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The Effect of Two Mycorrhizal Fungi upon Growth and Nutrition of Avocado Seedlings Grown with Six Fertilizer Treatments[1]

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ABSTRACT. Seedlings of 'Topa Topa' avocado *(Persea americana* Mill.) were grown in steamed loamy sand soil with no fertilizer, complete fertilizer (N, P, K, S, Ca, Mg, Cu, Zn, Mn, Fe, Mo, B), -P, -Zn, -P and -Zn, and -Zn+10xP (640 ppm P). Seedlings were inoculated separately with one of 2 isolates of *Glomus fasciculatus* (Thaxter) Gerd. & Trappe (GF) or were inoculated with a water filtrate of the mycorrhizal inoculum plus autoclaved mycorrhizal inoculum. Growth of mycorrhizal seedlings was 49-254% larger than nonmycorrhizal avocados except at the -Zn+10xP regime where mycorrhizal and nonmycorrhizal avocados were of similar size. Both mycorrhizal isolates increased absorption of N, P, and Cu at all fertilizer treatments and absorption of Zn was increased with all fertilizer treatments by one mycorrhizal isolate. Fertilization with P did not alter P concentrations in leaves of nonmycorrhizal plants but increased P concentrations in leaves of mycorrhizal seedlings. Fertilization with 10xP increased P concentrations in both mycorrhizal and nonmycorrhizal seedlings. One GF isolate appeared to be superior to the other based on mineral nutrition of the host avocados. Differences between the isolates apparently were related to their rate of growth or ability to infect. Poor growth of avocado seedlings in steamed or fumigated soil can be related to poor mineral nutrition due to the destruction of mycorrhizal fungi.

Avocado seeds are normally germinated and grown in steamed or fumigated soil and are frequently transplanted to fumigated orchard sites in order to avoid root diseases. Avocado seedlings which are grown in steamed or fumigated soil frequently becomes stunted and show a reduced capacity to absorb P (11). Martin et al. (11) suggested 2 hypotheses to explain this phenomenon: 1) Microorganisms which recolonize steamed or fumigated soil may excrete chemicals which could interfere with P absorption. Other microorganisms which normally metabolize these excreted chemicals may be destroyed by steam treatment or fumigation. 2) Steam treatments or soil fumigation may destroy

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mycorrhizal fungi which have been associated with improved P nutrition of many plants (5, 15).

Mycorrhizal fungi are commonly associated with avocado trees in the orchard (6), but it has only recently been shown (12) that mycorrhizal fungi improve growth of avocado seedlings. Mycorrhizal fungi commonly aid their hosts by increasing host absorption of P, Zn, Cu, and other mineral nutrients. It is not known to what extent mycorrhizal fungi influence the mineral nutrition of avocado trees, nor under what fertility conditions mycorrhizal fungi improve their growth. Purposes of this study were to determine if lack of mycorrhizal fungi was the cause of reduced growth and P absorption of avocado seedlings in steam treated or fumigated soil and to determine if either or both of 2 mycorrhizal fungi had an effect upon growth and mineral nutrition of avocado seedlings subjected to 6 fertilizer treatments.

Materials and Methods

A loamy sand soil was steamed for 2 hr at 121°C and cooled for 12 hr prior to use. Fertilizer treatments consisted of a control (no fertilizer), "complete" fertilizer (N, P, K, S, Ca, Mg, Zn, Cu, Mn, Fe, Mo, B), -P, -Zn, -P and -Zn, and -Zn+10xP with 7 replicates per mycorrhizal isolate as noted below. Source materials and amounts mixed into the soil in the "complete" fertilizer treatment are shown in Table 1. The pH and macro- and micro-nutrient composition of the loamy sand soil are shown in Table 2. Soil from each fertilizer regime was added to 21 twelve-liter plastic containers. Three samples of soil from each fertilizer regime were analyzed before and after the experiment (Table 2). Pots were watered daily alternating with solutions containing 173 ppm N [420 ppm NH_4NO_3 + 60 ppm $Ca(NO_3)_2$ + 120 ppm KNO_3] and 240 ppm $MgSO_4$.

