DIVISION S-3—SOIL MICROBIOLOGY AND BIOCHEMISTRY

Plant Response to Mycorrhizal Fungi: Host, Endophyte, and Soil Effects[1]

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ABSTRACT

Interactions and growth responses in soybean [*Glycine max* (L.) Merr.] and sorghum [*Sorghum bicolor* (L.) Moench] colonized by the vesicular-arbuscular mycorrhizal (VAM) fungi [*Glomus fasciculatum* (Thaxt. *sensu* Gerd.) Gerd. and Trappe] or [*Glomus mosseae* (Nicol. & Gerd.) Gerd. and Trappe] as grown in three northern California soil types were investigated in a 2 by 2 by 3 factorial experiment. Growth and development of both symbiotic partners were significantly influenced by all three factors (host plant, endophyte, soil). Growth responses to VAM-fungal colonization varied with soil type from −10 to 400%. Phosphorus concentrations increased significantly in all soybean and some sorghum plants relative to non-VAM controls as a result of VAM-fungal colonization. Shoot dry matter as percent of fresh weight increased significantly in only those VAM plants which had also experienced a significant growth enhancement. Root/shoot ratios of most VAM plants were lower than those of the controls. Changes in root/shoot ratios were inversely related to changes in dry weight. The results show that soil type, as well as the host-endophyte combination, is a significant factor in modifying the VAM growth effect independently of mineral nutrient availability.

***Additional Index Words:* *Glomus*, sorghum, soybean, plant nutrition, plant symbiosis, mycorrhiza-soil interactions.**

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THE ECOPHYSIOLOGY of vesicular-arbuscular mycorrhizal (VAM) associations has been subject to increasingly intensive study in recent years (14, 19, 33). Some of the interest is based on the premise that enhanced nutrient uptake by the VAM fungal symbiont and the resulting growth enhancement of the host plant may be utilized in agriculture (1, 17, 29). Although most crop plants require VAM fungi to achieve maximum growth in nutrient-poor soils, commercial use of the fungi in modern agricultural practice is limited at the present time (17). In developing countries, however, where fertilizer availability is restricted, applied research involving VAM fungi in crop growth is of major interest (24).

The dependence of plants on VAM fungi for optimal growth in a given environment (12, 23) appears to be influenced by factors in addition to the compatibility of the symbionts (14). Important among these is the edaphic environment of the VAM association (15, 28). The proper selection of efficient VAM fungi (25) for the right crop and soil therefore appears to be a key to successful applications of mycorrhizal research to crop productivity (34).

Although proof of the usefulness of selected VAM fungi in enhancing crop growth can come only from their introduction into untreated soils under field conditions (1), experimentation under controlled conditions will aid in pinpointing combinations of interest for further testing. The purpose of this work was to determine if different soil types affect host plant growth response to VAM fungi under equalized nutritional conditions.

MATERIALS AND METHODS

Experimental Design

Two plant species (a grass and a legume), two species of VAM fungus, and three soils were used in this 2 by 2 by 3 factorial experiment. Plants not colonized by VAM fungi were grown as controls with each of the 12 treatment combinations. Five replications were used for a total of 120 units. A unit consisted of one legume or two grass plants. The design was completely random and plants were rotated regularly to avoid any positional effects.

Biological Materials and Soils

Soybean [*Glycine max* (L.) Merr. cv. Amsoy] and sorghum [*Sorghum bicolor* (L.) Moench cv. G766] seeds were surface sterilized (2), and planted in soil inoculated with the VAM fungi [*Glomus fasciculatum* (Thaxt. *sensu* Gerd.) Gerd. and Trappe] or [*Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe], or grown in uninoculated soil as controls. The *G. fasciculatum* inoculum was originally purchased from Abbott Laboratories (Long Grove, IL 60047) as the Gerdemann isolate obtained from croplands. The *G. mosseae* isolate was collected from a desert site (6) and recultured in the greenhouse on sorghum.

