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Title: APPLE MYCORRHIZAE AND THEIR EFFECTS ON GROWTH AND NUTRIENT CONCENTRATION IN APPLE SEEDLINGS GROWN IN TWO SOILS WITH VARIED LEVELS OF P

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A study was conducted to characterize the vesicular-arbuscular (VA) fungi of apples grown in Oregon. Using roots and soil from apple orchards as inoculae, six different fungal species were found in pot cultures: Gigaspora margarita Becker and Hall, Glomus fasciculatum (Thaxter sensu Gerdemann) Gerd. and Trappe, Glomus mosseae (Nicol. and Gerd.) Gerd. and Trappe, Gigaspora calospora (Nicol. and Gerd.) Gerd. and Trappe, Glomus monosporum Gerd. and Trappe and Sclerocystis rubiformis Gerd. and Trappe. The first three species grew out of apple root inoculum, suggesting that they are strong competitors in colonizing apple roots in the field. Gigaspora margarita has not heretofore been reported in Oregon.

The effectiveness of Gigaspora margarita, Glomus fasciculatum and Glomus mosseae and applied P in promoting growth of apple seedlings grown in two soils which differ in their available P content was studied in a greenhouse experiment. Mycorrhizal inoculation could substitute for P application in low P soil with *G. fasciculatum* being the most effective in promoting growth and P uptake, *G. margarita* being the least effective, and *G. mosseae* intermediate. Also studied were the effects of soil-applied P and VA mycorrhizae on nutrient uptake and growth of maize grown in Willamette soil. Both treatments enhanced plant growth and P uptake. VA mycorrhizal inoculation significantly increased percent leaf Mg and Mn over the controls. Application of P to one-half of the root system did not reduce percent root colonization by VA mycorrhizae in the other half, while combining both treatments reduced percent root colonization.

APPLE MYCORRHIZAE AND THEIR EFFECTS ON GROWTH AND NUTRIENT CONCENTRATION IN APPLE SEEDLINGS GROWN IN TWO SOILS WITH VARIED LEVELS OF P

by

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Typed by Frances Gallivan for Yosef Ibrahim Geddeda

This thesis is dedicated to

my parents

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APPLE MYCORRHIZAE AND THEIR EFFECTS ON GROWTH AND NUTRIENT CONCENTRATION IN APPLE SEEDLINGS GROWN IN TWO SOILS WITH VARIED LEVELS OF P

I. Introduction

In 1980, Oregon produced 2.4% of total apple production in the U.S.A., and Hood River County produced 58% of the apple crop in Oregon (81). Poor shoot growth, shoot dieback and small fruit size at harvest were reported in some Hood River apple orchards (73). Review of reports of leaf analyses for the mid-Columbia area prepared by the Plant Analysis Laboratory, Department of Horticulture, Oregon State University, reveals that leaf P levels are below normal in some orchards. Maul (73) failed to increase leaf P in apples grown in the upper Hood River Valley by trenching P as superphosphate into the soil.

Plant growth and nutrient uptake, especially P, have been improved in many plant species by endomycorrhizal inoculation (5, 6, 37, 39, 48, 87, 93, 129). These effects also have been observed in the field under nonsterile conditions (3, 49, 61, 92, 94, 102). Not only has response to inoculation varied with the fungus used (5, 46, 89, 108, 112, 114) but also some mycorrhizal species have proven more effective than others in stimulating growth of some plants under certain conditions (29, 65, 110, 114). Commercial production and application of endophytes might be realized soon (29, 90, 93).

It will be most beneficial to use fungal species that are most effective.

The following studies were conducted to identify the vesicular-arbuscular mycorrhizae most competitive in colonizing roots of apples grown in Oregon and to test their effectiveness in promoting apple seedling growth and nutrient uptake. Effects of applied P and plant P on root colonization were investigated with maize.

This thesis consists of a literature review in three sections: Effects of Vesicular-Arbuscular Mycorrhizae on Plant Growth and Development, Relationships Between VA Mycorrhizae and Nutrient Uptake, and Some Factors Affecting VA Mycorrhizal Fungi. Data are presented in three papers in the form of journal articles to be submitted for publication. Literature cited throughout the thesis is presented in alphabetical order at the end.

II. Literature Review

Effects of Vesicular-Arbuscular Mycorrhizae on Plant Growth and Development

Vesicular-arbuscular (VA) mycorrhizal fungi are common to most soils of the world (33, 37, 82, 91, 99, 100, 120). More plant species form VA mycorrhizae than any other type (13, 34, 38, 39, 51, 70, 126, 136, 146). Because VA mycorrhizae are so widespread, it is easier to list the plant families in which VA are not known to occur than to list those in which they have been shown to occur (38, 44). VA mycorrhizae have been shown to increase plant growth of many species. Daft and Nicolson (24) studied the effects of three different species of *Endogonaceae* on growth of tobacco, maize and tomatoes. Colonization by all three species resulted in significant increases in dry matter of tobacco and maize compared with nonmycorrhizal controls. With tomato, only one fungal species significantly increased plant dry weight over the control. Baylis (5) found that noninoculated *Griselinia littoralis* seedlings became stunted and pale during their second year, while inoculated plants remained dark green and vigorous. The dry weight of mycorrhizal plants was significantly higher than that of nonmycorrhizal plants (17, 29, 125, 127, 128). Inoculated onion plants grew significantly larger than noninoculated controls (56,94,97, 102, 103, 121, 131, 133). Similar results were reported with many other annual crops: maize (35, 36, 98,), barley (29, 102), wheat (52), finger millet (3), rye grass (1, 110-112), alfalfa (102), tropical grass *Paspalum notatum* (85), sudan grass (29), clover (95, 107, 109, 111, 112), cowpea (3), potato (12), strawberry (59), lily (2), cotton (3, 29), and marigold (43).

Crews et al. (21), who studied effects of VA mycorrhizal fungus inoculation on *Viburnum*, *Podocarpus* and *Pittosporum*, reported greater plant height, stem caliper, root and shoot fresh weights of inoculated plants over controls. An increase of two- to three-fold in overall plant growth resulted from inoculation. Sycamore seedlings inoculated with *Glomus fasciculatum* grew 73% taller and had 200% greater dry weight than noninoculated plants (105). Mycorrhizal red maple seedlings produced more leaves with greater leaf area and weighed significantly more than nonmycorrhizal seedlings growing in the same medium (23). Similarly, eucalyptus (148), sweetgum (63, 139) and *Griselinia littoralis* (5) produced greater biomass when inoculated with VA mycorrhizae than when they were not inoculated. Marx et al. (71) found that rough lemon seedlings inoculated with *Glomus mosseae* produced significantly more dry weight and were twice as large as nonmycorrhizal seedlings. They measured no difference in plant height or dry weights of mycorrhizal and nonmycorrhizal sour orange, although 52% of the roots were mycorrhizal. Menge et al. (75, 77) reported that the mean plant dry weights of each of six citrus cultivars inoculated with *G. fasciculatum* were greater than the mean dry weights of noninoculated plants. Mycorrhizal citrus plants had extensive root systems and dark, large leaves, while nonmycorrhizal plants had poorly developed roots and chlorotic leaves

(62). Stunting and chlorosis of nursery citrus seedlings can be prevented by seed inoculation with VA mycorrhizal fungi (49).

Mycorrhizal peach seedlings produced a dry weight nearly five times that of the controls (42), and mycorrhizal grapes were twice as big as nonmycorrhizal ones (30). Benson and Covey (8) reported that apple seedlings inoculated with VA mycorrhizal fungi had a significantly increased shoot weight over nonmycorrhizal seedlings. Other investigators, using either apple seedlings or apple leaf-bud rooted cuttings, found that mycorrhizal plants grow significantly larger, while nonmycorrhizal plants were stunted with short internodes and had very dark green, hard leaves (20, 84). Trappe et al. (147) attributed stunting of apple trees grown in high arsenic soils to a lack of VA mycorrhizal fungi.

Although little is known about endomycorrhizal relations in tropical plants (80, 119), a few papers indicate a positive effect of VA mycorrhizae on the growth and development of crops grown in the tropics. Growth of lowland tropical rain forest trees was significantly increased by VA mycorrhizae inoculation (60), and dry matter weight of VA inoculated *Khaya grandifoliola* was six times greater than the controls (118). Ramirez et al. (114) studied the effects of three VA species on growth of papaya grown in fertilized and non-fertilized soils. Plants were significantly taller when inoculated with *Gigaspora calospora* and *Glomus macrocarpum* and grown in fertilized soil than when inoculated with *Gigaspora heterogama* or not inoculated. Plant height did not differ as a result of any treatment when plants were grown in non-fertilized soil.

VA mycorrhizae can become established in competition with indigenous mycorrhizae and can improve plant growth and development where indigenous endophytes are sparse (61) or less efficient (89). Cotton, cowpea and finger millet plants inoculated with *Glomus fasciculatum* and grown in nonsterile soil had greater root and shoot weights than those grown in nonsterilized soil (3). Khan (61), having transplanted VA inoculated and noninoculated maize to a field, observed that inoculated plants contained more P and had significantly higher top and root and total dry weights than noninoculated plants after 45 days. Inoculated plants grew tall and had well-developed root systems and thick stems. The noninoculated plants were stunted and showed P deficiency symptoms. Although the same results were obtained 60 and 90 days after transplanting, he noted improvement in the growth of noninoculated plants as they became colonized with the indigenous VA population. He attributed the slow improvement in growth of noninoculated plants to the initial small number of VA spores and/or to competition from other microflora in the field. Similarly, mycorrhizal barley plants transplanted to a P deficient field grew taller with better-developed roots, produced greater dry weight, yielded more tillers and assimilated more P than nonmycorrhizal barley plants transplanted to the same field (129). Mosse and Hayman (92) studied effects of VA inoculation on growth of onions in both sterilized and nonsterilized soils. Inoculated plants grew more than noninoculated ones in both soils with greater difference over time.

Owusu-Bennoah and Mosse (102) seeded onion, alfalfa and barley directly above a small VA inoculum in a field containing a reasonably high level of indigenous endophytes. They observed an increase in shoot growth of the tree crops by 77%, 79% and 33%, respectively, when Glomus mosseae was used and by four-, six-fold and 30% when Glomus caledonium was used. Black and Tinker (12) spread a soil containing many spores of VA mycorrhizal fungi down the furrows of a potato crop and reported a 20% increase in tuber production as compared to a nonfertilized field. Hattingh and Gerdemann (49) prevented stunting and chlorosis of sour orange seedlings grown in a nursery field fumigated with methyl bromide by pelleting the seeds with Glomus fasciculatum inoculum prior to planting. In a greenhouse experiment, Powell (111) found that the shoot growths of rye grass and clover were 48% and 91%, respectively, over the control when the seeds were pelleted with VA mycorrhizae. In the field, he reported that clover shoot dry matter was 37% more when pelleted with Glomus tenue and 79% greater when pelleted with Gigaspora margarita over plants grown from nontreated seeds. In comparing the effects of G. fasciculatum mycorrhizal fungi to the indigenous VA mycorrhiza, G. fasciculatum was reported to have more than doubled the dry matter of clover over clover with the indigenous fungi (112). Powell (110) showed it was possible to increase phosphate recovery of rye grass plants by 56% when efficient mycorrhizal fungi were introduced into nonsterilized soils.