Table 1. Source materials and amounts of fertilizers added to the soil of the "complete" fertilizer treatment.

Fertilizer source	Concn (ppm/dry wt soil)
$CaCO_3$	370.0
3 $Ca(H_2PO_4)_2$ + 7 $CaSO_4$	738.0 (64 ppm P)
$CuSO_4$-$5H_2O$	190.0
$ZnSO_4$	76.0
$MnSO_4$	66.0
$Fe2(SO_4)_3$	76.0
$(NH_4)_6$ Mo_7O_{24}•$4H_2O$	1.0
H_3BO_3	0.4

Seedlings were inoculated with GF isolate 0-1 or 463 by adding 10 aliquots of pot-culture inoculum to each pot. Control pots received 10 g aliquots of autoclaved GF 0-1 inoculum plus 10 ml of a water filtrate (through 10 µm nylon mesh) of 0-1 and 463 innoculum. This procedure assured that bacteria, actinomycetes, and small-spored fungi that might have been present in the mycorrhizal inoculum were also added to nonmycorrhizal controls. Pot-culture inoculum consisted of roots and soil from a sudangrass plant (*Sorghum vulgare* Pers.) in case of isolate 0-1 and an avocado seedling in the case of isolate 463. The sudangrass plant had been infected with isolate

0-1 for 3 months while the avocado seedlings had been infected with isolate 463 for 9 months. Isolate 0-1 was originally isolated from *Citrus* sp. while isolate 463 was originally isolated from an avocado tree. Isolate 463 produced few chlamydospores outside host roots and was previously described as *G. fasciculatus* Type 3 (13).

Two 'Topa Topa' avocado seeds previously heat treated at 49°C for 6 min were planted 3 cm apart on top of the mycorrhizal innoculum in each pot. One of the avocados was removed 2 months after planting and 10 g of the appropriate mycorrhizal innoculum was buried next to the roots of the remaining seedling. Seedlings were grown in a greenhouse at 20 to 280.

Three 1.2-cm diameter soil cores containing roots were taken from each pot 9 months after planting. Mycorrhizal spores were removed from the soil samples by wet-sieving and decanting (4) and counted under a dissecting microscope. Ten 1-cm root pieces were selected at random from each seedling, cleared in KOH, stained with trypan blue (19), and lengths of mycorrhizal hyphae per cm root estimated. Plant dry weights were obtained and leaf tissues from each seedling were analyzed for N, P, K, Ca, Mg, Na, Zn, Cu, Mn, and Fe (8) and data were analyzed statistically (2).

Results

SOIL FERTILITY. Nonfertilized soil was deficient in P, Cu, and Zn. P and Zn fertilization substantially increased available soil P and Zn, and the "complete" fertilization treatment was adequate for growth of avocado seedlings. Available soil P in the "complete" and -Zn treatments dropped from 34-49 ppm P to 7 ppm during the course of the experiment (Table 2). Available Zn and Cu and pH changed little during the experiment, except in the -Zn+10xP treatment where the addition of 640 ppm P initially reduced the pH from 7.8 to 6.2 and increased the availability of Mg, Na, Mn, and Zn. However, by the end of the experiment, the pH of the -Zn+10xP treatment had risen to 7.5.