To provide wide variety, the soils were selected from different orders (Ultisoils, Entisoils, and Alfisoils). All soils were collected from a depth of 0- to 25-cm, sieved (10-mm mesh) and sterilized with ethylene oxide. One soil from Mendocino County, California was a reddish-brown, medium textured, acid (pH 5.4) loam in the Josephine series (Mesic Typic Haploxerults), developed from sandstone and shale. It was moderately aggregated, of subangular, blocky structure and slightly sticky when wet. This soil was limed (10 g $CaCO_3$ kg^{-1} soil) to alleviate Mn toxicity to the plants (22). Soil pH after liming was 6.9. The other two soils used were from Yolo County, California. The Balcom-series silty clay loam (Typic Xerorthents) was light brownish gray, fine textured, moderately alkaline (pH 8.0), of moderate, subangular blocky structure, and friable, slightly sticky with plastic consistency when moist, and derived from sandstone and shale. The Corning-series soil (Typic Palexeralfs) was a reddish-brown, gravelly, moderately acid (pH 6.1) loam, of medium, angular blocky structure, and hard, friable, slightly sticky with plastic consistency. Corning soils are formed in softly consolidated, mixed, gravelly alluvium.

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Table 1. Nutrient levels in Corning, Balcom, and Josephine soils.

Soil type	Soil data																	
	Plant available nutrients†									Total nutrients‡						Other soil data		
	P	K	SO_4-S	B	Cu	Fe	Mn	Mo	Zn	Ca§	Fe	K	N	P	S	pH§	OM	Salts§
	mg/kg soil									%							$g\ kg^{-1}$	dS/m
Corning	3.5	85	1.0	0.20	2.3	20	30.6	0.02	20.0	0.59	2.95	0.76	0.09	0.07	0.01	6.1	10	0.1
Balcom	3.3	114	6.0	0.39	1.6	4	3.5	0.01	3.8	2.22	3.97	1.30	0.07	0.08	0.01	8.0	17	0.3
Josephine	4.6	328	<1.0	0.41	2.5	34	16.5	<0.01	1.3	0.82	4.25	0.99	0.19	0.06	0.03	6.9	57	1.0

† Extractants were: 1 *M* KCl for SO_4-S, hot water for B, and NH_4HCO_3-diethyl triamine penta acetic acid for all others (21).
‡ Total nutrients were extracted in hydrofluoric-perchloric acid (21).
§ Calcium and pH values of the Josephine soil reflect the effects of liming (10 g $CaCO_3$/kg soil). pH and salts were determined in a 1:1 (w/w) water extract.

Levels of key available and total nutrients, pH, organic matter (OM) and electrolytic conductivity of the soils are described in Table 1.

Growth Conditions

Plants were grown in 1.5-L white plastic pots in a greenhouse at Albany, CA, March through August and harvested after 56 d. Automatic heating and cooling systems were operational at temperatures above 25°C and below 18°C, minimizing temperature variations. Daylength was extended to 16 h by General Electric 1000 W metal halide lamps mounted vertically in parabolic reflectors, and providing supplementary photosynthetic photon flux density of 500 μmol $m^{-2}s^{-1}$ at the soil surface level.

Soybean seeds were germinated in an incubator (2 d, 28°C) and selected for uniformity at planting. Three soybean seedlings and several sorghum seeds were planted, and thinned to one and two plants, respectively, at 14 d. The VAM-fungal inoculum added per pot consisted of approximately 100 colonized root segments and 500 spores for *G. mosseae*, and 50 root segments and 750 spores for *G. fasciculatum*, in soil. The inocula were mixed into the soil to a depth of 5 cm. Control plants were initially watered with washings of the inoculum free of VAM fungi. The soil was covered by a reflective 2-cm layer of white perlite. Plants were watered with a nutrient solution without P twice every 7 d for the first 35 d of growth and as needed to prevent wilting during the final 21 d. The solution consisted of 1.3 m*M* $Ca(NO_3)_2$, 1.3 m*M* KNO_3, 0.25 m*M* $MgSO_4$, and 0.02 m*M* Fe (chelate). Micronutrients were according to Johnson et al. (16) at one-quarter strength.

