Stunting of Citrus Seedlings in Fumigated Nursery Soils Related to the Absence of Endomycorrhizae

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ABSTRACT

Stunted and chlorotic citrus seedlings growing in fumigated nurseries in California and Florida were nonmycorrhizal, and *Endogone* spores were not found associated with their roots; whereas seedlings growing normally in scattered areas of these nurseries were mycorrhizal, and *Endogone* spores were present. Stunted plants from nurseries grew normally after inoculation with *Endogone mosseae*, an endomycorrhizal fungus. Noninoculated citrus seedlings grew poorly in steamed, autoclaved, or methyl-bromide-treated soil in greenhouse experiments. Plants inoculated with *E. mosseae* produced excellent growth in these treated soils. Inoculation also improved the growth of citrus seedlings in an Illinois field plot that had been fumigated with methyl bromide. All mycorrhizal plants had a greater dry weight and a higher percentage of phosphorus than did nonmycorrhizal plants. Stunting and chlorosis of citrus in fumigated or heat-treated soils have been previously attributed to soil toxicity. Our evidence indicates that the major cause of this problem is inadequate nutrition brought about by the killing of mycorrhizal fungi.

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Citrus seedlings grown in fumigated nursery soils and in heat-treated or fumigated soil in greenhouse experiments commonly are stunted and chlorotic. This condition has been attributed to "soil toxicity" (9, 11). Compounds toxic to plants have been found in some heat-treated soils (20). However, phytotoxic components (toxins) have not been recovered or identified from any treated citrus soil (9, 10, 11). It was postulated that a "toxin" produced in treated soils inhibited phosphorus absorption (11). Although the water-soluble phosphate in soil increases after soil sterilization (1), the percentage of phosphorus in the stunted citrus plants was less than in the healthy plants (11). Phosphate fertilizers overcame the effect of the "toxin" when applied to some heat-treated or fumigated soils (11, 18, 22). The addition of nontreated soil, which probably contained endomycorrhizal fungi (5), shortened the duration of the inhibitory effect (18).

Mycorrhizal plants are known to take up more phosphorus than nonmycorrhizal plants (1, 8, 19). Phosphorus-deficiency symptoms on corn grown in steamed soil can be prevented by inoculation of the plants with an endomycorrhizal fungus (3). A higher fertility level is known to be required for normal plant growth when endomycorrhizal fungi are absent (1, 2, 3, 5, 19).

The beneficial effect of endomycorrhizal fungi on citrus has been questioned (14, 15, 16, 17). Sabet (21), however, reported that chlorotic orange seedlings had fewer endomycorrhizal root cells than did healthy plants, and that the number of mycorrhizal root cells increased as the plants recovered. Marx et al. (13) obtained increased growth of citrus plants in steamed soil by inoculation with *Endogone mosseae* Nicol. & Gerd., an endomycorrhizal (vesicular-arbuscular) fungus. We undertook our research to determine whether citrus stunting and chlorosis in partially sterilized or sterilized soils is related to killing of endomycorrhizal fungi.

MATERIALS AND METHODS.—*Soil treatments and inoculation of plants.*—A standard soil mix (2:1 loam plus sand) was used in all greenhouse experiments. This soil mixture tested 29 lb./acre available phosphorus (P_1), 73 lb./acre available and acid-soluble phosphorus (P_2), and 242 lb./acre exchangeable potassium (K). It was partially sterilized by (i) autoclaving for 2 hr at 121 C and 15 psi; (ii) aerated-steaming for 1 hr at 82 C; or (iii) fumigating in a sealed plastic container into which a mixture of 98% methyl bromide and 2% chloropicrin was injected. The soil mixtures were aerated for at least 7 days after treatment.

We increased sporocarps of *E. mosseae* by planting Sudangrass (*Sorghum vulgare* Pers.) in the autoclaved soil mixture to which 200 to 250 sporocarps had been added. After 4 months, sporocarps of *E. mosseae* to be used as inoculum were collected by a procedure involving wet-sieving and decanting of soil from the Sudangrass roots (6). Between 200 and 250 sporocarps were placed in the soil of each 15-cm plastic pot, and ca. 1,000 sporocarps were placed in the soil of each 31-cm clay pot. The effect of soil microorganisms present on sporocarps was assessed by washing the sporocarps, filtering the sporocarps from the resulting microbial suspension, and adding the suspension to the soil. Each greenhouse

experiment was arranged in a completely randomized design and included the following treatments: (i) inoculated with sporocarps of *E. mosseae;* (ii) inoculated with microbial suspension from the sporocarps; (iii) noninoculated.