Plant growth response of many species may not relate to percentage root colonization by VA mycorrhizae. Skipper et al. (140)

found no relationship between the percentage of root colonization and soybean growth. Similarly, no correlation was found between the dry weight of aerial parts of tomato and maize (26), Paspalum notatum (85), sudan grass (29) or clover (107). Daniels and Menge (29) could not correlate growth responses to VA inoculation with amount of root colonization in cotton and citrus. On the other hand, Pope (105) reported a positive correlation between growth of sycamore seedlings and root colonization.

Relationships Between VA Mycorrhizae and Nutrient Uptake

Plants with VA mycorrhizae take up more nutrients than nonmycorrhizal plants (5, 14, 37, 84, 87, 129). Mycorrhizal onions had significantly higher P in their dry matter than nonmycorrhizal onions grown in the same soil (50, 55, 88, 97, 103, 131, 132). Using $Na_2{}^{35}SO_4$, Rhodes and Gerdemann (122) detected ^{35}S in the roots of mycorrhizal onions, but not in roots of nonmycorrhizal plants. Maize grown in low phosphorus soil contained more P when inoculated with VA mycorrhizae than noninoculated (29, 134, 144). Gerdemann (36) reported that mycorrhizal maize removed more P and K from the soil than nonmycorrhizal plants. However, the concentrations of K, Mg, and B were higher in the roots and tops of nonmycorrhizal maize plants (35). Leaf Zn of maize and wheat were significantly increased by VA inoculation, but not by $ZnSO_4$ soil application (144). Mycorrhizal inoculation of cowpea grown in soil containing added insoluble $Ca_3\ (PO_4)_2$ increased shoot and root P from 3.2 and 2.0 mg to 6.8 and 3.2 mg, respectively, and also resulted in a greater N uptake (134).

The elements N, P, Ca, and Cu concentrations in leaves of mycorrhizal soybeans were greater than their concentrations in the leaves of nonmycorrhizal plants (124). In tomatoes, mycorrhizal plants contained more P and N than the controls (134). Phosphorus and Zn contents of cotton, cowpea and finger millet were significantly increased by inoculation with Glomus fasciculatum, but it did not affect Mn (3). Holeves (59) reported that strawberry plants grown under a low P regime contained significantly higher P than nonmycorrhizal plants, but he detected no difference in the concentrations of N, K, Ca and Mg.

Inoculated red maple seedlings grown in sand or anthracite waste contained more leaf percent P and had higher total K, Ca, Mg, S, Mn, Fe, B, Zn, Mo, Na and Al than nonmycorrhizal ones (23). Pope (105) showed that sycamore seedlings inoculated with Glomus fasciculatum had 39% more leaf N than noninoculated seedlings and 21, 17 and 3% more when seedlings received 1x, 2x and 4x Hoagland's No. 2 solution. Leaf K increased 54% over the control and 40, 12 and 4% more in 1x, 2x and 4x treatments, respectively. Leaf P was increased 50, 36, 0 and 15% over noninoculated seedlings at 0, 1x, 2x and 4x treatments. Inoculation of hoop pine enhanced Zn absorption, with the metabolically mediated absorption rate of mycorrhizal roots being 2.6 times that of noncolonized roots (15). Gray and Gerdemann (45) demonstrated the increase of ^{32}P uptake from nutrient solution and from soil by mycorrhizal inoculation of sweetgum and tuliptree seedlings.

Sour orange and citrange seedlings grown in fumigated soil became stunted, developed chlorosis and had low percent leaf

P (62, 77). When inoculated with Glomus mosseae, they grew more and had higher percent leaf P than noninoculated plants. Also, mycorrhizal plants removed more K from the soil than nonmycorrhizal plants (62, 75). Deficiency symptoms of Zn were eliminated from peach seedlings by introduction of VA fungi (42). La Rue et al. (66) studied the effects of Glomus fasciculatum alone and in combination with P and Zn treatments and found that mycorrhizal plants grew vigorously and showed no nutrient deficiency. P and Zn treated plants showed moderate Zn deficiency while nontreated controls were stunted and Zn deficient. Levels of leaf Zn were found to be significantly higher in mycorrhizal-treated plants than in nonmycorrhizal plants. K and P levels were similar in all treatments, but N and Mn were significantly higher in the nontreated plants. Mycorrhizal apple seedlings and rooted apple cuttings had higher K, Fe and Cu content and strikingly lower Mn (84). Benson and Covey (8) showed that inoculation of apple seedlings with VA fungi resulted in higher total Zn uptake over the controls. When they combined the mycorrhizal fungi with 5 ppm Zn as $ZnSO_4$, total Zn uptake was increased by more than 5 times over nonmycorrhizal $ZnSO_4$ treatments.

Mycorrhizal and nonmycorrhizal plants appear to use the same nutrient sources. Sanders and Tinker (131) reported that the specific activity of phosphorus in onion plants and the specific activity of P in equilibrium with the soil solution were similar. Hayman and Mosse (56) grew onions in soils labelled with ^{32}P and found that the proportion of ^{32}P to total P taken up by mycorrhizal and nonmycorrhizal plants to be similar. This was confirmed by

Sanders, et al (133), who showed that mycorrhizal plants inoculated with different strains of VA fungi and nonmycorrhizal plants absorb P in the same proportions from the same or similarly labelled fractions of soil P. Powell (106) measured the specific activity of P absorbed by mycorrhizal and nonmycorrhizal plants and found it to be identical.

The enhancement of nutrient uptake by VA mycorrhiza is attributed to the increased absorbing surface area of fungal hyphae extending out from the roots into the soil, thereby covering a larger soil volume than roots alone. Hattingh et al. (50) used soil chambers to study absorption of ^{32}P by mycorrhizal plants and nonmycorrhizal plants. Rhodes and Gerdemann (121) compared the zones of uptake of mycorrhizal and nonmycorrhizal onion roots using ^{32}P injected into the soil at 1 cm intervals up to a distance of 8 cm from the confined roots. They concluded that a mycorrhizal fungus can extend the P uptake zone to a distance of at least 7 cm from the root surface, making mycorrhizal plants accessible to P which is considerably beyond the 1-2 mm zone normally assumed to be the region of P depletion (68). Similarly, ^{35}S injected into the soil 8 cm from onion roots was reported to appear only in the roots of mycorrhizal plants and not in nonmycorrhizal plants (123).

Some Factors Affecting VA Mycorrhizal Fungi

Vesicular-arbuscular mycorrhizal fungi are obligate symbionts and can only multiply and spread in association with a host plant (16, 37, 48, 69). They receive photosynthates from their host plants and mineral nutrients from the soil (58, 87). Therefore, host and soil factors are of great importance for fungal establishment and development. Members of the Cruciferae and Chenopodiaceae do not form mycorrhizae associations (37, 38, 87). Ocampo et al. (101) observed no colonization in cabbage, kale, rape or swede and saw only traces in sugar beets when all of these plants were grown among heavily VA colonized plants. They attributed the lack of colonization in "non-host" plants to intrinsic barriers that could be related to characteristics of root cortex or epidermis rather than to any colonization-inhibitors that might be released in root exudates, as was suggested by others (48, 115).

An increased supply of mineral nutrients may reduce colonization (54, 86), and colonization is favored in nutrient stress situations (26, 116, 146). Applied P reduced the percentage of colonization in maize and tobacco (24, 83) and wheat colonization was highest at low N (52). With several other Gramineae hosts, highest colonization levels were recorded in April in P deficient soil low in moisture and in July under wet soil conditions (113). Mosse and Phillips (96) found that colonization of clover grown in a medium containing 250 ppm P occurred only when N was withheld and Fe was included in the medium. Lambert et al. (67) reported that P reduced percentage of root colonization in clover, but B deficiency had no effect. They found no relationship between N and alfalfa root colonization; however, B deficiency delayed the onset of mycorrhizal colonization and the subsequent spread of the fungi within the roots. Colonization declined in onion with added P, and it did not occur when 1.5 g or more of monocalcium phosphate was added per Kg soil (88). Sanders (130) demonstrated that high levels of P in onions, induced by foliar application of phosphorus, could inhibit colonization by mycorrhizal fungi. The number of spores produced by Glomus fasciculatum on sudan grass roots was significantly reduced by increased plant P and was not affected by soil P (78). In tomato, percentage of colonization decreased from 46.5 to 18.5% with increased amount of phosphate, and in Coprosma robusta from 58 to 20%. Sycamore seedlings inoculated with G. fasciculatum showed a decline in the percentage of root colonization as available soil P increased (105). Mason (72) indicated that the number of spores produced on strawberry and raspberry decreased with production of new roots and increased with cessation of root growth and onset of senescence. Menge et al. (75) reported that increased fertilization significantly decreased the number of spores produced by VA mycorrhizae on citrus seedlings. This reduction was from 776 spores/gm soil at 0 fertilizer to 534 spores/gm soil at the 1/2 fertilizer regime and to 276 spores/gm soil at full fertilizer regimes (complete nutrient solution minus P).

Partial defoliation of tomato and maize plants greatly decreased the percentage of root colonization and total defoliation of grasses and alfalfa reduced mycorrhizal colonization by 50% (22). Mycorrhizal colonization was favored in maize and alfalfa by long day (22) and in pine by light exceeding 25% full daylight combined with deficiency of easily-available N and P (11). Hayman (53) reported that Glomus fasciculatum colonization in onion at 23°C with 25,000 lux was twice as much as that developed under 23°C with 13,000 lux treatment. On the other hand, shading to about one-third full daylight did not reduce the level of mycorrhizal colonization in Coprosma robusta seedlings (4). Furlan and Fortin (32) found the rate of Gigaspora calospora colonization in onion roots to be more rapid and with higher percentage at 5,000 and 10,000 lux than at 15,000 and 20,000 lux under 21/16°C day/night temperature.

Schenk and Schroder (137) used light and temperature treatments ranging from 17 to 41°C to study their effects on the growth of VA mycorrhizae in soybeans. Their results showed that arbuscule development reached a maximum near 30°C, root surface mycelium was greatest between 28 and 34°C and spore production was most numerous at 35°C. VA colonization in onion grown in low P soil was much sparser under 6-hour daylight than under 12-hour with 18°C, but very low colonization occurred with 14°C (53). Furlan and Fortin (31) found that the amount of VA colonization in onions at day/night temperature regimes of 26/21, 21/16 and 16/11°C to be 82, 73 and 11%, with spore production of 2600, 1800 and 50 spores/plant, respectively. Initiation of colonization in onion caused by Gigaspora calospora could start in 4-8 weeks depending on temperature (31).