Evaluation and Assays

Plant parts were weighed immediately after harvest, and after drying at 80°C for 2 d. Phosphorus contents of all roots, sorghum shoots, and soybean leaf blades were determined according to Allen (3). Total and available soil P was determined according to Shelton and Harper (30) and Watanabe and Olsen (36), respectively. Other soil parameters (Table 1) were determined according to standard analytical methods (21) by the Soil Testing Laboratory, Colorado State Univ., Fort Collins, CO 80523.

The chitin [poly-β-(1,4)-*N*-acetylglucosamine] content of extraradical mycelia of *G. fasciculatum* and *G. mosseae* and of VAM roots was determined spectrophometrically (5, 7). A standard curve based on purified chitin was used in the assay of fungal mycelia. To account for contamination by chitin-containing organisms other than VAM fungi, root material from the non-VAM controls mixed with chitin was used in the standard curves of the VAM-root chitin assays (5). Separate standard curves were constructed for each soil-host combination. Intraradical VAM-fungal biomass was calculated from the chitin content of the VAM-fungal mycelium and the VAM roots. Control plants were checked for chance contamination by VAM fungi by staining. The amount of dry matter in the shoots relative to fresh weight was calculated as percentage dry matter.

Percent change between VAM and control plants in any plant parameter was calculated as [(VAM − control)/control] × 100. Controls and VAM plants were ranked for each parameter and replicates of equal ranking were paired. A separate percent change value was calculated for each pair. Means and SE were derived from these values. Differences between shoot parameters were evaluated for significance by Student's *t*-test (host or endophyte effects) or Duncan's multiple range test (soil effects). The significance of main effects and interaction between factors was determined by analysis of variance on total plant growth enhancement and percent VAM fungal biomass within the VAM roots.

RESULTS

Shoot Dry Weight

Colonization of soybeans by either VAM fungus resulted in large, positive changes (enhancement) in shoot dry weight when grown in Josephine soil, intermediate levels of enhancement in Balcom, and no significant change in Corning soil (Table 2). Differences due to VAM-fungal species were not significant. In sorghum, there was no significant difference between VAM plants and controls in Corning soil. In the other two soils, the growth response pattern was more complex: in Balcom soil the response of sorghum to *G. mosseae* was seven times higher than the response to *G. fasciculatum*, while in Josephine soil this response was reversed. The effect of host-plant species on growth enhancement in Josephine soil was significant with both endophytes. The change due to colonization was over 400% in soybean, and variable (30 and 300%) in sorghum. In Corning soil, host effects were not significant. Host effects of soybean and sorghum in Balcom soil were significantly different only with *G. fasciculatum* but not with *G. mosseae* as the endophyte.

Root/Shoot Ratios

The root/shoot (R/S) ratios of VAM plants were significantly ($p < 0.05$) lower than those of controls except for soybean and sorghum grown with *G. fasciculatum* in Corning soil (Fig. 1). Enhancement of total dry weight by VAM fungi was largest when the change in R/S ratios was most negative (Fig. 1). In soybean, the largest positive change in dry weight and the largest negative change in the R/S ratio for both fungi was in Josephine soil. In Balcom soil the two parameters were nearly identical for both soybean-en-

Table 2. Changes in plant leaf parameters as a result of colonization by VAM fungi.†

Plant leaf parameter	Soil type: Corning	Balcom	Josephine
	% change		
Soybean			
Dry weight			
G. mosseae	6 aA x	228*** aA y	425*** aA z
G. fasciculatum	−3 a Ax	228*** a Ay	468*** a Az
P concentration			
G. mosseae	39.8***aA x	31.4***aA xy	23.8***aA y
G. fasciculatum	18.4***b Ax	32.6***a Ay	47.6***b Az
Dry matter‡			
G. mosseae	1.8 aA x	11.0** aA xy	13.3***aA y
G. fasciculatum	1.6 a Ax	17.3***b Ay	12.6** b Ay
Sorghum			
Dry weight			
G. mosseae	4 aA x	268*** aA y	29* aB z
G. fasciculatum	−9 b Ax	37* b By	292*** b Bz
P concentration			
G. mosseae	−9.2* aB x	−2.2 aB x	21.8** aA y
G. fasiculatum	5.6 b Bx	22.0** b By	9.4 b Bx
Dry matter‡			
G. mosseae	−3.9 aA x	18.2* aA y	2.1 aB x
G. fasciculatum	−1.8 a Bx	−5.1 b Bx	18.4* b Ay

*,**,*** Significant differences at 5, 1, and 0.1%, respectively, between VAM and control plants from which percent change was calcalculated.