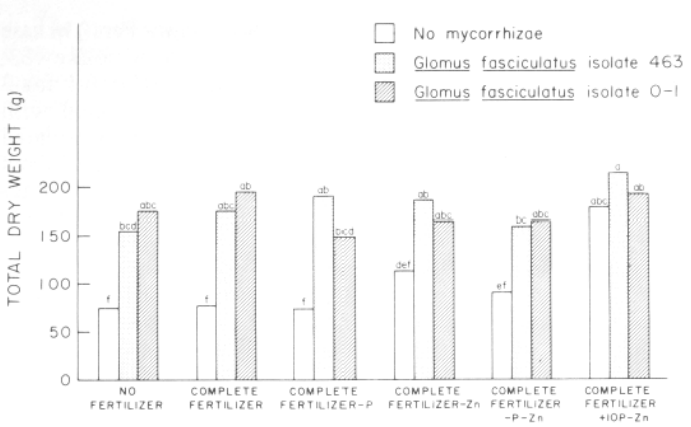

Fig. 1. Growth responses of seedlings of 'Topa Topa' avocado to 6 fertilizer treatments and 2 isolates of mycorrhizal fungi. (Bars without identical letters are significantly different at the 5% level.)

GROWTH RESPONSE. Growth of nonmycorrhizal plants (dry weight) was significantly influenced only by the -Zn+10xP fertilizer treatment which increased growth 142% and 133% over the no fertilizer and complete fertilizer treatments, respectively (Fig. 1). All

mycorrhizal plants, except those given -Zn+10xP, were larger (98% larger on the average) than non-mycorrhizal plants given the same fertilizer treatments (Fig. 1).

None of the mycorrhizal plants differed in size from non-mycorrhizal plants given -Zn+10xP (Fig. 1). Seedlings inoculated with isolates 463 and 0-1 GF did not differ in size when given the same fertilizer treatments (Fig. 1).

Table 2. Macro- and micro-nutrient content[z] and pH of soil used with several fertilizer treatments before and after the experiment.[y]

	Before Experiment									After experiment[x]			
Fertilizer regime	pH	P (ppm)	Ca (me/ liter)	Mg (me/ liter)	Na (me/ liter)	Zn (ppm)	Cu (ppm)	Mn (ppm)	Fe (ppm)	pH	P (ppm)	Zn (ppm)	Cu (ppm)
No fertilizer	7.8b	2.4c	1.8d	0.1c	0.8c	0.2d	0.3b	2.1b	8.9a	7.9ab	3.2c	0.5c	0.1b
Complete fertilizer[w]	8.1ab	49.0b	7.6bc	3.6b	1.3b	3.0a	3.4a	3.0b	14.0a	8.1a	7.9b	1.8a	2.0a
-P	8.4 a	3.3c	3.8d	1.0c	0.9c	2.4a	2.6a	2.8b	9.5 a	7.9ab	3.8c	1.6a	1.8a
-Zn	8.1ab	34.0b	4.6cd	0.8c	0.6c	0.3c	1.7a	2.6b	12.0a	7.7ab	7.2b	0.5c	1.8a
-P, -Zn	8.5a	2.6c	3.1d	0.5c	0.6c	0.3c	2.0a	2.7b	7.7a	7.9ab	4.5c	0.4c	1.6a
-Zn+10xP	6.2c	169.0a	25.8a	10.0a	2.6a	0.7b	1.6a	4.8a	10.0a	7.5b	28.0a	1.1b	1.8a

[z]Soil was analyzed for P (Olsen analysis) (1), Zn, Cu, Mn, Fe (DTPA extraction) (9), and Ca, Mg, Na (ammonium acetate) (1).
[y]Each value is the mean of 3 individual determinations. Values in each column not followed by an identical letter are significantly different at the 5% level using Duncan's multiple range test.
[x]From non-mycorrhizal treatments only.
[w]Complete fertilizer is shown in Table 1. N, K, and Mg were added daily in the water during the experiment.

CONCENTRATIONS OF MACRO- AND MICRONUTRIENTS IN LEAVES. Irrespective of the fertilizer treatment, both isolates of GF consistently increased concentrations of P, N, Zn, and Cu and reduced concentrations of Ca and Na in the leaves (Tables 2 and 3).