VA mycorrhizal fungi spores can survive a wide range of temperature. Spores of Gigaspora margarita stored at 4°C remained viable for at least one year without loss of their germination ability or hyphal growth compared to nonstored spores (79). Glomus mosseae spores aged at 10°C for at least 4 months germinated more rapidly than fresh ones (28). Schenk et al. (135) tested effects of light and temperature on germination of Gigaspora coralloida and Gigaspora heterogama from Florida and Glomus fasciculatum of Washington. Their results revealed that spores of all species germinated better in the dark, with Florida VA species having maximum germination at 34°C, while Washington spores had maximum germination at 20°C, leading them to conclude that Florida isolates are adapted to high temperatures and Washington isolates to moderate temperatures. Menge et al. (76) exposed one cm root segments of troyer citrange containing vesicles, arbuscules and chlamydospores of G. fasciculatum to seven temperature treatments for 10 minutes, then used them to inoculate sudan grass seedlings. Colonization occurred when the inoculum was treated at 38, 43, 49 and 51.5°C but not when treated at 52.5, 53 or 55°C.

Different mycorrhizal fungi species respond differently to soil pH. Mosse (85) tested the effects of four different strains of VA fungi on the growth of Paspalum notatum and observed an 11-fold growth increase over nonmycorrhizal controls in limed soil compared to five-fold increase in nonlimed soil. Vigorous mycelial growth was observed on clover roots in a growth medium with a pH of 7 to 8, whereas at pH 4.5 fungus growth and colonization were inhibited (95). Skipper et al. (140) compared growth responses of soybeans to inoculation with Gigaspora gigantea and Glomus mosseae at soil pH's of 5.1 and 6.2 and found that plants failed to respond to G. mosseae inoculation at soil pH 5.1 but grew well at pH 6.2. Inoculation with Gigaspora gigantea increased growth greatly at pH 5.1 and moderately at pH 6.2. In comparing the level of root colonization, they found no difference between the two fungal species in each soil. Thus they attributed the lack of response to _G. mosseae_ at low pH to lack of effectiveness rather than lack of colonization. At pH 4.3 _Tagetes minuta_ inoculated with _Glomus macrocarpum_ grew well, while _Giozotia abyssinica_ similarly inoculated grew only when soil pH was elevated to 6.6 (43).

III. Characterization of Vesicular-Arbuscular Mycorrhizae in Apples Grown in Oregon

Abstract

Vesicular-arbuscular fungi from roots and soil from apple orchards were characterized. *Gigaspora margarita* Becker and Hall, is reported for the first time in Oregon; *Glomus fasciculatum* (Thaxter sensu Gerdemann) Gerd. and Trappe and *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe were found to be the most competitive species in colonizing apple roots in Oregon orchards. Other mycorrhizal fungi also were found in association with apples.

Introduction

Inoculation of plants with vesicular-arbuscular (VA) mycorrhizal fungi often results in improved plant growth and nutrient uptake (39, 48, 51, 87, 93). However, plants respond differently to different species of VA fungi (5, 46, 108, 112, 114) and the host-fungus interaction can be affected by soil and other environmental factors (32, 53, 54, 65, 67, 69, 86, 140). Inoculated plants typically grow better than noninoculated plants in nursery and field (3, 49, 61, 87, 90, 94). Commercial production and application of the endophytes might be realized soon (29, 93). Crop production can be potentially increased by use of fungal species that are most effective.

In this paper we report the VA mycorrhizal fungi most competitive in colonizing roots of apples grown in Oregon. Studies of the relative efficiency of these endophytes will be reported elsewhere.

Materials and Methods

Fine roots of apples and surrounding soil were gathered from mature apple orchards in Oregon. Five orchards were sampled: Lewis Brown Horticultural Research Farm near Corvallis, Oregon (A) and four other orchards located in the Hood River area, referred to as B, C, D and E. All the orchards had grasses and forbs as a cover crop. From each orchard, twelve samples were collected from the top 15 cm of soil, sealed in clear plastic bags and transported to the laboratory in a Coleman ice chest packed with ice to prevent dryness. Root subsamples from each sample were checked for VA mycorrhizae by the clearing and staining method of Phillips and Hayman (104).

For each orchard, the eight samples with highest VA mycorrhizal colonization were combined. Roots were washed with distilled water, chopped into small pieces and thoroughly hand-mixed. The corresponding soil samples were mixed well after being sieved to remove large stones and debris.

Wheat, bell pepper, and 4-leaf stage apple seedling grown in vermiculite from sterilized seeds were used as test plants. Inoculae consisting of either 150 cc soil or 100 cc apple roots was placed in a layer under seeds (wheat and pepper) or plants (apple) at planting time by the modification of Gerdemann's (33) funnel technique used by Ames (2) to ensure contact between growing roots and the inoculum.

Plants were grown in 4 x 4" plastic containers in steam-sterilized sandy loam soil mixed with vermiculite. Containers were placed on Na O Cl-treated benches in a greenhouse. Five replicates of each inoculum plus one noninoculated control were established for each test plant for a total of 18 plants per location per treatment. All plants received Long Ashton mineral nutrient solution (57) with P at one-fourth strength, on a bi-weekly basis, and watered regularly with distilled water.

After eight months from the planting date, VA spores were recovered by wet sieving and decanting (40) and mycorrhizal fungi species were identified (41, 47). Root samples from control test plants were cleared and stained and checked for mycorrhizal colonization (104).

Results and Discussion

Six different VA mycorrhizal fungi species were found in the pot cultures inoculated with roots and soil from Oregon apple orchards: *Gigaspora margarita* Becker and Hall, *Glomus fasciculatum* (Thaxter sensu Gerdemann) Gerd. and Trappe, *Glomus mosseae* (Nicol. and Gerd.) Gerd. and Trappe, *Gigaspora calospora* (Nicol. and Gerd.) Gerd. and Trappe, *Glomus monosporum* Gerd. and Trappe and *Sclerocystis rubiformis* Gerd. and Trappe (Table 1). The first three species grew out of apple root inoculum, suggesting that they are strongly competitive in colonizing apple roots. The other three species resulted from field soil inoculum, indicating that they are associated with plants other than apples. None of the control test plants became mycorrhizal. More than one VA mycorrhizal fungus species are commonly associated with one field (27, 34, 91, 136) or one plant (54, 87, 126). The number of species in any orchard is determined by its agricultural history, soil and environmental characteristics and vegetation types (65, 86, 140).

Gigaspora margarita Becker and Hall (7) has not heretofore been reported in Oregon (41). It was found in the Hood River area but not in the Willamette Valley (Table 2). The distribution of the different species throughout the sample orchards is presented in Table 3. Wheat seems to be a better test plant than pepper in that it was colonized by more species than pepper (Table 1).

Table 1. Species of VA mycorrhizal fungi (*Endogonaceae*) isolated from apple orchards in Oregon by use of apple roots and field soil as inoculum.

VA Species	Apple Root Inoculum			Soil Inoculum		
	Apple	Pepper	Wheat	Apple	Pepper	Wheat
Gigaspora margarita	x	-	x	x	-	-
Gigaspora calospora	-	-	-	-	-	x
Glomus fasciculatum	x	x	x	x	x	-
Glomus mosseae	x	-	x	x	-	x
Glomus monosporum	-	-	-	-	x	x
Sclerocystis rubiformis	-	-	-	-	x	x

x = present, - = absent

Table 2. Species of VA mycorrhizal fungi (Endogonaceae) isolated from different apple orchards in Oregon by use of apple roots as inoculum.

VA Species	Orchards[1]				
	A	B	C	D	E
Gigaspora margarita	-	x	-	x	x
Glomus fasciculatum	x	-	x	x	x
Glomus mosseae	x	x	x	-	x

x = present, - = absent

[1]A located in Willamette Valley; B, C, D and E located in Hood River.

Table 3. Species of VA mycorrhizal fungi (*Endogonaceae*) isolated from different apple orchards in Oregon by use of apple roots and field soil as inoculum.

VA Species	Orchards[1]				
	A	B	C	D	E
Gigaspora margarita	-	x	-	x	x
Gigaspora calospora	x	-	x	x	x
Glomus fasciculatum	x	x	x	x	x
Glomus monosporum	x	-	x	-	-
Glomus mosseae	x	x	x	x	x
Sclerocystis rubiformis	x	x	-	x	-

x = present, - = absent

[1]A located in Willamette Valley; B, C, D and E located in Hood River.

IV. Effects of Some VA Mycorrhizal Fungi and Applied Phosphorus On Growth and Leaf Nutrient Concentration of Apple Seedlings Grown In Two Oregon Soils With Different Levels of Available P

Abstract

Mycorrhizal inoculation of apple seedlings could substitute for P application in some soils. Of three VA-mycorrhiza species, *Gigaspora margarita* was the least effective in promoting plant growth, *Glomus fasciculatum* was the most effective, and *Glomus mosseae* was intermediate. Combining the three species was no more effective than *G. fasciculatum* alone. Effects of VA mycorrhizae on nutrient concentrations in apple leaves are reported. Percent of root colonization was not significantly related to VA-mycorrhizal effectiveness.

Introduction

Vesicular-arbuscular (VA) mycorrhizae improve growth and nutrient uptake of many plant species (20, 37, 93). Recent research indicates that some VA fungal species are more effective than others under given conditions (43, 85, 140) and can benefit some plants but not others (24, 114). Daft and Nicolson (24) reported that dry matter of tobacco and maize were increased over the control when inoculated with any one of three species of *Endogonaceae*. However, only one fungal species increased tomato plant dry weight over noninulated plants. Growth of inoculated onion plants was increased 77%

when the inoculum was Glomus mosseae and by 400% when it was Glomus caledonis, compared with noninoculated plants (102). Inoculation of rough lemon seedlings with G. mosseae produced plants twice as large as the controls; but when sour orange seedlings were similarly inoculated, no growth response was measured (71). Papaya plants grew significantly taller when inoculated with Gigaspora calospora or Glomus macrocarpum than those inoculated with Gigaspora heterogama or not inoculated (114).

Some species of Endogonaceae are more effective in promoting P uptake than others (110). Mosse et al. (97) reported that Glomus fasciculatum was more effective in increasing P uptake by onions and clover over Acaulospora laevis mycorrhizal fungi. Apples inoculated with G. fasciculatum took up more Zn than plants inoculated with G. mosseae (8).

In this paper we report on the effects of P application and three VA mycorrhizal fungi, found to be strongly competitive in colonizing apple roots (this thesis), on growth and nutrient uptake of apple seedlings grown in two soils that differ in their available P content.

Materials and Methods

Parkdale loam soil with low available P and Willamette silty loam soil with high available P (Table 4), as determined by the Oregon State University Soil Testing Laboratory by the Bary No. 1 method (9), were used. Mature apple trees growing in soil A failed to absorb high rates of P trenched into the root zone (73). Maize grown in Willamette soil responded to applied P in the field (74) and in the greenhouse (this thesis).

Equal volumes of Parkdale and Willamette soils were collected from the top 15 cm. Samples were shredded, sifted and mixed with 20% vermiculite in a concrete mixer, and steam sterilized.