† Numbers denote percent enhancement or inhibition (−) of VAM plants relative to controls [(VAM plant-control)/control] × 100. Differences among endophytes (within same host and soil type) are not significant ($p > 0.05$) for values followed by same letter (a, b). Differences among hosts (within same endophyte and soil type) are not significant ($p > 0.05$) when followed by same letter (A, B). Differences among soil types (within same host-endophyte combination) are not significant ($p > 0.05$) when followed (horizontally) by same letter (x, y, z).

‡ Dry matter was calculated as a percentage of fresh weight.

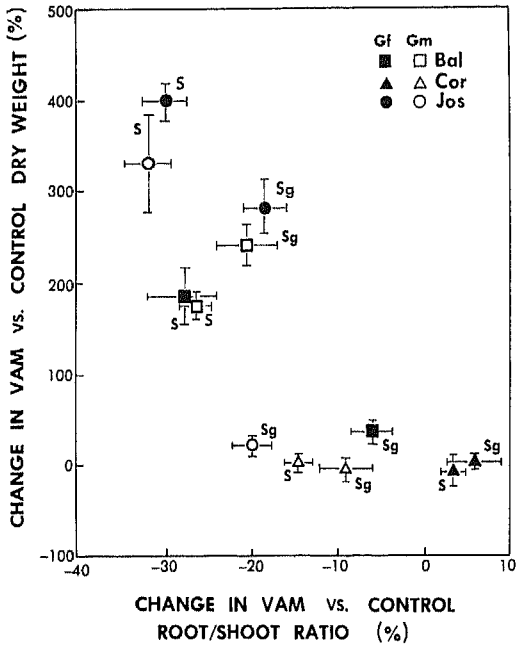


Fig. 1. Percent change in root/shoot ratio and total dry weight in vesicular-arbuscular mycorrhizal (VAM) plants relative to non-VAM controls. Four symbiotic combinations between soybean (S) and sorghum (Sg) plants and the VAM fungi *Glomus mosseae* (Gm) and *Glomus fasciculatum* (Gf) were grown in Corning (Cor), Balcom (Bal) and Josephine (Jos) series soils. Bars denote standard errors of the mean.

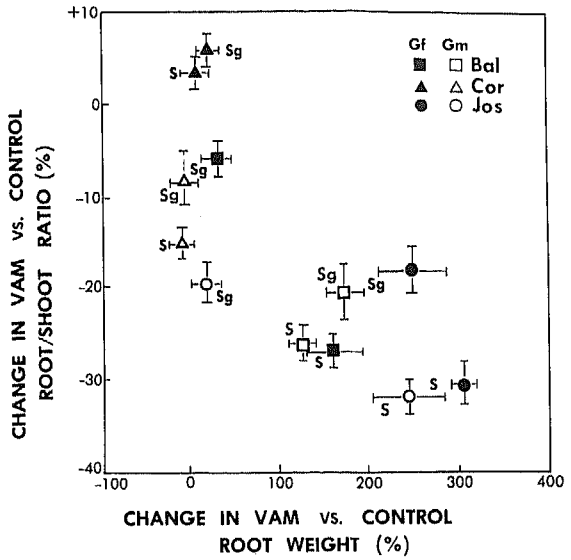


Fig. 2. Percent change in root dry weight and R/S ratio in VAM plants relative to non-VAM controls. Annotations are as in Fig. 1.

dophyte combinations. In Corning soil, no significant ($p > 0.05$) growth enhancement was observed for either host.