Concentrations of K, Mg, Mn, and Fe did not show consistently significant effects of mycorrhizal inoculation. P was available in sufficient amounts to increase P concentrations significantly in leaves and increase growth of nonmycorrhizal seedlings only in the -Zn+10xP treatment (Fig. 1 and Table 3). Fertilization with 64 ppm P in the "complete" and -Zn treatments did not result in significant increases in P concentration in leaves of nonmycorrhizal plants but did result in significant increases in P concentration in leaves of mycorrhizal seedlings (Table 3). Concentrations of N in leaves were directly correlated with concentrations of P. Only in the -Zn+10xP fertilizer treatment were concentrations of N in leaves of mycorrhizal seedlings not significantly greater than in leaves of non-mycorrhizal seedlings (Table 3). Greatest concentrations of Zn were found in mycorrhizal plants grown on Zn-fertilized soil. Soil analysis indicated the soil was Zn-deficient when not fertilized with Zn, but was not deficient in leaves from any treatment. Fertilization with Zn consistently resulted in greater concentrations of Zn in leaves than were found in leaves of avocados not receiving Zn (Table 4). In 3 of the 6 fertilizer treatments, concentrations of N, P, or Zn were greater in leaves of seedlings inoculated with GF 0-1 than in those inoculated with GF 463. Only in the -Zn+10xP treatment were concentrations of P or Zn greater in leaves of seedlings inoculated with GF 463 than in those inoculated with GF 0-1. Similar amounts of all other nutrients were found in mycorrhizal seedlings in the same fertilizer treatment irrespective of the mycorrhizal inoculant.

Table 3. Macronutrient concentrations of leaves of mycorrhizal and non-mycorrhizal avocado grown with 6 fertilizer treatments.[z]

Fertilizer treatment	Mycorrhizal condition	Leaf concn (%)					
		N	P	K	Ca	Mg	Na
No fertilizer	No mycorrhizae	0.90f	0.04ij	0.46bcde	1.11b	0.46cd	0.03ab
	Isolate 463	1.42cd	0.07fg	0.67a	0.84cdef	0.43cd	0.02c
	Isolate 0-1	1.43cd	0.07fg	0.44cde	0.84cdef	0.50bcd	0.02bc
Complete	No mycorrhizae	0.97ef	0.03j	0.43cde	0.92bcde	0.48bcd	0.03abc
fertilizer	Isolate 463	1.38d	0.08ef	0.58abc	0.89bcdef	0.59ab	0.02c
	Isolate 0-1	1.62ab	0.1]be	0.51abcd	0.80def	0.47bcd	0.02c
-P	No mycorrhizae	0.93f	0.03ij	0.34de	0.82cdef	0.41d	0.03ab
	Isolate 463	1.33d	0.06gh	0.42cde	0.65f	0.51bcd	0.03a
	Isolate 0-1	1.57abc	0.08fg	0.42cde	0.77ef	0.49bcd	0.02bc
-Zn	No mycorrhizae	1.09w	0.05hi	0.38de	1.03bcd	0.50bcd	0.03abc
	Isolate 463	1.61ab	0.10de	0.47bcde	0.82cdef	0.59ab	0.02bc
	Isolate 0-1	1.61ab	0.12ab	0.62ab	0.79def	0.53abcd	0.02c
-P, -Zn	No mycorrhizae	0.91f	0.03j	0.45bcde	1.04bc	0.54abc	0.03ab
	Isolate 463	1.38d	0.06gh	0.58abc	0.78ef	0.65a	0.02c
	Isolate 0-1	1.68a	0.08f	0.51abcd	0.78ef	0.5lbcd	0.02c
-Zn+10xP	No mycorrhizae	1.39d	0.08f	0.52abcd	1.35a	0.53abcd	0.02bc
	Isolate 463	1.43cd	0.13a	0.66a	0.99bcde	0.50bcd	0.02d
	Isolate 0-1	1.48bcd	0.10cd	0.40 de	0.98bcde	0.43cd	0.02d

[z]Each value is a mean of 7 individual determinants. Values in each column not followed by an identical letter are significantly different at the 5% level as indicated by Duncan's multiple range test.