Experiments with seedlings from nurseries.—Healthy and stunted 10-month-old seedlings of Brazilian sour orange (*Citrus aurantium* L. 'Brazilian'), Yuma citrange [*Citrus* sp. × *Poncirus trifoliata* (L.) Raf.], and rough lemon [*Citrus limon* (L.) Burm. f.] were received from Willits & Newcomb, Inc., Thermal, Calif. They had been grown in a nursery soil fumigated with 400 lb./acre of a mixture containing 75% methyl bromide and 25% chloropicrin. Root samples were washed free of soil and cleared and stained (4), and 200 1-cm segments from each group of seedlings were sectioned free-hand and examined for endomycorrhizae. Soil collected from near the roots was processed by wet-sieving and decanting (6), then examined for live spores of *Endogone* spp.

Each lot of healthy or stunted seedlings was divided randomly into three groups of three seedlings, and these then were transplanted into 31-cm pots that contained autoclaved soil mixture which had been inoculated as described above or not inoculated. One pot was used for each treatment. All pots were kept in a greenhouse. The plants were removed from the pots 32 weeks after transplanting, and the mineral content of tops and roots was determined by emission spectrographic analysis. Healthy and stunted Cleopatra mandarin (*Citrus reticulata* Blanco) seedlings collected from a fumigated nursery in Florida were tested in a similar experiment (Fig. 1).

Experiments with plants grown from seed in the greenhouse.—Rough lemon, Keen sour orange (*Citrus aurantium* L. 'Keen'), Cleopatra mandarin, Troyer citrange [*Citrus sinensis* (L.) Osb. × *Poncirus trifoliata* (L.) Raf.], sweet orange [*Citrus sinensis* (L.) Osb.], and Brazilian sour orange were seeded in flats containing the autoclaved soil mixture. We grew seedlings for 5 weeks before transplanting them into soil mixtures that had been inoculated as described above or not inoculated.

Troyer citrange, Cleopatra mandarin, and rough lemon were tested in steamed soil. Keen sour orange, Brazilian sour orange, and sweet orange were tested in the autoclaved soil mixture. For each variety, there were two seedlings in each 15-cm pot, and each treatment was replicated 4 times. Rough lemon was tested in a similar experiment using both fumigated and nonfumigated soil, and the experiment was replicated 8 times. Troyer citrange was used in a similar experiment, except that the seeds were planted directly into the pots.

In all these experiments, plant height was measured biweekly. We removed plants from the pots 21 weeks after transplanting the seedlings, or 28 weeks after seeding in the case of Troyer citrange. The root systems were compared for size and examined for presence of endomycorrhizae. Dry weights were recorded, and the mineral composition of the tops and roots was determined by emission spectrographic analysis. The soil in each pot was tested for P_1, P_2, and K.

Experiments with plants in a fumigated field plot.—A field plot near Urbana, Ill., was fumigated with a mixture of 98% methyl bromide and 2% chloropicrin at a rate of 435 lb./acre, sealed with a plastic tarp for 4 days, then aerated for 7 days. The soil tested 63 lb./acre P_1, 91 lb./acre P_2, and 367 lb./acre K. One 15-cm pot culture of *E. mosseae* was mixed with an equal volume of steamed sand and distributed evenly 4 cm deep in a 2.5-m row in the fumigated field plot. Soil and roots from a pot of Sudangrass, grown in autoclaved soil mixture and inoculated with the microbial suspension obtained from *E. mosseae* sporocarps, were applied similarly in a second row and served as the control. Seeds of rough lemon, Cleopatra mandarin, Troyer citrange, or Keen sour orange were planted directly on the inoculum or control mixture. The plants were removed from the soil 18 weeks after planting, and the height and dry weight of each plant recorded. The mineral content of the tops and roots was determined by emission spectrographic analysis.