Greatest depression of R/S ratios and greatest enhancement of dry weight in sorghum was found in Josephine soil with *G. fasciculatum*, and in Balcom soil with *G. mosseae*. The relationship between the increase in root dry weight and the decrease in R/S ratios of VAM vs. control plants was inverse (Fig. 2). Large increases in root weight were accompanied by large decreases in the R/S ratios. Analysis of variance of plant growth enhancement by VAM fungi showed highly significant main effects for soil and host, and a significant effect ($p < 0.055$) for the endophyte factor. Soil-host and soil-endophyte interactions were highly significant.

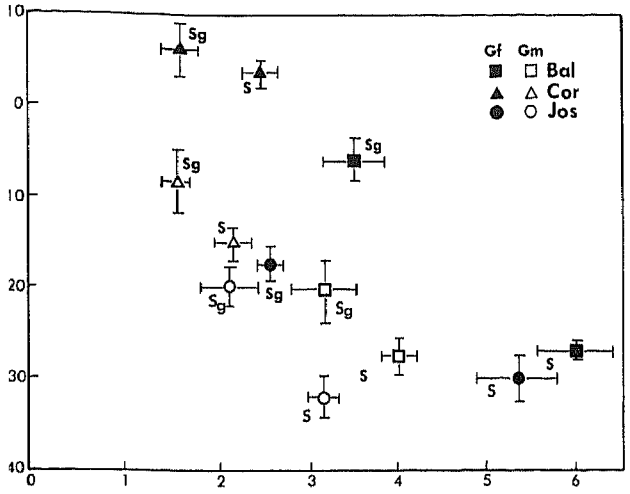
Fungal Biomass

Percent VAM-fungal biomass in roots was lowest in all four host-endophyte combinations when grown in Corning soil, coinciding with the lowest depressions of R/S ratios (Fig. 3). Fungal proliferation was greatest in Balcom soil for both hosts and endophytes. There was less VAM-fungal biomass in the roots of both hosts in Josephine than in Balcom soil, but the drop in the R/S ratios of plants in Josephine soil was greater than that in Balcom soil. The analysis of percent fungal biomass showed highly significant main effects and interactions for all three factors.

Phosphorus Concentration

Enhancement of P concentration increased with increasing percent fungal biomass in the VAM roots for the soybean-*G. mosseae* and sorghum-*G. fasciculatum* combinations (Fig. 4). In the other two host-endophyte combinations the linear relationship of these two parameters was not repeated.

Phosphorus concentrations in the shoots were significantly higher for VAM plants than controls for all soybean-endophyte-soil combinations (Table 2), but



. 3. Percent change in R/S ratio in VAM plants relative to non-
/AM controls as a function of VAM-fungal biomass in host-plant
oot. Annotations are as in Fig. 1.

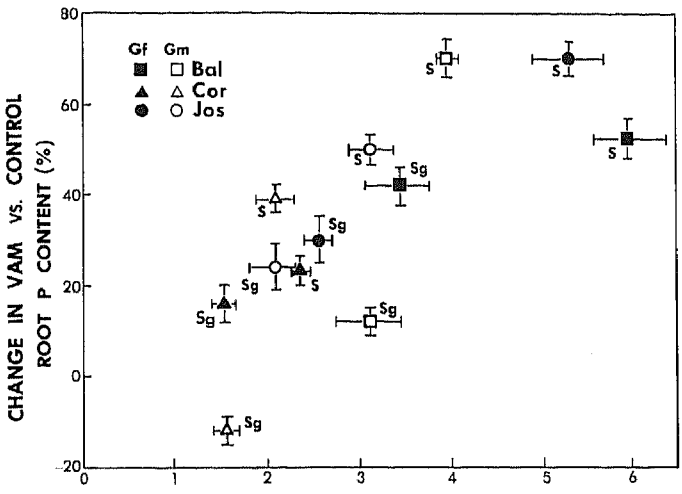


Fig. 4. Percent change in P concentration in VAM plants relative to non-VAM controls as a function of VAM-fungal biomass in host-plant root. Annotations are as in Fig. 1.

ly two of the sorghum combinations were enhanced P content. In sorghum, the enhancement of shoot y weight and P concentration did not always agree relative magnitude. Dry matter concentration in AM plants was significantly higher than in controls almost all cases where significant enhancement of y weight had also occurred (Table 2).