Table 4. Micronutrient concentrations of leaves of mycorrhizal and nonmycorrhizal avocado grown with 6 fertilizer treatments.[z]

Fertilizer treatment	Mycorrhizal condition	Leaf concn (%)			
		Zn	Cu	Mn	Fe
No fertilizer	No mycorrhizae	11.6hi	2.73g	89.1ef	101.9a
	Isolate 463	14.0ghi	3.30fg	52.0f	76.3bcd
	Isolate 0-1	17.7efg	4.89def	88.3de	75.3bcd
Complete	No mycorrhizae	14.7fgh	2.87g	104.3cd	72.4cd
fertilizer	Isolate 463	18.0ef	6.23bcd	122.4bc	97.3ab
	Isolate 0-1	22.lbcd	7.51bc	89.3de	77.4bcd
-P	No mycorrhizae	18.7def	2.76g	56.4f	83.9abcd
	Isolate 463	22.7bc	5.86cd	65.3ef	92.0abc
	Isolate 0-1	29.7a	5.64cde	89.3de	77.4bcd
-Zn	No mycorrhizae	12.3hi	3.84efg	72.0ef	71.1cd
	Isolate 463	16.0efg	7.27bc	51.4f	92.6abc
	Isolate 0-1	18.1ef	8.00b	55.4f	71.0cd
-P, -Zn	No mycorrhizae	10.6i	2.70g	82.3def	62.7d
	Isolate 463	12.0hi	6.53bcd	82.4def	88.9abc
	Isolate 0-1	17.lefg	6.67bcd	74.2def	81.4abcd
-Zn+10xP	No mycorrhizae	10.4i	3.56fg	166.4a	80.7abcd
	Isolate 463	19.0cde	10.03a	105.1 cd	91.6abc
	Isolate 0-1	19.4cde	6.39bcd	141.1ab	88.6abc

[z]Each value is a mean of 7 individual determinants. Values in each column not followed by an identical letter are significantly different at the 5% level as indicated by Duncan's multiple range test.

MYCORRHIZAL INFECTION AND SPORE PRODUCTION. Infection and spore production by isolate GF 0-1 were greater over all treatments than occurred with isolate GF 463. Mean spore production over all fertilizer treatments was 15.2 spores/g of soil for GF 0-1 but only 0.3 spores/g soil for GF 463. Similarly, the mean length of mycorrhizal hyphae

within 1 cm of root was 8.5 mm for GF 0-1 but only 0.6 mm for GF 463. Infection by GF 463 was sporadic and isolated in patches along the roots. Only 10% of the 1 cm root sections examined were infected with GF 463, whereas 100% of the 1 cm root sections were infected by GF 0-1. Fertilizer treatments did not significantly affect the infection per cm of root by either GF isolate. Spore production of 22.4 spores/g of soil by GF 0-1 in the nonfertilized treatment was significantly greater than the 11.2-14.8 spores/g of soil which occurred in the other fertilizer treatments. GF 463 produced significantly more spores, 0.7 spores/g soil in the -Zn+10xP fertilizer treatment than in any of the other fertilizer treatments which produced 0.1-0.3 spores/g soil.

Discussion

Both mycorrhizae and heavy P fertilization eliminated P deficiencies in leaf tissues and restored normal growth of avocado seedlings. P appeared to limit the growth of avocado seedlings in steamed soil as concluded in the study by Martin et al. (11). The second hypothesis of Martin et al. (11) is supported by data from this study; that is, an absence of mycorrhizal fungi, which can be destroyed by fumigation or steam treatment, may result in a P deficiency. It could be argued that microorganisms associated with inoculum of the mycorrhizal fungus could degrade toxins which might be responsible for the inhibition of P uptake. However, since filtrates of mycorrhizal inoculum were added to non-mycorrhizal avocados, and P absorption was not improved, the toxin hypothesis is not likely to be correct.