RESULTS.—*Experiments with seedlings from nurseries.*—The Brazilian sour orange and Yuma citrange seedlings, collected by D. A. Newcomb from the fumigated nursery at Thermal, Calif., and classified by him as stunted, were nonmycorrhizal. Seedlings that he classified as healthy were mycorrhizal. Spores and sporocarps of *Endogone fasciculata* Thaxter were found in soil collected near mycorrhizal plants, but not in soil collected near the nonmycorrhizal plants. Healthy plants transplanted to pots of autoclaved soil and placed in a greenhouse continued to grow, and the stunted plants, inoculated with *E. mosseae*, made excellent growth. After 32 weeks, stunted plants that had been inoculated were nearly equal in size to plants originally classified as healthy (Fig. 2). Noninoculated stunted plants grew only slightly. The rough lemon seedlings, classified by D. A. Newcomb as healthy or stunted, were all nonmycorrhizal when we received them, and they did not differ appreciably in size. Seedlings from both

Fig. 1-3. 1) Healthy (mycorrhizal) and stunted (nonmycorrhizal) citrus seedlings growing in a fumigated nursery in Florida. **2)** Healthy and stunted Brazilian sour orange seedlings obtained from a fumigated nursery in California and transplanted into autoclaved soil. The pot on the left contains plants which were growing normally (mycorrhizal) and the three pots on the right contain plants which were stunted (nonmycorrhizal). From left to right: noninoculated; inoculated with *Endogone mosseae* sporocarps; inoculated with microbial suspension from the sporocarps; noninoculated. **3)** Rough lemon seedlings growing in nonfumigated soil (three pots on left) and methyl-bromide-fumigated soil (three pots on right). From left to right: inoculated with *E. mosseae* sporocarps; inoculated with microbial suspension from the sporocarps; noninoculated; inoculated with *E. mosseae* sporocarps; inoculated with microbial suspension from the sporocarps; noninoculated.

groups grew well when they were inoculated with *E. mosseae*, whereas noninoculated plants from both groups made little additional growth.

All mycorrhizal plants had large, dark-green leaves and extensive root systems. Leaves of the nonmycorrhizal plants were small and chlorotic, and although the root systems appeared healthy they were poorly developed. The mycorrhizal plants contained a higher percentage of phosphorus than did the nonmycorrhizal plants. The percentage of phosphorus for mycorrhizal and nonmycorrhizal plants, respectively, were Brazilian sour orange, 0.15 and 0.10%; Yuma citrange, 0.25 and 0.13%; and rough lemon, 0.14 and 0.10%

Healthy Cleopatra mandarin seedlings from the fumigated Florida nursery were mycorrhizal, whereas stunted and chlorotic seedlings were nonmycorrhizal (Fig. 1). The results from greenhouse experiments with these seedlings were similar to those obtained with the seedlings from the California nursery.

Experiments with plants grown from seed in the greenhouse.—All citrus seedlings inoculated with *E. mosseae* or grown in nonsterilized soil became mycorrhizal. Those seedlings grown in partially sterilized soils not inoculated with *E. mosseae* were nonmycorrhizal.

The nonmycorrhizal plants were stunted, and the leaves were small and chlorotic, whereas the mycorrhizal plants grew normally and had large, dark-green leaves (Fig. 3). The root systems of the nonmycorrhizal plants appeared healthy, but were poorly developed (Fig. 4). Growth differences between mycorrhizal and nonmycorrhizal plants appeared between 4 and 6 weeks after inoculation (Fig. 5). About 10 weeks elapsed before differences were observed for Troyer citrange plants grown from seed in pots. Dry weights of all mycorrhizal plants were significantly greater than dry weights of nonmycorrhizal plants. Similar results were obtained with all varieties in autoclaved, steamed, and methyl-bromide-fumigated soils. Typical results are given in Tables 1 and 2. In some experiments, inoculation of nonsterilized soil with *E. mosseae* also significantly increased the growth of the plants (Table 2).

Fig. 4. Keen sour orange seedlings grown in autoclaved soil. From left to right: inoculated with *Endogone mosseae* sporocarps; inoculated with microbial suspension from the sporocarps; noninoculated.

