants remained symptomless even though *F. oxysporum* f. sp. *dianthi* was isolated from most of the symptomless plants (9). Regardless of the cause of this phenomenon, it is important that the pathogen existed in symptomless plants, because reproduction of the pathogen in these plants may provide inoculum for the following season. Thus, it should be recommended to remove all plants by the end of the season to reduce the amount of initial inoculum in the following year.

Fumigation of soil with methyl bromide before planting is a common practice in carnation production in Israel. In addition, growers tend to grow susceptible cultivars because of their higher profitability. However, fumigation alone does not always provide an optimal solution for disease control, even though it significantly

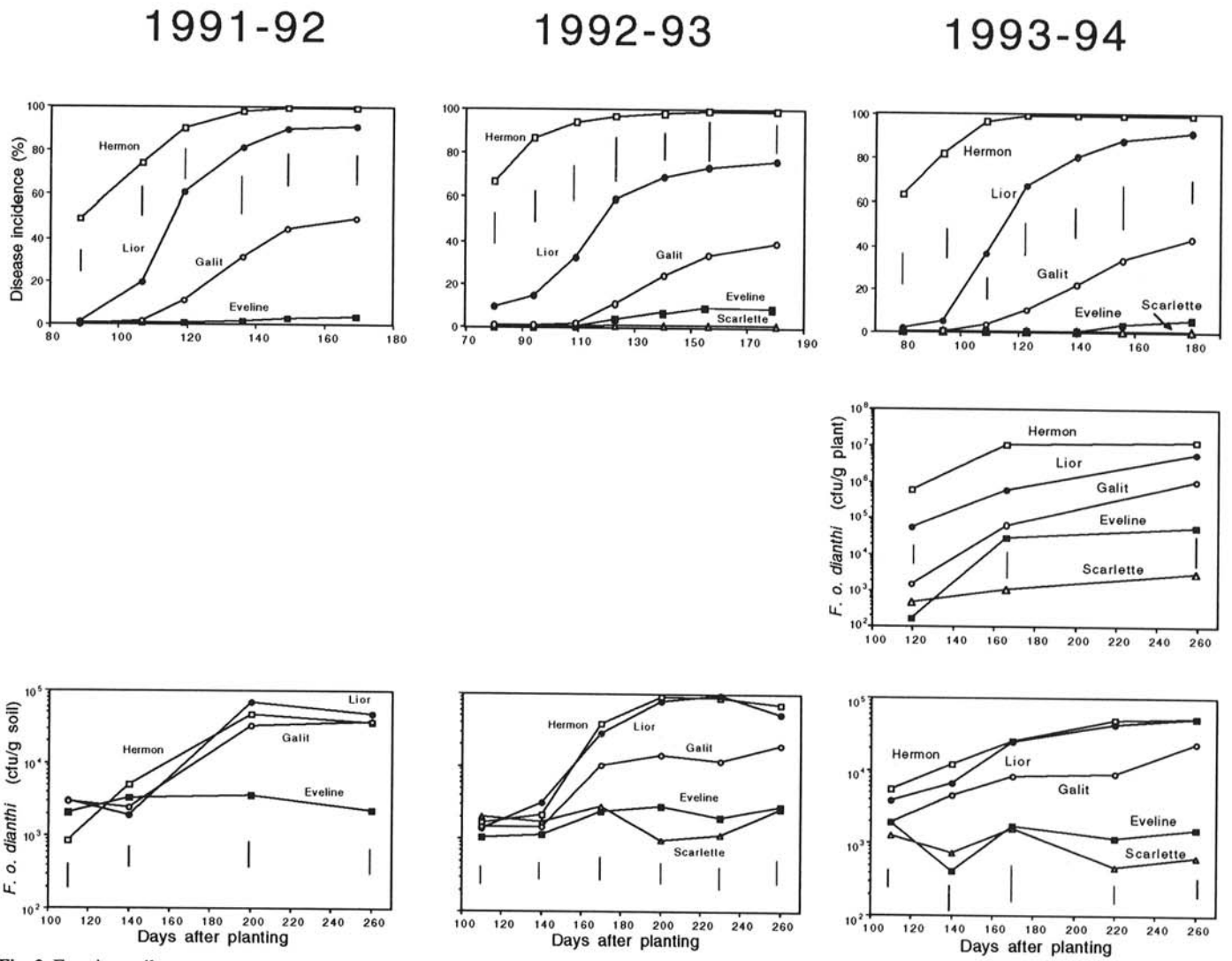

Fig. 2. Fusarium wilt progress curves and the population density of *Fusarium oxysporum* f. sp. *dianthi* on plant stems and in soil beneath the plants for carnation cultivars with diverse levels of resistance to the pathogen. Experiments were conducted in the field in Israel in 1991 to 1992, 1992 to 1993, and 1993 to 1994. For each sampling date, the bars indicate the least significant difference at $P < 0.05$.

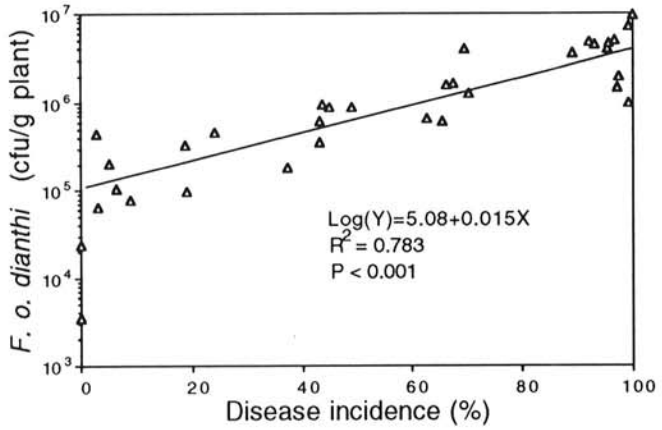

Fig. 3. The relationship between the disease incidence and the population density of *Fusarium oxysporum* f. sp. *dianthi* on plant stems for carnation cultivars with diverse levels of resistance to the pathogen. Results are for experiments conducted in the field in 1993 to 1994. The disease incidence was assessed 180 days after planting. The number of *F. oxysporum* f. sp. *dianthi* CFU was determined 260 days after planting. Only cultivars with disease incidence >0% were included in the regression analysis.