DISCUSSION

A determination of the host and soil preferences of given species of VAM fungus appears to be a key to potential agricultural utilization (10, 15). While a k of host specificity and an inverse relationship be-een plant growth response to VAM fungi and avail-le soil P are generally observed, deviations from ch rules (9, 11, 25) make a determination of the fluence of plant, soil, and endophyte on the overall owth response of interest. In this study, the analysis the effects and interactions of the factors indicates at plant, soil, and endophyte individually and in mbination influence the level of biomass produc-n of both symbionts.

Comparability of the effectiveness of the two inoc-a used was shown both by the similarity in response soybean and by the dissimilarity in sorghum in lcom and Josephine soils (Table 2). Lack of re-onse to either fungal species by either host in Corn-g soil indicated [according to the characteristics of AM-fungal efficiency suggested by Abbott and Rob-n, (1)] that the fungi were unable to form extensive ycelia in this soil. This suggestion is supported by e relatively low levels of intraradical VAM-fungal omass found in roots growing in Corning soil. The le of mineral uptake by VAM fungi in relation to il nutrient levels was investigated by Menge et al. 8) in several California soils. They found that soil trient levels could be used predictively in deter-ining the dependence of Troyer citrange on its fun-l endophyte. In the present experiment, growth ef-cts could not be attributed to differences in nutrient ailability, as all soils had similarly low levels of available P, and received the same complete nutrient amendments (without P). These amendments were calculated to exceed the levels of available nutrients (Table 1) by an order of magnitude. As all soils were initially sterilized and inoculated with the microflora from the VAM inoculum, differences in biological interactions were minimized. Differences in the physical characteristics of these soils appear to be responsible for the variation observed in the biological responses. These differences were mainly textural, but are likely to have included structural features not destroyed by the potting procedure, such as water-stable micro and macro aggregates.

Environmental factors are known to affect R/S ratios markedly (35). Development of roots and shoots is balanced, and the partition of assimilates controlled, to provide optimal utilization of resources to the CO_2 assimilation and nutrient- and water-uptake functions of the above- and below-ground organs of the plant. This balance is often altered in the presence of VAM fungi due to changed uptake capability of VAM roots (31). As a result, R/S ratios are an important parameter in evaluating growth responses in VAM associations.

The relatively low levels of VAM-fungal development in Corning soil were associated with a trend towards small changes in the R/S ratios (Fig. 4) and the absence of growth enhancement (Fig. 1). Conversely, large increases in dry weight (Fig. 1), large decreases in R/S ratios, and high levels of VAM fungal colonization in Balcom and Josephine soils (Fig. 3) suggested the presence of a symbiotic mechanism efficient at absorbing P (26). Although large increases in VAM-root weights relative to controls occurred in these soils, these changes were accompanied by large decreases in the root/shoot ratios (Fig. 2) indicating the VAM plant's ability to channel energy to increased shoot production when a large root mass was not required, corroborating similar findings by Nemec (20).

The low R/S ratios generally observed in VAM plants (27) may serve as indicators of VAM-fungal effectiveness, i.e., the capability of the fungus to sub-

stitute for relatively large amounts of root matter in P uptake. Intraradical VAM fungal biomass, however, may be an unreliable measure of P uptake by the extraradical hyphae (4, 13). Thus the large percentages of intraradical VAM fungal biomass found in Balcom soil (Fig. 3, 4) may not have translated into comparably large decreases in the VAM R/S ratios (Fig. 4) or increases in root P concentrations (Fig. 4) because of a lesser degree of extraradical development of the uptake hyphae. Measurement of these hyphae by the chitin method (5) was not feasible in these soils. Such soil-dependent imbalances in the development of the intraradical and extraradical mycelia of *G. fasciculatum* and *G. mosseae* may have contributed to the differences in growth response and P concentrations of sorghum shoots in the Balcom and Josephine soils (Table 2).