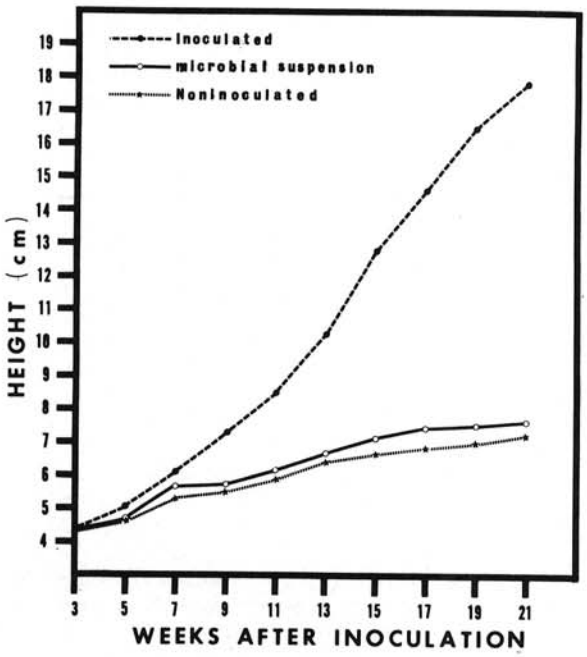

Fig. 5. Growth of mycorrhizal and nomycorrhizal Keen sour orange seedlings in autoclaved soil. Inoculated = inoculated with *Endogone mosseae* sporocarps; Microbial suspension = inoculated with the microbial suspension obtained by washing with *E. mosseae* sporocarps.

Because the nonmycorrhizal plants grew poorly, it was necessary to bulk plants from the two control treatments to have sufficient material for mineral analysis. All mycorrhizal plants had a significantly greater percentage of phosphorus than did the nonmycorrhizal plants; however, the concentration of other minerals usually was greater in the nonmycorrhizal plants (Tables 3, 4). Since the mycorrhizal plants had much greater dry weights, they contained larger amounts of all minerals. The concentration of some minerals was too high in the root samples to be measured by the emission spectrograph. The mycorrhizal plants removed a greater amount of P_1, P_2, and K from the soil mixture than did the nonmycorrhizal plants (Table 5).

Experiments with plants in a fumigated field plot.—The dry weights of rough lemon, Cleopatra mandarin, and Troyer citrange plants inoculated with

TABLE 1. The effect of *Endogone mosseae* on the growth of citrus in steamed soil[a]

Treatment[b]	Mean dry wt (g) per pot		
	Cleopatra mandarin	Rough lemon	Troyer citrange
Inoculated	10.09**[c]	13.43**	14.94**
Microbial suspension	0.44	0.52	2.17
Noninoculated	0.47	0.54	2.81

[a] Soil was treated with aerated steam for 1 hr at 82 C.
[b] Inoculated = inoculated with *E. mosseae* sporocarps. Microbial suspension = inoculated with microbial suspension obtained by washing *E. mosseae* sporocarps.
[c] ** = Significant at the .01 level of probability.

TABLE 2. The effect of *Endogone mosseae* on the growth of citrus in soil fumigated with methyl bromide

Treatment[a]	Mean dry wt (g) per pot	
	Rough lemon	Troyer citrange
Fumigated		
Inoculated	11.29 x[b]	6.34 xy
Microbial suspension	0.75 z	0.90 z
Noninoculated	0.67 z	0.90 z
Nonfumigated		
Inoculated	10.29 x	6.90 x
Microbial suspension	6.51 y	5.53 y
Noninoculated	5.61 y	5.38 y

[a] Inoculated = inoculated with *E. mosseae* sporocarps. Microbial suspension = inoculated with microbial suspension obtained by washing *E. mosseae* sporocarps.
[b] Means not followed by the same letter are significantly different at the .01 level of probability as determined by Duncan's multiple range test.