Apple seedlings were grown from sterlized seeds in sterile vermiculite in plastic test tube-shaped containers. At the four-leaf stage, single seedlings of uniform size were planted in 4 x 4" plastic pots in each soil and were placed on greenhouse benches lined with plastic sheets. A split strip randomized block design (19) with 9 replications was used.

Treatments consisted of 0 (P_0), 50 (P_1), and 100 (P_2) ppm P_2O_5 as Ca $(H_2PO_4)_2$ per pot. Phosphorus was dissolved in distilled water and applied at planting time in combination with the following mycorrhizal fungus treatments: no mycorrhizae (M_0), Glomus mosseae (Nicol. and Gerd.) Gerd. and Trappe (M_1), Glomus fasciculatum (Thaxter sensu Gerdemann) Gerd. and Trappe (M_2), Gigaspora margarita Becker and Hall (M_3), and a combination of the three mycorrhizal fungi (M_4). Spores of the three fungi were produced in pot culture started with single spores inoculated onto germinated clover seedlings and grown in sterilized sand-soil mixture in the greenhouse. Each of the three treatments consisted of 60 cc of spore-containing, pot culture soil and root fragments. Treatment M_4 was made of 20 cc of each of M_1, M_2 and M_3 as above. All plants not receiving mycorrhizal inoculae received 60 cc of soil and root fragments of clover grown in the same soil used for mycorrhiza pot culture but noninoculated and lacking mycorrhizae. They also received 25 ml of twice-filtered washings from all inoculae. Mycorrhizal-treated plants, on the other hand, received 25 ml of filtered washings of the nonmycorrhizal clover roots and sand-soil mixture. This was to insure that, except for VA fungi, each treatment was exposed to the same array of microorganisms.

After planting, seedlings were watered as needed, and all received Long Ashton mineral nutrient solution (57), withholding P, on a weekly basis.

Shoot growth was recorded every two weeks, starting 45 days after planting. On the 90th day, fresh and dry weights of leaves and stems were measured. Leaves were washed, dried at 80°C for 48 hours, and ground in a Wiley mill to pass a 40-mesh screen. Total nitrogen was determined with a Technicon Auto Analyzer using Kjeldahl procedure (139). The elements P, K, Ca, Mg, Fe, Mn, Zn, Cu and B were analyzed with a Jarrell-Ash 3/4 meter direct reading emission spectrometer (18).

Mycorrhizal colonization of the roots was assessed on root samples taken from each experimental plant. Root samples were cleared and stained by the procedure used by Kormanik et al. (64), and percent of root colonization was determined using the Biermann and Linderman (10) method.

The data were subjected to analysis of variance to test the relationship of applied P and different mycorrhizal fungi to the measured responses (19).

Results

Final shoot height and shoot fresh and dry weights of apple seedlings grown in Parkdale soil were significantly increased over the control by phosphorus and mycorrhizal treatments (Tables 5 & 6), (Figs. 1, 2, 7 & 8). Over all, phosphorus treatments P_1 and P_2 increased final plant height 35 and 63% and fresh weight 55 and 98% and shoot dry weight 51 and 104%, respectively, over no phosphorus treatment. Over all VA mycorrhizal fungi M_1, M_2, M_3 and M_4 resulted in 576, 726, 370 and 735% increases in final plant height; 872, 1184, 433 and 1211% increases in shoot fresh weight; and 826, 1122, 410 and 1161% increases in dry weight, respectively, over nonmycorrhizal controls. Applied P increased growth response to VA mycorrhizal inoculation. Sheffe's method for mean separation revealed no significant differences in height or fresh and dry weights of nonmycorrhizal plants grown with P_1 or without P. However, when these two treatments were analyzed separately from the rest of the experiment, it was found that P_1 significantly increased plant growth over P_0. This is more meaningful since nonmycorrhizal seedlings grew very little compared to mycorrhizal ones and, thus, differences between P_1 and P_0 were very small when compared to differences between mycorrhizal vs. nonmycorrhizal treatments.

Mycorrhizal plants grown in Parkdale soil contained higher concentrations of K and P in their leaves than nonmycorrhizal plants (Table 7). While no significant difference in leaf K concentration resulted due to different mycorrhizal fungi inoculation, plants inoculated with Glomus fasciculatum and the three-fungi combination had significantly higher leaf P concentrations than plants inoculated with Gigaspora margarita or Glomus mosseae. Nonmycorrhizal controls contained higher leaf concentrations of Mn and Fe than mycorrhizal plants (Table 8). There was no significant difference between treatments in leaf concentrations of N, Ca, Mg, Cu, B and Zn (Tables 7 & 8). Nitrogen content of the control plants could not be determined because there was not enough tissue from these plants. Applied P had no significant effects on the leaf concentrations on any of the elements analyzed (Tables 7 & 8).

Forty-five days after planting, all mycorrhizal-inoculated apple seedlings grown in Parkdale soil were taller than nonmycorrhizal controls (Table 5 and Fig. 3). Plants inoculated with Glomus fasciculatum and the three fungi combined were significantly taller than the plants inoculated with Gigaspora margarita. At 60 days, plants inoculated with G. fasciculatum and the three fungi combined were significantly the tallest, followed by plants inoculated with G. mosseae which, in turn, were significantly taller than plants inoculated with G. margarita. This growth rate continued throughout the experiment's duration. Both P treatments resulted in plants significantly taller than the control, with the highest P level producing significantly taller plants than the lower P level (Table 5 and Fig. 4).

Apple seedlings grown in Willamette soil did not respond significantly to mycorrhizal fungi treatments. Final plant height, fresh and dry weights increased significantly with phosphorus treatments (Tables 6 & 9 and Fig. 2). There were no significant differences in plant response to P_1 and P_2; and the highest P level resulted in 15, 17.5 and 18% increases in shoot height, fresh and dry weights, respectively, over no P treatments.

Leaf P concentration of apple seedlings grown in Willamette soil differed according to the fungus used. Plants inoculated with Glomus fasciculatum or the three-fungi combination had significantly higher leaf P concentration than plants inoculated with Glomus mosseae, Gigaspora margarita or noninoculated (Table 10). Applied P had no significant effect on leaf P. Leaf concentrations of N, K, Ca, Mg, Mn, Fe, Cu, B, and Zn were not significantly affected by VA mycorrhizae nor by P treatments (Tables 10 & 11).

The growth rate of apple seedlings grown in Willamette soil was affected differently by different fungi used (Table 9 and Fig. 5). At the end of the 45-day period after planting, plants inoculated with G. margarita or noninoculated were significantly shorter than plants inoculated with G. mosseae, G. fasciculatum or the three-fungi combination. By seventy-five days after planting, plants inoculated with G. margarita grew less than plants inoculated with the other mycorrhizal fungi, as well as noninoculated controls. However, by the end of the experimental period, there were no significant differences in plant heights as a result of the various mycorrhizal inoculae. Forty-five days after planting, P treatments resulted in taller seedlings over the control, with the highest P level producing significantly taller plants than the lower P levels. However, 60, 75 and 90 days after planting, there was no significant difference in plant height between applied phosphorus levels, which remained significantly different over the no-phosphorus treatment (Table 9, Fig. 6).

All noninoculated plants remained nonmycorrhizal and inoculated plants became mycorrhizal. Percentage of root colonization of inoculated plants grown in both soils varied according to the fungus involved. Plants inoculated with G. margarita or the three-fungi combination had the highest level of root colonization when compared to plants inoculated with G. mosseae or G. fasciculatum. Phosphorus treatments reduced percent of colonization of apple roots grown in both soils (Table 6).

Discussion

The results demonstrate that VA mycorrhizal association in apples can strikingly increase plant growth and nutrient uptake where available P is low in the soil. Mycorrhizal inoculation alone resulted in a several-fold increase in plant height, fresh and dry weights over the highest level of applied P. Phosphorus uptake was significantly increased by VA mycorrhizae, as reported for apples by Covey et al. (20). Mycorrhizal inoculation resulted in lower concentrations of leaf Mn and Fe in plants grown in Parkdale soil over the controls, but had no such effects on plants grown in Willamette soil. Those results can be explained by either of two facts. First: control plants grown in Parkdale soil had very little growth compared to mycorrhizal plants; growth of mycorrhizal and nonmycorrhizal plants in Willamette soil did not differ at the end of the experiment. Therefore, the lower leaf concentration of Mn and Fe in mycorrhizal plants may have been a result of growth dilution. Second: the improved P nutrition of plants is known to decrease root membrane permeability (115). Thus, mycorrhizal plants which had higher P than the controls were less permeable to Mn and Fe. Since both mycorrhizal and nonmycorrhizal plants had higher P content, no difference between Mn and Fe concentrations existed in plants grown in Willamette soil.

This experiment shows that differences in effectiveness of VA mycorrhizal fungi can exist even between indigenous species that are strongly competitive in colonizing roots of apples grown in the field. The tested species range according to their efficiency as follows: Glomus fasciculatum, Glomus mosseae and Gigaspora margarita. Combining species together is at least as effective as G. fasciculatum alone. This will be of great help in determining what fungi to use in inoculating apples to be grown in Oregon before releasing them from the nursery or in the field.

Percentage of root colonization alone should not be used to determine mycorrhizal effectiveness. No relationships were found between percent of root colonization and fungus effectiveness. Gigaspora margarita had the highest level of colonization, yet it is the least effective of the three species used in stimulating growth or increasing nutrient uptake. Lack of correlation between percent of root colonization and plant growth has been reported with clover (107), maize (26), citrus (29) and other crops (85, 140).

Table 4. Soil analysis[1] for Parkdale loam soil and Willamette silty loam soil[2].

Soil Type	P (ppm)	K (ppm)	Ca (meq/100g)	Mg (meq/100g)	PH
Parkdale soil	13	149	2.5	0.38	5.7
Willamette soil	117	264	8.7	1.20	6.2

[1]Means pooled over 10 replications for soil A and 4 replications for soil B.

[2]Pachic Ultic Argixeralls, fine, silty, mixed, mesic.

Table 5. The effect of VA mycorrhizae and P treatments on shoot growth, measured at 15 day intervals, of apple seedlings grown in Parkdale soil.

Treatment	Shoot Height Measured On			
	July 15	July 30	Aug. 14	Aug. 29
M_0P_0	0.6c	0.7d	0.7d	0.7e
M_0P_1	1.0c	2.1d	2.6d	3.0e
M_0P_2	4.0c	7.3c	11.4d	15.2d
M_1P_0	7.4b	12.7c	22.8c	31.0c
M_1P_1	11.8b	23.8b	36.2b	45.9b
M_1P_2	14.4a	30.7a	42.1a	50.8a
M_2P_0	10.0c	19.2b	32.4b	43.2b
M_2P_1	13.2a	31.0a	44.2a	53.7a
M_2P_2	18.3a	37.3a	50.2a	59.4a
M_3P_0	3.9c	10.4c	17.9c	20.5c
M_3P_1	5.8c	13.1c	23.4c	30.3c
M_3P_2	9.1b	16.5b	31.2b	38.1b
M_4P_0	10.1b	19.4b	34.1b	42.9b
M_4P_1	13.2a	30.3a	45.2a	53.8a
M_4P_2	17.9a	38.3a	51.4a	61.2a
M_0	1.9c	3.4d	4.9d	6.3d
M_1	11.2a	22.4b	33.7b	42.6b
M_2	13.8a	29.2a	42.3a	52.1a
M_3	6.3b	13.3c	24.2c	29.6c
M_4	13.7a	29.4a	43.6a	52.6a
P_0	6.4c	12.5c	21.6c	27.7c
P_1	9.0b	20.1b	30.3b	37.3b
P_2	12.7a	26.0a	37.3a	45.0a

Data within group/within column followed by different letters are significantly different using Scheffe's test at P = .05. Data followed by the same letter are not significantly different.