P deficiency and growth retardation in avocado frequently occurred in soils which had more than adequate amounts of available P (11). In the present study, non-mycorrhizal avocado seedlings did not respond to fertilization with 64 ppm P (Fig. 1, Table 3). Mycorrhizal seedlings, however, were able to absorb sufficient P from soil receiving no P fertilizer, and addition of 64 ppm P further increased P absorption by mycorrhizae. Fertilizer P frequently becomes insoluble and unavailable especially in alkaline or calcareous soils (18). Although less than 3% of the soil P was absorbed by plants, the available P dropped from 34-49 ppm to 7 ppm in P-fertilized soil during the course of the experiment. Non-mycorrhizal avocado may be relatively inefficient at absorbing P from some soils, especially those where the amount of soluble P is low. Responses to modest P fertilization in such soils is more likely to occur when avocado seedlings are mycorrhizal because mycorrhizal fungi can explore a larger volume of soil to extract available P. Heavy P fertilization alleviated P deficiency and improved growth of non-mycorrhizal avocado; however, mycorrhizal fungi could be equated with fertilization with 640 ppm P (ca. 1289 kg P/ha) in the soil used in this study.

N was added every other day at rates which should have been adequate for growth of avocado seedlings, but absorption of N was significantly increased in mycorrhizal seedlings in most of the fertilizer treatments. Concentrations of N in leaf tissues were directly correlated with concentrations of P. Furthermore, heavy P fertilization (640 ppm) also improved N absorption in non-mycorrhizal plants, which indicates that it was improved P nutrition and not mycorrhizal fungi which resulted in increased absorption of N in avocados. N and P uptake and metabolism are closely interrelated and a P deficiency may result in a feedback mechanism which could decrease N uptake. A second hypothesis is that the large shoot size of mycorrhizal plants may have initiated greater transpiration which would have increased the flow of water plus dissolved N to

the roots of mycorrhizal plants. The integrity of the phospholipid membranes in roots can be impaired in P-deficient plants and this could explain the suboptimal absorption of N in nonmycorrhizal seedlings in this experiment (21). Root weights were not consistently increased by mycorrhizal fungi so that increased root absorptive surface in such plants cannot be used to explain increased N absorption. Results from this study substantiate data from Embleton et al. (3) who found that applications of P stimulated N absorption by avocado trees in the field. Lynch et al. (10), however, found no effect of P applications on N content of avocado leaves. Haines and Best (7) found that the mycorrhizal fungus *(Glomus mosseae)* could reduce leaching losses of N in a P-deficient forest soil under tree seedlings. Regardless of the mechanism, an improvement in the efficiency of N fertilization caused by mycorrhizal fungi could be of great importance to avocado nurserymen.

Addition of mycorrhizal fungi to fumigated or steamed soil improved P, Zn, Cu, and even N nutrition of avocado seedlings in this experiment. Implications are that mycorrhizal fungi added to fumigated or steamed soils could improve growth of avocado seedlings grown in the nursery or greenhouse as well as reduce the cost of fertilization.

It has been shown that different endomycorrhizal fungi can improve growth of host plants to different degrees (14, 16, 17, 20, 22). In this study, growth of avocado was stimulated equally by both GF isolates. However, GF 0-1 consistently improved the P and Zn nutrition of avocado more than GF 463 (Table 2 and 3). GF 463, however, appeared to improve the P and Cu nutrition to a greater extent than did isolate 0-1 when avocados were fertilized with 640 ppm P (Tables 3 and 4). Perhaps GF 463 is better suited to high phosphate soils than GF 0-1.

Sanders et al. (22) showed that P uptake and beneficial response were directly related to the percentage of roots infected by specific mycorrhizal fungi. Our results support this conclusion because differences in nutrient absorption provided by the 2 GF isolates appeared to be associated with differences in infection or to differences in initial inoculum density. GF 463 produced far fewer spores than GF 0-1 and, therefore, infection by GF 463 may have been slower. However, both fungi should have had an equal chance to occupy all available root material after 9 months in a closed container. GF 463 probably grew more slowly or was not as well adapted to the conditions of these experiments as was GF 0-1.

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