E. mosseae in a fumigated field plot were significantly greater than those for noninoculated control plants. The difference in dry weights of inoculated and noninoculated Keen sour orange seedlings was not significant. The mean dry weights for inoculated and noninoculated plants, respectively, were rough lemon 0.17 and 0.07 g; Cleopatra mandarin 0.10 and 0.06 g; Troyer citrange 0.31 and 0.23 g; Keen sour orange 0.23 and 0.21 g. The inoculated plants also had a consistently greater percentage of phosphorus than the noninoculated plants. The percentage of phosphorus for inoculated and noninoculated plants, respectively, was: Troyer citrange 0.16 and 0.12%; rough lemon 0.42 and 0.15%; Cleopatra mandarin 0.16 and 0.06%; Keen sour orange 0.13 and 0.11%.

DISCUSSION.—Our results indicate that the major cause of poor growth of citrus in fumigated or heat-treated soil is the absence of endomycorrhizae rather than soil toxicity. Stunted and chlorotic plants growing in fumigated citrus nurseries are nonmycorrhizal, whereas healthy plants growing in patches of these nurseries are mycorrhizal. Stunted plants recovered when inoculated with an endomycorrhizal fungus. Seedlings grown in steamed soil, autoclaved soil, or soil fumigated with methyl bromide were stunted and chlorotic, and appeared similar to the unhealthy seedlings from fumigated citrus nurseries. Citrus plants grew well in these soils when they were inoculated with *E. mosseae*. It seems unlikely that all three soil treatments would produce toxins in the soil which are somehow neutralized by inoculation with *E. mosseae*. A much more likely explanation is that all three treatments kill the endomycorrhizal fungi, and that only the plants with endomycorrhizae are capable of absorbing enough nutrients for normal growth. It is well known that endomycorrhizal fungi increase nutrient uptake. This has been particularly well demonstrated for phosphorus (1, 2, 3, 8, 19) and zinc (7).

It has been suggested that the bromine ion may be toxic to citrus, and indeed, a higher concentration of bromine was found in stunted plants grown in fumigated soil (12). However, a higher concentration of bromine does not necessarily indicate that it is the cause of stunting. In our experiments with both heat-treated and methyl-bromide-treated soil, nonmycorrhizal plants contained a higher concentration of most minerals other than phosphorus. It is likely that when one element, such as phosphorus, is limiting growth, other elements tend to accumulate in higher concentrations.

Soil fumigation increased the growth of citrus

TABLE 3. The mineral content of mycorrhizal and nonmycorrhizal Keen sour orange seedlings grown in autoclaved soil[a]

Treatment	% dry wt					μg/g						
	Mg	Ca	P	K	Si	Zn	B	Fe	Mn	Na	Al	Cu
Tops												
Mycorrhizal	0.33	2.76	0.20**	0.91	0.43	38	52	130	38	733	162	20
Nonmycorrhizal	0.46**[b]	3.79**	0.12	1.85**	1.10**	46	80	242**	80**	1,314**	404**	16
Roots												
Mycorrhizal	0.31	2.39**	0.20**	0.59	0.43	97	58	–[c]	250	–	–	32
Nonmycorrhizal	0.34	1.33	0.16	1.51**	1.10**	92	62	–	367**	–	–	18

[a] Soil was autoclaved for 2 hr at 121 C and 15 psi.
[b] ** = Significant at the .01 level of probability.
[c] – = Levels were too high to be measured by the emission spectrograph.

TABLE 4. The mineral content of *Endogone mosseae* inoculated and noninoculated rough lemon seedlings grown in fumigated and nonfumigated soil

Treatment[a]	% dry wt					μg/g						
	Mg	Ca	P	K	Si	Zn	B	Fe	Mn	Na	Al	Cu
Tops												
Fumigated												
Inoculated	0.31 x[b]	3.05 x	0.17 x	0.67 y	0.65 y	52 y	97 y	103 y	42 y	1,195 y	169 y	11 y
M.S. + N.	0.37 x	3.15 x	0.10 y	1.51 x	1.42 x	114 x	125 x	237 x	53 x	1,837 y	299 x	8 x
Nonfumigated												
Inoculated	0.32 x	2.97 xy	0.19 x	0.84 y	0.61 y	47 y	80 y	98 y	47 y	1,346 y	162 y	11 x
M.S. + N.	0.31 x	2.59 y	0.19 x	0.81 y	0.56 y	46 y	67 z	94 y	50 x	1,376 y	150 y	11 x
Roots												
Fumigated												
Inoculated	0.51 x	0.80 x	0.21 x	0.69 y	–[c]	123 y	48 x	–	150 y	–	–	24 x
M.S. + N.	0.57 x	1.03 y	0.17 y	2.99 x	–	243 x	58 x	–	268 x	–	–	27 x
Nonfumigated												
Inoculated	0.47 x	0.80 x	0.23 x	0.93 y	–	128 y	48 x	–	172 y	–	–	25 x
M.S. + N.	0.49 x	0.78 x	0.24 x	1.24 y	–	96 y	51 x	–	199 y	–	–	22 x