Table 6. The effect of VA mycorrhizae and P treatments on fresh and dry weights and percentage root colonization of apple seedlings grown in Parkdale and Willamette soils.

Treatment	PARKDALE SOIL Shoot Fresh Wt(g)	PARKDALE SOIL Shoot Dry Wt(g)	PARKDALE SOIL Root Col. %	WILLAMETTE SOIL Shoot Fresh Wt(g)	WILLAMETTE SOIL Shoot Dry Wt(g)	WILLAMETTE SOIL Root Col. %
M_0P_0	0.2d	0.1d	00 d	8.8a	4.1b	00 e
M_0P_1	0.6d	0.3d	00 d	11.1a	5.0a	00 e
M_0P_2	2.3d	1.1c	00 d	12.2a	5.5a	00 e
M_1P_0	5.8c	2.5c	68 b	11.3a	5.2a	70 b
M_1P_1	11.4b	5.1b	60 c	11.9a	5.7a	68 b
M_1P_2	12.8a	5.9a	53 c	12.2a	5.8a	63 c
M_2P_0	9.4b	4.2b	64 b	11.5a	5.2a	61 c
M_2P_1	13.6a	6.2a	61 c	12.4a	5.8a	59 c
M_2P_2	16.7a	7.6a	53 c	12.6a	5.9a	48 d
M_3P_0	3.1c	1.6c	82 a	9.0a	4.3b	85 a
M_3P_1	5.1c	2.3c	75 a	10.8a	5.2a	75 b
M_3P_2	8.2b	3.6b	74 a	11.7a	5.4a	70 b
M_4P_0	10.1b	4.3b	75 a	11.9a	5.5a	80 a
M_4P_1	13.8a	6.5a	72 b	12.5a	5.9a	76 b
M_4P_2	16.6a	7.7a	69 b	12.9a	6.1a	74 b
M_0	1.0d	0.5d	00 c	10.7a	4.8a	00 d
M_1	10.0b	4.5b	61 b	11.8a	5.6a	67 b
M_2	13.2a	6.0a	59 b	12.2a	5.7a	56 c
M_3	5.5c	2.5c	77 a	10.5a	5.0a	77 a
M_4	13.5a	6.2a	72 a	12.5a	5.9a	76 a
P_0	5.7c	2.5c	58 a	10.5b	4.9b	60 a
P_1	8.9b	4.1b	54 b	11.8a	5.5a	56 b
P_2	11.3a	5.2a	50 c	12.3a	5.7a	51 c

Data within group/within column followed by different letters are significantly different using Scheffe's test at P = .05. Data followed by the same letter are not significantly different.

Table 7. The effects of VA mycorrhizae and P treatments on the concentration of N, K, P, Ca, and Mg. in the leaves of apple seedlings grown in Parkdale soil.

Treatment	Nutrient Concentration (% Dry Leaf Wt.)				
	N	K	P	Ca	Mg
M_0P_0	----*	0.58b	.04b	0.87	.21
M_0P_1	----	0.83b	.06b	0.95	.20
M_0P_2	----	1.28a	.10a	0.81	.23
M_1P_0	2.01	1.65a	.10a	0.96	.29
M_1P_1	1.98	1.67a	.12a	0.92	.27
M_1P_2	2.05	1.43a	.13a	0.96	.29
M_2P_0	2.09	1.54a	.13a	0.98	.26
M_2P_1	2.13	1.38a	.13a	1.03	.26
M_2P_2	2.02	1.51a	.16a	1.10	.26
M_3P_0	2.15	1.61a	.09a	1.01	.30
M_3P_1	1.99	1.55a	.10a	1.06	.28
M_3P_2	2.12	1.60a	.10a	0.93	.25
M_4P_0	2.16	1.80a	.16a	1.02	.29
M_4P_1	2.08	1.58a	.18a	1.04	.27
M_4P_2	2.02	1.56a	.21a	1.16	.27
M_0	----	0.89b	.07c	0.88	.21
M_1	2.01	1.58a	.12b	0.95	.28
M_2	2.08	1.48a	.14a	1.04	.26
M_3	2.09	1.59a	.10b	1.00	.28
M_4	2.09	1.63a	.19a	1.08	.28
P_0	2.10	1.44a	.10c	0.97	.27
P_1	2.05	1.41a	.12b	1.00	.26
P_2	2.05	1.48a	.14a	0.99	.26

Data within group/within column followed by different letters are significantly different using Scheffe's test at P = .05. Data followed by the same letter or no letter are not significantly different.

*---- = no N analysis was run due to lack of tissue.

Table 8. The effects of VA mycorrhizae and P treatments on the concentration of Mn, Fe, Cu, B and Zn in the leaves of apple seedlings grown in Parkdale soil.

Treatment	Nutrient Concentration (PPM Dry Leaf Wt.)				
	Mn	Fe	Cu	B	Zn
M_0P_0	301a	181a	6	59	21
M_0P_1	310a	167a	7	50	24
M_0P_2	260a	125a	8	61	25
M_1P_0	87b	69b	9	60	30
M_1P_1	82b	67b	7	53	22
M_1P_2	68b	45b	5	44	21
M_2P_0	72b	67b	7	49	24
M_2P_1	68b	53b	5	44	19
M_2P_2	85b	66b	6	50	25
M_3P_0	72b	62b	7	48	26
M_3P_1	74b	57b	5	46	26
M_3P_2	72b	58b	6	44	25
M_4P_0	76b	63b	8	47	31
M_4P_1	71b	51b	7	47	24
M_4P_2	64b	44b	8	47	28
M_0	290a	158a	7	57	23
M_1	79b	60b	7	52	24
M_2	75b	62b	6	47	22
M_3	73b	59b	8	46	25
M_4	70b	52b	6	47	28
P_0	121a	88a	7	52	26
P_1	121a	79a	6	48	23
P_2	110a	68a	6	49	25

Data within group/within column followed by different letters are significantly different using Scheffe's test at P = .05. Data followed by the same letter or no letter are not significantly different.

Table 9. The effect of VA mycorrhizae and P treatments on shoot growth, measured at 15 day intervals, of apple seedlings grown in Willamette soil.

Treatment	Shoot Height Measured On			
	July 15	July 30	Aug. 14	Aug. 29
M_0P_0	10.3b	23.2b	35.6b	42.4b
M_0P_1	13.7b	29.6a	43.3a	52.3a
M_0P_2	18.3a	33.0a	46.7a	54.1a
M_1P_0	13.8b	28.9a	40.4a	49.7a
M_1P_1	16.4a	32.1a	43.6a	52.4a
M_1P_2	18.8a	33.9a	45.1a	54.2a
M_2P_0	15.7a	28.9a	42.5a	50.8a
M_2P_1	17.2a	32.5a	45.9a	53.0a
M_2P_2	20.1a	35.2a	46.3a	54.3a
M_3P_0	9.6b	23.2b	33.2b	41.8b
M_3P_1	13.2b	30.6a	38.6b	49.1a
M_3P_2	16.3a	31.7a	43.7a	52.4a
M_4P_0	15.9a	31.1a	42.2a	51.7a
M_4P_1	18.9a	32.6a	45.9a	53.7a
M_4P_2	20.5a	35.3a	47.3a	55.9a
M_0	14.1b	28.6a	41.9a	49.6a
M_1	16.4a	31.7a	43.9a	52.1a
M_2	17.7a	32.2a	44.9a	52.7a
M_3	13.0b	28.5a	38.5b	47.8a
M_4	18.4a	32.9a	45.1a	53.8a
P_0	13.1c	27.1b	38.8b	47.3b
P_1	15.9b	31.5a	43.5a	52.1a
P_2	18.8a	33.8a	45.8a	54.2a

Data within group/within column followed by different letters are significantly different using Scheffe's test at P = .05. Data followed by the same letter are not significantly different.

Table 10. The effects of VA mycorrhizae and P treatments on the concentration of N, K, P, Ca, and Mg. in the leaves of apple seedlings grown in Willamette soil.

Treatment	Nutrient Concentration (% Dry Leaf Wt.)				
	N	K	P	Ca	Mg
M_0P_0	2.10	1.51	.14b	1.18	.23
M_0P_1	2.03	1.65	.16b	1.11	.24
M_0P_2	2.11	1.64	.20a	1.21	.23
M_1P_0	2.03	1.51	.21a	1.08	.25
M_1P_1	2.10	1.48	.20a	1.11	.27
M_1P_2	2.05	1.41	.24a	1.06	.27
M_2P_0	2.11	1.47	.24a	1.14	.26
M_2P_1	2.07	1.41	.23a	1.08	.28
M_2P_2	2.09	1.49	.24a	1.12	.28
M_3P_0	1.92	1.53	.17b	0.95	.23
M_3P_1	2.06	1.60	.20a	1.09	.21
M_3P_2	2.00	1.53	.21a	1.00	.21
M_4P_0	2.04	1.60	.29a	1.14	.24
M_4P_1	1.96	1.56	.27a	1.11	.23
M_4P_2	2.11	1.68	.31a	1.20	.27
M_0	2.08	1.60	.16b	1.17	.23
M_1	2.06	1.47	.21b	1.09	.26
M_2	2.09	1.46	.24a	1.11	.27
M_3	1.99	1.55	.19b	1.01	.22
M_4	2.04	1.62	.29a	1.15	.25
P_0	2.04	1.53	.21a	1.10	.24
P_1	2.04	1.54	.21a	1.10	.25
P_2	2.07	1.55	.23a	1.12	.25

Data within group/within column followed by different letters are significantly different using Scheffe's test at P = .05. Data followed by the same letter or no letter are not significantly different.

Table 11. The effects of VA mycorrhizae and P treatments on the concentration of Mn, Fe, Cu, B and Zn in the leaves of apple seedlings grown in Willamette soil.

Treatment	Nutrient Concentration (PPM Dry Leaf Wt.)				
	Mn	Fe	Cu	B	Zn
M_0P_0	80	59	4	53	19
M_0P_1	84	63	4	50	16
M_0P_2	82	58	5	58	21
M_1P_0	87	51	6	50	19
M_1P_1	90	61	5	47	20
M_1P_2	78	51	5	46	19
M_2P_0	75	57	5	46	22
M_2P_1	72	55	5	45	19
M_2P_2	68	57	6	53	27
M_3P_0	71	66	4	42	18
M_3P_1	70	55	5	55	20
M_3P_2	62	40	4	46	18
M_4P_0	83	53	6	49	23
M_4P_1	83	57	6	45	22
M_4P_2	90	54	6	50	25
M_0	82	60	4	53	18
M_1	85	54	5	48	19
M_2	72	56	6	48	23
M_3	67	53	5	48	19
M_4	85	55	6	48	23
P_0	79	57	5	48	20
P_1	80	58	5	48	19
P_2	76	52	5	51	22

Data within column are not significantly different.