The significant increase in dry matter concentrations of only those VAM plants which have also experienced growth enhancement as a result of colonization (Table 2) does not confirm previous observations by others (32). The physiological basis for this phenomenon is obscure. It is suggested that the leaves incorporated C which would otherwise be exported to the relatively large root systems of unenhanced VAM plants. The similar R/S ratios and shoot dry matter concentrations of plants grown in Corning soil support this view. Further support is offered by Buwalda and Goh (8) who found that the C content of grass shoots was lowered in plants under growth depression. These observations indicate an increase in shoot dry matter content when the VAM symbiosis is mutualistic and a decrease when the endophyte acts as a parasite in competing for C.

REFERENCES

1. Abbott, L.K., and A.D. Robson. 1982. The role of vesicular-arbuscular mycorrhizal fungi in agriculture and the selection of fungi for inoculation. Aust. J. Agric. Res. 33:389–408.
2. Abdul-Baki, A.A. 1974. Pitfalls in using sodium hypochlorite as a seed disinfectant in ^{14}C incorporation studies. Plant Physiol. 53:768–771.
3. Allen, R.J. 1940. The estimation of phosphorus. Biochem. J. 34B:858–860.
4. Bethlenfalvay, G.J., H.G. Bayne, and R.S. Pacovsky. 1983. Parasitic and mutualistic associations between a mycorrhizal fungus and soybean: The effect of phosphorus on host plant-endophyte interactions. Physiol. Plant. 57:543–548.
5. Bethlenfalvay, G.J., M.S. Brown, and R.S. Pacovsky. 1982. Relationships between host and endophyte development in mycorrhizal soybeans. New Phytol. 90:537–543.
6. Bethlenfalvay, G.J., S. Dakessian, and R.S. Pacovsky. 1984. Mycorrhizae in a Southern California desert: ecological implications. Can. J. Bot. 62:519–524.
7. Bethlenfalvay, G.J., R.S. Pacovsky, and M.S. Brown. 1981. Measurement of mycorrhizal infection in soybeans. Soil Sci. Soc. Am. J. 45:871–875.
8. Buwalda, J.G., and K.M. Goh. 1982. Host-fungus competition for carbon as a cause of growth depression in vesicular-arbuscular mycorrhizal ryegrass. Soil Biol. Biochem. 14:103–106.
9. Carling, D.E., and M.F. Brown. 1980. Relative effect of vesicular-arbuscular mycorrhizal fungi on growth and yield of soybeans. Soil Sci. Soc. Am. J. 44:528–532.
10. Davis, E.A., J.L. Young, and R.G. Linderman. 1983. Soil lime level (pH) and VA mycorrhizal effects on growth responses of sweetgum seedlings. Soil Sci. Soc. Amer. J. 47:251–256.
11. Dodd, J., J. Krikum, and J. Haas. 1983. Relative effectiveness of indigenous populations of vesicular-arbuscular mycorrhizal fungi from four sites in the Negev. Isr. J. Bot. 32:10–21.
12. Gerdemann, J.W. 1975. Vesicular-arbuscular mycorrhizae. The development and function of roots. p. 575–591. *In* J.G. Torrey and D.T. Clarkson (ed.) Academic Press, London.
13. Graham, J.H., R.G. Linderman, and J.A. Menge. 1982. Development of external hyphae by different isolates of mycorrhizal *Glomus* spp. in relation to root colonization and growth of Troyer citrange. New Phytol. 91:183–189.
14. Hayman, D.S. 1983. The physiology of vesicular-arbuscular endomycorrhizal symbiosis. Can. J. Bot. 61:944–963.
15. Hayman, D.S. 1982. Influence of soils and fertility on activity and survival of vesicular-arbuscular mycorrhizal fungi. Phytopathology 72:1119–1125.