[a] Inoculated = inoculated with *E. mosseae* sporocarps; M.S. + N. = combination of plants inoculated with microbial suspension + noninoculated.

[b] Means not followed by the same letter are significantly different at the .01 level of probability as determined by Duncan's multiple range test. Means of tops and roots are not comparable.

[c] – = Levels were too high to be measured by the emission spectrograph.

TABLE 5. Available phosphorus (P_1), available and acid-soluble phosphorus (P_2), and exchangeable potassium (K) content in autoclaved soil in which mycorrhizal and nonmycorrhizal Keen sour orange had grown[a]

Treatment[b]	lb./acre		
	P_1	P_2	K
Original level	29.0	73.0	242
Inoculated	18.6**[c]	47.6**	192**
Microbial suspension	27.0	58.0	219
Noninoculated	27.3	55.3	215

[a] Soil was autoclaved for 2 hr at 121 C and 15 psi.

[b] Inoculated = inoculated with *Endogone mosseae* sporocarps. Microbial suspension = inoculated with microbial suspension obtained by washing *E. mosseae* sporocarps.

[c] ** = Significant at the .01 level of probability.

seedlings in established citrus groves. However, this growth was less than that obtained in nonfumigated soil which had not been previously planted to citrus (10). Fumigation of soil not previously planted to citrus reduced seedling growth. Both harmful and beneficial organisms are killed by soil fumigation. The soil from the established citrus grove probably contained numerous pathogens. When the pathogens were killed, the citrus plants grew better, but this growth still did not equal that obtained in a nonfumigated soil which probably contained endomycorrhizal fungi and few pathogens.

Citrus plants appear to be highly mycorrhiza-dependent. Phosphorus applications partially overcame the effects of fumigation or heat-treatment (11, 18, 22). However, heavy fertilization of a citrus nursery has not produced growth that is entirely satisfactory. The present practice of Willits & Newcomb, Inc., is to apply 4,000 lb. of 16-20-0 chemical fertilizer and 15 T of chicken manure (2.5% N, 3.5% P_2O_5) per acre, 6-8 weeks prior to planting seed. This combination of fertilizer material contains approximately 640 lb. NH_4^+, 750 lb. organic N, 800 lb. P_2O_5 in soluble form, and 1,000 lb. P_2O_5 in organic form. The fertilizer is incorporated into the beds which are then flooded with 3 inches of water at weekly intervals until planting. This amount of fertilizer is necessary to partially overcome the effect of soil fumigation. This program has improved the growth of citrus seedlings, but the more susceptible varieties still produce only about 25% normal growth. In a limited nursery experiment, Mr. Newcomb recently obtained excellent growth responses following inoculation of seedlings with *E. mosseae*.

As soil nutrient levels are increased, differences in growth between mycorrhizal and nonmycorrhizal plants become less. When high levels of soluble phosphorus are added to the soil, nonmycorrhizal plants grow as well or nearly as well as mycorrhizal plants (1, 2, 19). However, if a species is highly dependent on mycorrhizal fungi for nutrient uptake, it may be more practical to artificially inoculate fumigated soil with mycorrhizal fungi than to reach nutrient levels high enough for satisfactory growth without them.

The failure of vesicular-arbuscular mycorrhizal fungi to grow in axenic culture should not be an insurmountable obstacle to large scale field inoculation. Inoculum could be produced in quantity in small fumigated field plots. Such inoculum could be incorporated into the row at the time of planting.

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