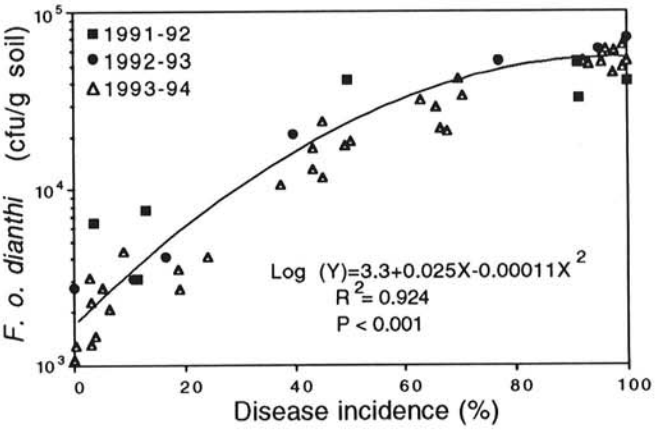

Fig. 4. The relationship between the disease incidence and the population density of *Fusarium oxysporum* f. sp. *dianthi* in soil beneath the carnation cultivars with diverse levels of resistance to the pathogen. The disease incidence was assessed 180 days after planting. The number of CFU was determined 260 days after planting. Experiments were conducted in the field in 1991 to 1992, 1992 to 1993, and 1993 to 1994. Only cultivars with disease incidence >0% were included in the regression analysis.

reduces the population of the pathogen in soil (8). Results of this study may have implications for the development of strategies for effective management of Fusarium wilt in carnation. Resistant cultivars may be used as a means to reduce the accumulation of *F. oxysporum* f. sp. *dianthi* CFU in soil, especially beyond the efficacy of fumigation. Another implication may be in the reduction of methyl bromide use. It may be possible to grow several cycles of carnation after one successful fumigation with methyl bromide, provided that resistant cultivars are planted. However, implementation of these conclusions should await determination of threshold levels (i.e., number of CFU) for each group of resistance and evaluation in separate experiments.

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