16. Johnson, C.M., P.R. Stout, T.C. Broyer, and A.B. Carlton. 1957. Comparative chlorine requirements of different plant species. Plant Soil 8:337–353.
17. Menge, J.A. 1983. Utilization of vesicular-arbuscular mycorrhizal fungi in agriculture. Can. J. Bot. 61:1015–1024.
18. Menge, J.A., W.M. Jarrell, C.K. Labanauskas, J.C. Ohala, C. Huszar, E.L.V. Johnson, and D. Sibert. 1982. Predicting mycorrhizal dependency of Troyer citrange on *Glomus fasciculatum* in California citrus soils and nursery mixes. Soil Sci. Soc. Am. J. 46:762–768.
19. Mosse, B., D.P. Stribley, and F. LeTacon. 1981. Ecology of mycorrhizae and mycorrhizal fungi. p. 137–210. *In* M. Alexander (ed.) Advances in microbial ecology, Vol. 5. Plenum Press, New York.
20. Nemec, S. 1978. Response of six citrus rootstocks to three species of *Glomus*, a mycorrhizal fungus. Proc. Fla. State Hortic. Soc. 91:10–14.
21. Page, A.L., R.H. Miller, and B.R. Keeney. 1982. Methods of soil analysis, Part 2. Agronomy 9.
22. Pearson, R.W., F. Adams, (ed.). 1967. Soil acidity and liming. Agronomy 12.
23. Plenchette, C., J.A. Fortin, and V. Furlan. 1983. Growth responses of several plant species to mycorrhizae in a soil of moderate P fertility. I. Mycorrhizal dependency under field conditions. Plant Soil 70:199–209.
24. Plucknett, D.L., and Nigel J.H. Smith 1982 Agricultural research and third world food production. Science 217:215–220.
25. Powell, C.L.L. 1982. Selection of efficient VA mycorrhizal fungi. Plant Soil 68:3–9.
26. Redente, E.F., and F.B. Reeves. 1981. Interactions between vesicular-arbuscular mycorrhiza and Rhizobium and their effect on sweetvetch growth. Soil Sci. 132:410–415.
27. Rhodes, L.H., and J.W. Gerdemann. 1980. Nutrient translocation in vesicular-arbuscular mycorrhizae. p. 173–195. *In* C.B. Cook et al. (ed.) Cellular interactions in symbiosis and parasitism. Ohio State University Press, Columbus.
28. Ross, J.P. 1980. Effect of nontreated field soil on sporulation of vesicular mycorrhizal fungi associated with soybean. Phytopathology 70:1200–1205.
29. Safir, G.R. 1980. Vesicular-arbuscular mycorrhizae and crop productivity. p. 231–252. *In* P.S. Carlson (ed.) The biology of crop productivity, Academic Press, New York.
30. Shelton, W.R., and H.T. Harper. 1941. A rapid method for the determination of total phosphorus in soil and plant material. Iowa State Coll. J. Sci. 15:405–413.
31. Smith, S.E. 1980. Mycorrhizas of autotrophic higher plants. Biol. Rev. Cambridge Philos. Soc. 55:475–510.
32. Snellgrove, R.C., W.E. Splittstoesser, D.P. Stribley, and P.B. Tinker. 1982. The distribution of carbon and the demand of the fungal symbiont in leek plants with vesicular-arbuscular mycorrhizas. New Phytol. 92:75–87.
33. St. John, T.V., D.C. Coleman. 1983. The role of mycorrhizae in plant ecology. Can. J. Bot. 61:1005–1014.
34. Trappe, J.M. 1982. Synoptic keys to the genera and the species of zygomycetous mycorrhizal fungi. Phytopathology 72:1102–1108.
35. Wareing, P.F., and J. Patrick. 1975. Source-sink relations and the partition of assimilates in the plant. p. 489–499. *In* J.P. Cooper (ed.) Photosynthesis and productivity in different environments, Cambridge Univ. Press, Cambridge, UK.
36. Watanabe, F.S., and S.R. Olsen. 1965. Test of an ascorbic acid method for determining phosphorus in water and $NaHCO_3$ extracts from soil. Soil Sci. Soc. Am. Proc. 29:677–678.