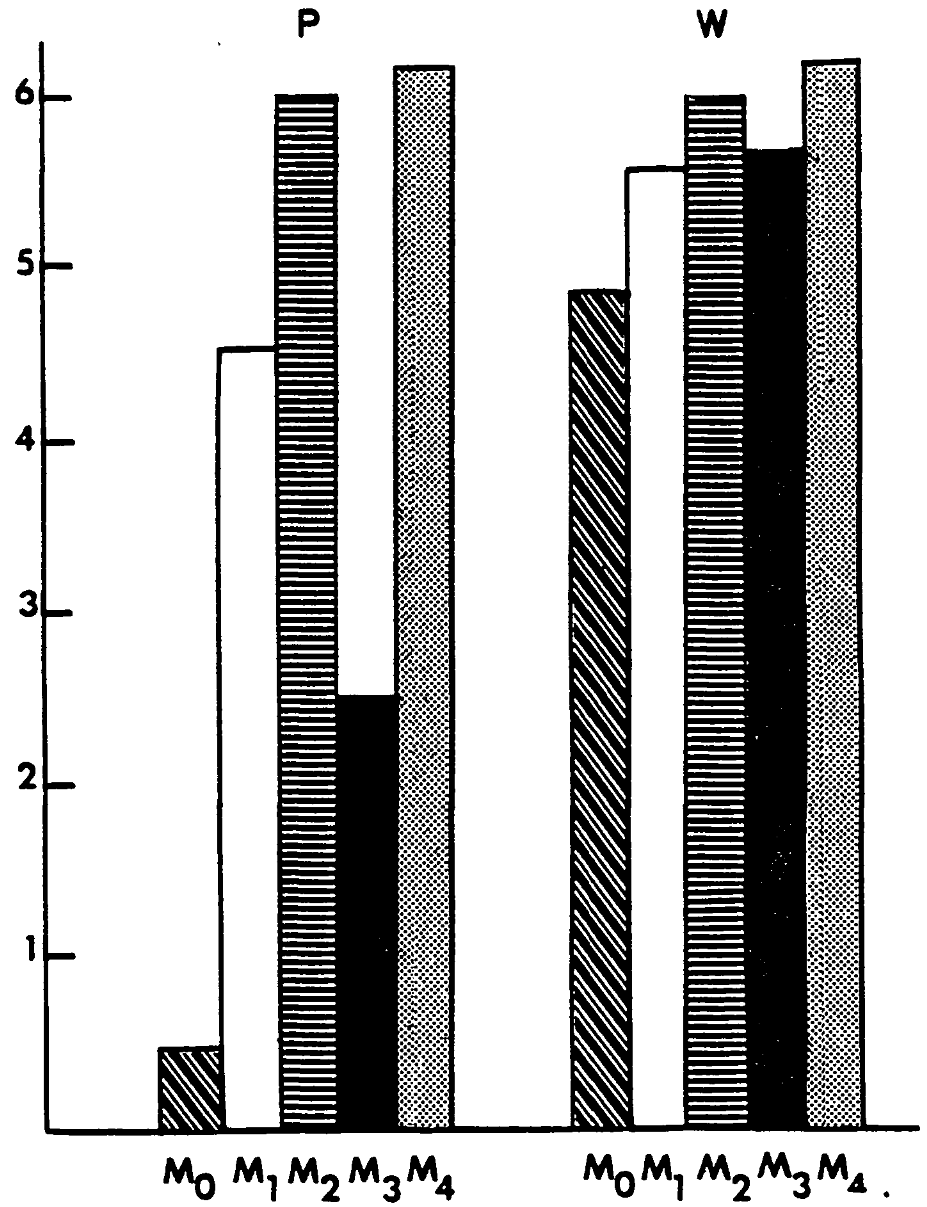

Figure 1. The effect of no VA mycorrhizae (M_0), Glomus mosseae (M_1), Glomus fasciculatum (M_2), Gigaspora margarita (M_3), and $M_1 + M_2 + M_3$ (M_4) on the dry weight of apple seedlings grown in Parkdale (P) and Willamette (W) soils. Data labelled with different letters are significantly different at P = .05.

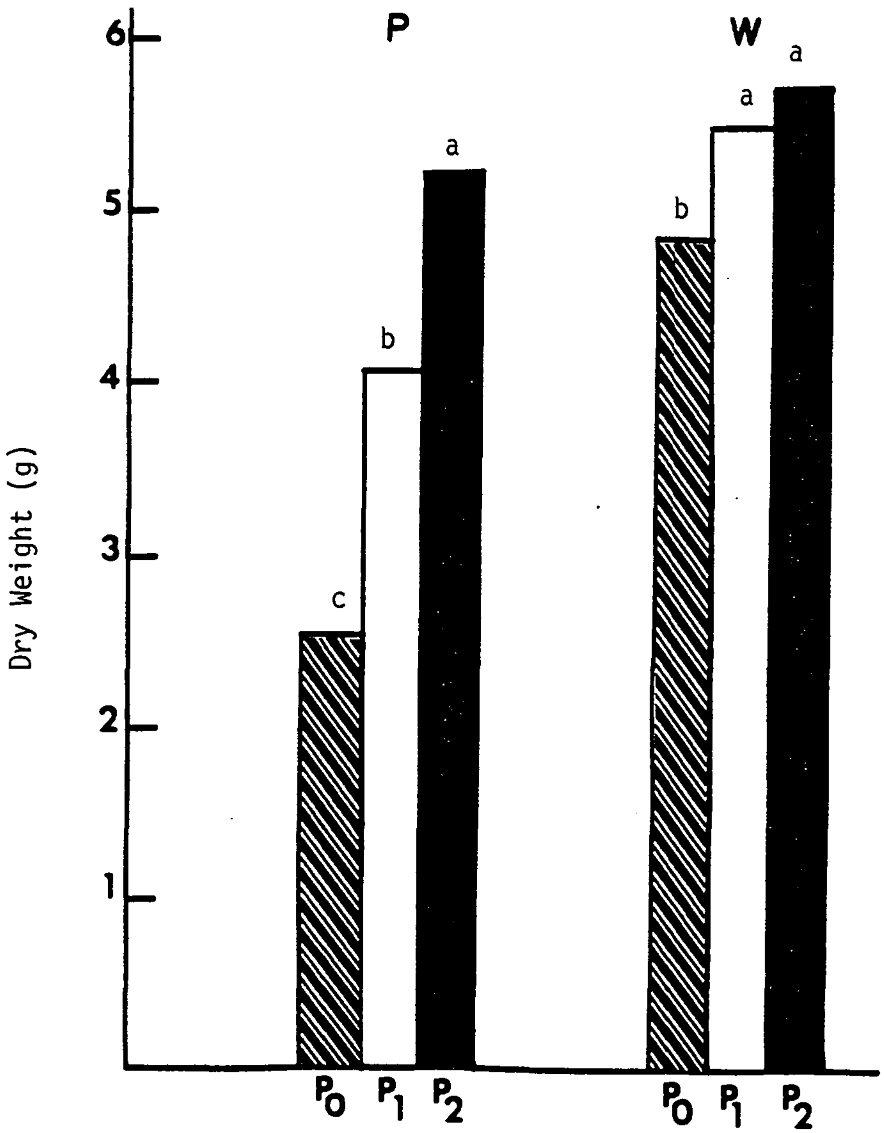

Figure 2. The effects of phosphorus treatment at 0 ppm P_2O_5 (P_0), 50 ppm P_2O_5 (P_1) and 100 ppm P_2O_5 (P_2) on the dry weight of apple seedlings grown in Parkdale (P) and Willamette (W) soils. Data labelled with different letters are significantly different.

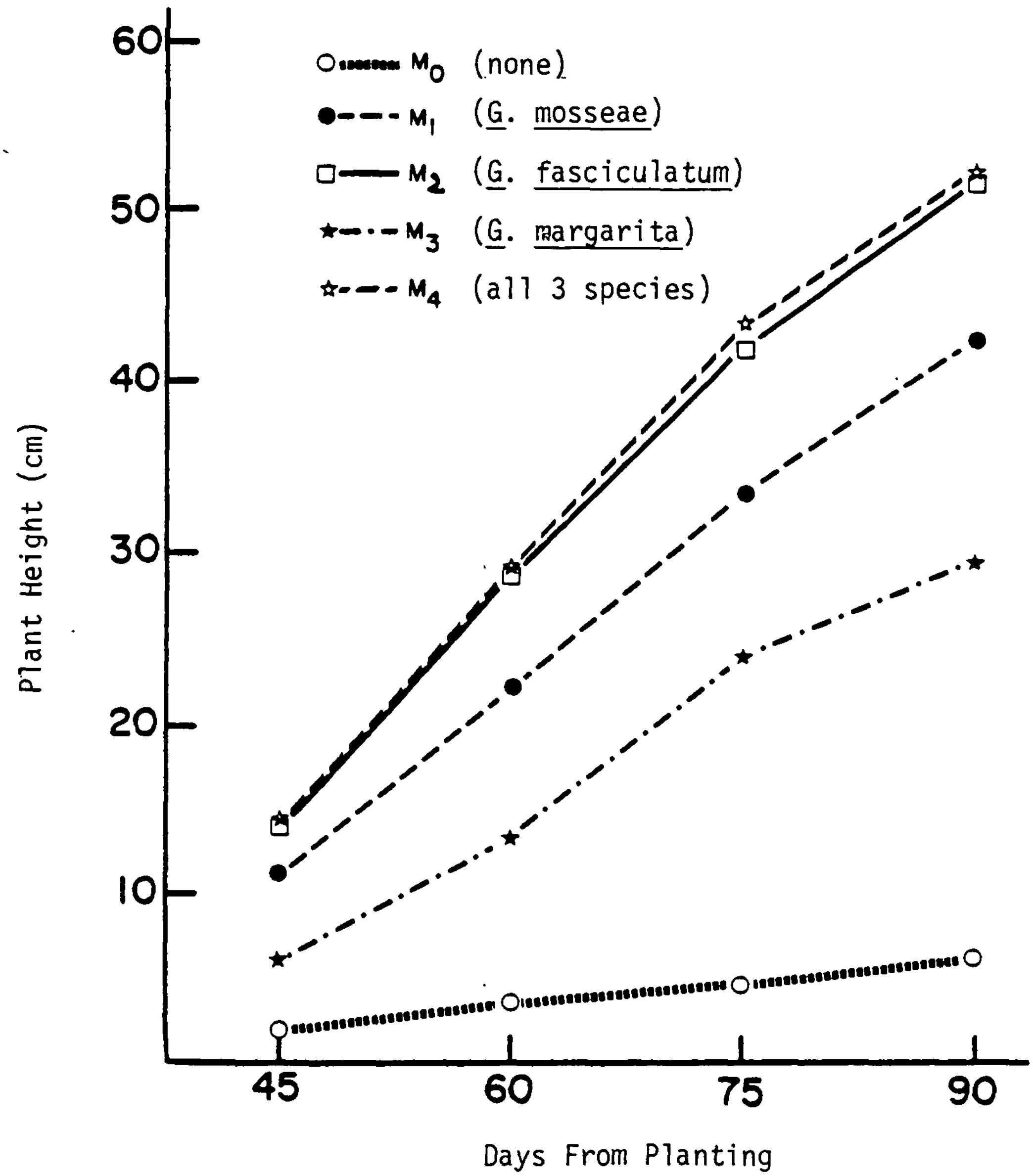

Figure 3. The effects of different VA mycorrhizal species on the growth of apple seedlings grown in Parkdale soil.

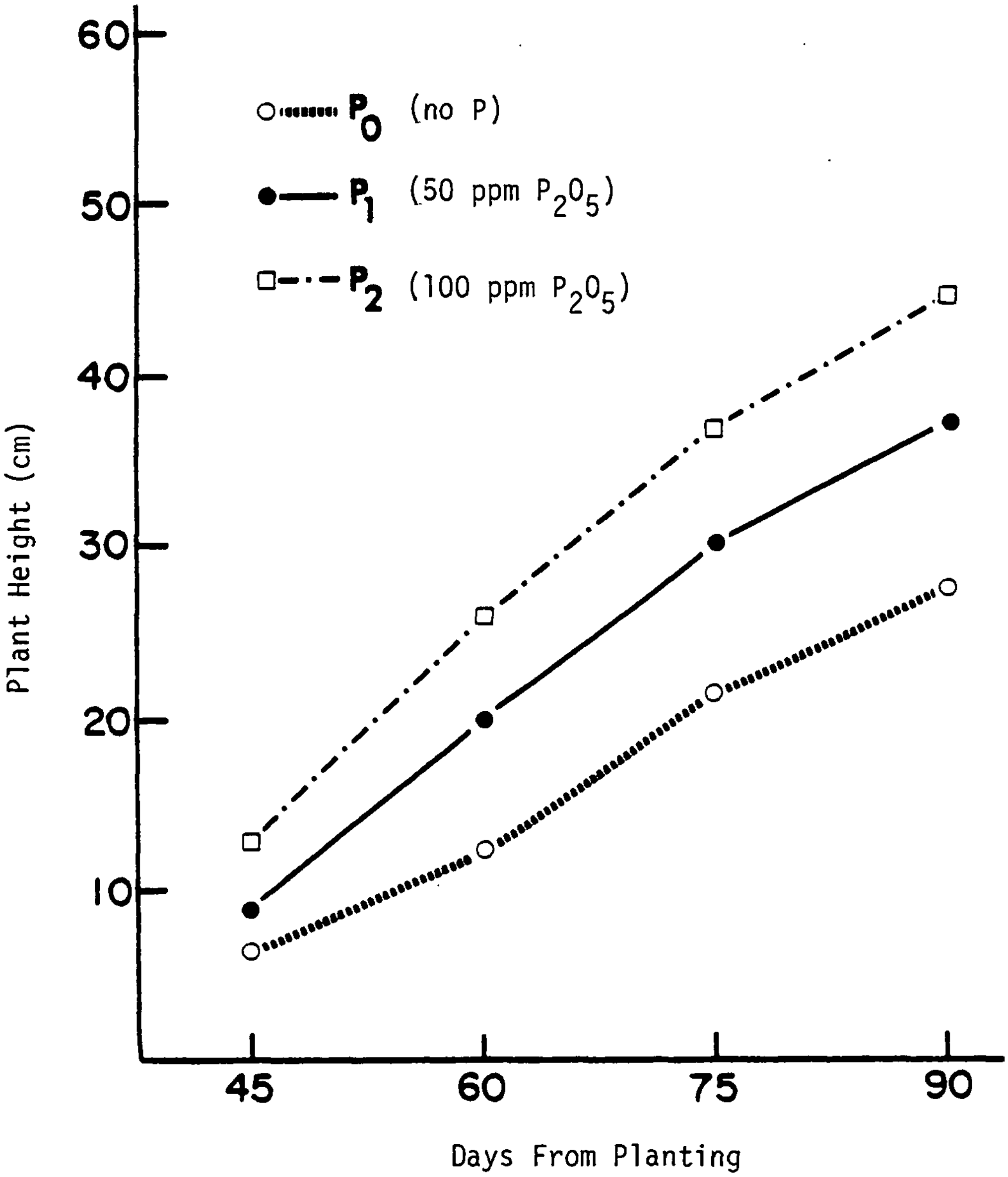

Figure 4. The effect of P treatment on the growth of apple seedlings grown in Parkdale soil.

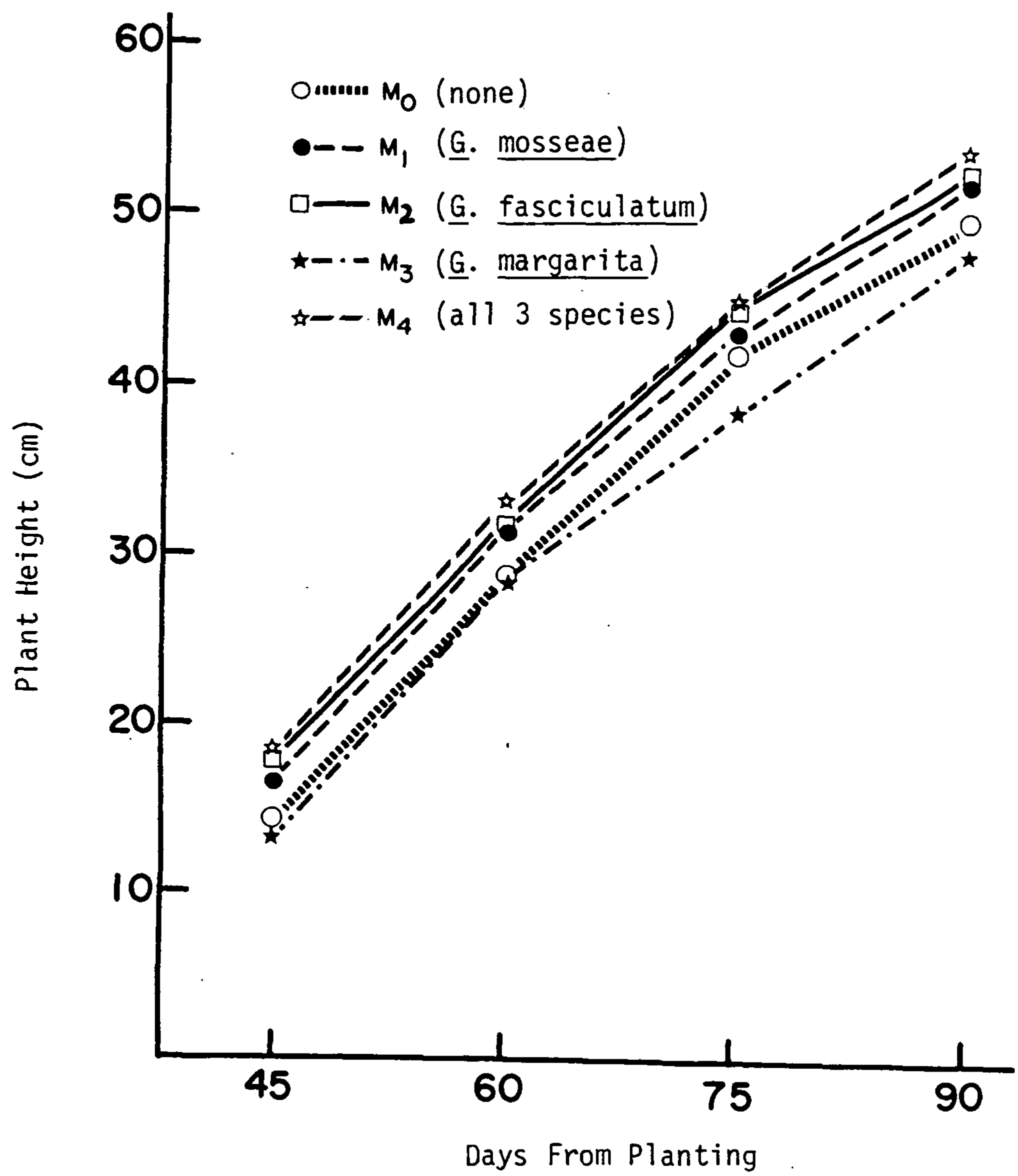

Figure 5. The effects of different VA mycorrhizal species on the growth of apple seedlings grown in Willamette soil.

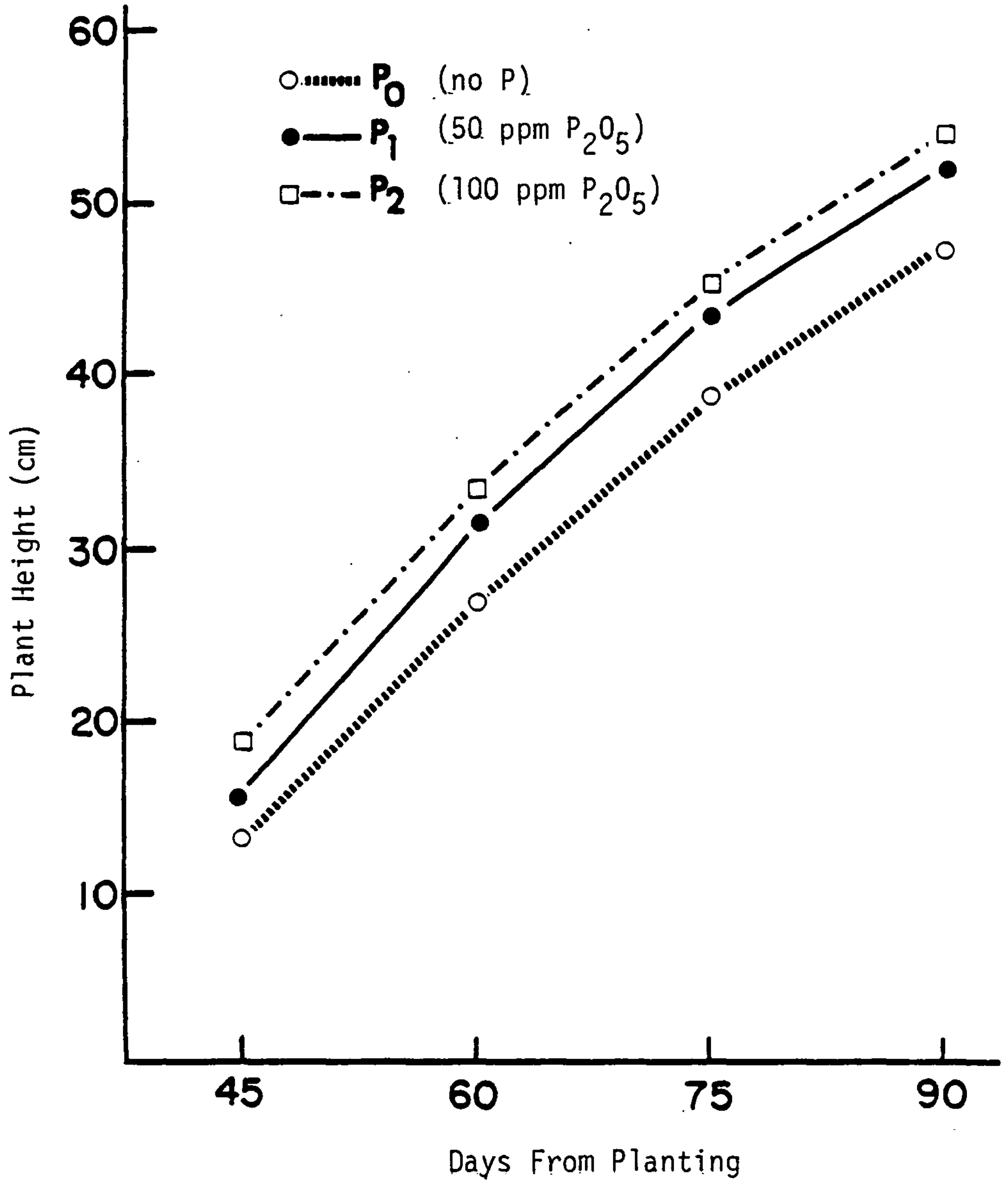

Figure 6. The effect of P treatment on the growth of apple seedlings grown in Willamette soil.

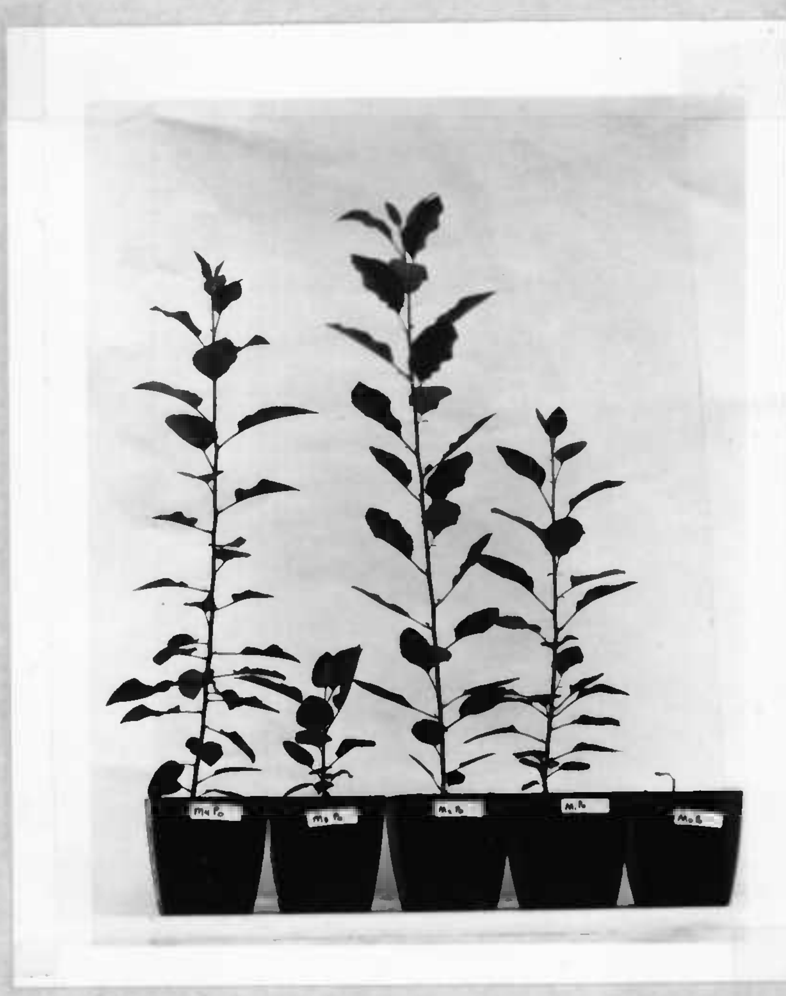

Figure 7. The effects of no VA mycorrhizae (M_0), Glomus mosseae (M_1), Glomus fasciculatum (M_2), Gigaspora margarita (M_3), and $M_1 + M_2 + M_3$ (M_4) (right to left) on growth of apple seedlings grown in Parkdale soil.

Figure 8. The effects of phosphorus treatment at 0 P_2O_5 (P_o), 50 ppm P_2O_5 (P_1) and 100 ppm P_2O_5 (P_2) (right to left) on growth of apple seedlings grown in Parkdale soil.

V. Response of Maize to VA Mycorrhizae and Phosphorus Treatments Applied Separately and in Combination in a Split Root Experiment

Abstract

The effects of soil-applied P and vesicular-arbuscular (VA) mycorrhizae on plant height, weight, leaf nutrient concentration and root colonization of sweet maize (*Zea mays* L. cv. Jubilee) were investigated in a split root experiment. Both treatments resulted in taller plants which weighed more and had higher leaf P concentration than the controls, but VA effects were greater than those of P. VA treatments also increased percent leaf Mg and Mn. Root colonization was reduced by applied P.

Introduction

Vesicular-arbuscular (VA) mycorrhizal fungi were known to increase plant growth and phosphorus (P) uptake by different plants grown in P-deficient soils (29, 107, 134). Application of P was reported to reduce the beneficial effects of VA mycorrhizal associations (87, 125, 145). However, reports are contradictory as to whether P concentration in the soil or within the plants is responsible for the lack of plant response to VA fungi inoculation. Soil-applied P was reported to reduce percentage of colonization in plants (25, 12). Sanders (130) found that high levels of P in onion plants, induced by foliar application of P, could inhibit mycorrhizal fungus colonization.

In this experiment we report on the effects of soil-applied P and VA mycorrhizal fungus inoculation separately and in combination on growth of maize, rate of colonization of roots and concentration of various nutrients in the plants.

Materials and Methods

Willamette silty loam soil containing high available P (Table 12), as determined by the Oregon State University Soil Testing Laboratory using Bray No. 1 method (9), was used in the experiment. Field-grown maize in this soil has shown a growth response to P application (74). The soil was shredded and mixed with 20% vermiculite for better aeration, then was steam sterilized and kept in an airtight 35-gallon can.

Sweet corn (*Zea mays* L. cv. Jubilee) seeds were grown individually in sterilized vermiculite in plastic test tube-shaped containers. At the four-leaf stage, 45 maize plants of uniform size were selected. The root system of each plant was parted in two. Each half was planted in one of two 4 x 4" plastic containers which were taped together.

Treatments consisted of 0 (P_0) and 50 (P_1) ppm P_2O_5 as Ca $(H_2PO_4)_2$ applied in solution at the time of planting in combination without vs. with mycorrhizal inoculum (M_1), which was a mixture of *Acaulospora elegans* Trappe and Gerdemann and *Glomus microcarpum* Tul. and Tul. *A. elegans* was produced on *Asparagus* sp. and was supplied by Mr. John Kough, USDA Agricultural Research Service, Horticultural Research Laboratory, Corvallis, Oregon. *Glomus microcarpum* was grown on *Coleus* sp. and was supplied by Dr. H. J. Larsen, Tree Research Center, Wenatchee, Washington. The M_1 treatment was applied around the roots at planting as 50 cc of sand containing spores and mycorrhizal plant root fragments. All nonmycorrhizal treatments (M_0) received 50 cc of double-filtered washings of M_1.

Treatments were randomized within the block and were replicated nine times. Each replicate consisted of five treatments, each of a single plant with divided root systems, as follows: P_0M_0 (roots in first pot) - P_0M_0 (roots in second pot), P_0M_1-P_0M_1, P_1M_0-P_1M_0, P_1M_1-P_1M_1 and P_1M_0-P_0M_1.

Plants were grown in a greenhouse, watered as needed, and fertilized weekly with 10 ppm N as $(NH)_2SO_4$ and 10 ppm N as KNO_3.

At boot stage, plant height and weight were measured. Leaves were washed, dried at 80°C for 48 hours, and ground in a Wiley mill to pass a 40-mesh screen. Total nitrogen was determined with a Technicon Auto Analyzer using Kjeldahl procedure (139). The elements P, K, Ca, Mg, Fe, Mn, Zn, Cu, B and Al were analyzed with a Jarrell-Ash 3/4 meter direct reading emission spectrometer (18).

Root samples from individual pots were collected, cleared and stained (104) and percent of root length with mycorrhizal colonization was determined (10).

The data were subjected to analysis of variance with comparison of individual treatment effects (142).

Results

Both P and VA mycorrhizal fungus treatments resulted in significantly taller plants with greater fresh weight over the control plants (Table 13). Plants with VA mycorrhizae on one (P_1M_0-P_0M_1) or both (P_1M_1-P_1M_1) parts of the root system in combination with P grew more than plants which received P but no mycorrhizal inoculum to both root parts (P_1M_0-P_1M_0). Applying VA mycorrhizal inoculum without P to both parts (P_0M_1-P_0M_1) produced plants as tall and as heavy as those which received P and VA mycorrhizal treatments (P_1M_1-P_1M_1) and P_1M_0-P_0M_1).

All treatments induced higher leaf P concentration over the control (Table 13). Although statistically not different, plants inoculated with VA mycorrhizae in one or both root parts (P_0M_1-P_0M_1, P_1M_1-P_1M_1 and P_1M_0-P_0M_1) had higher percent leaf P than plants treated with P but no VA mycorrhizae (P_1M_0-P_1M_0) in both parts. Combining VA mycorrhizae and P in both parts of the root system (P_1M_1-P_1M_1) resulted in plants with the highest percent leaf P. The VA mycorrhizal treatments (P_0M_1-P_0M_1, P_1M_1-P_1M_1 and P_1M_0-P_0M_1) also increased percent leaf Mg and Mn over the control, but P did not affect these elements (P_1M_0-P_1M_0).

Leaf concentrations of N, K, Fe, B, Zn and Al did not differ significantly between treatments. Roots in noninoculated pots remained nonmycorrhizal while inoculated ones became mycorrhizal (Table 14). Levels of colonization were highest when VA mycorrhizal inoculum was not combined with P (P_0M_1-P_0M_1 and P_1M_0-P_0M_1) and lowest when VA inoculation was combined with P treatment (P_1M_1-P_1M_1). Applying P to one part of the root system did not affect root colonization in the other part (P_1M_0-P_0M_1).

Discussion

Results confirm the reported response of maize grown in Willamette soil to applied P (74) and that VA inoculation increases plant growth and P uptake (35, 36, 98). Inoculation of maize grown in this soil substitutes for P application (Table 13). Moreover, inoculation improves Mg and Mn uptake. Although Daft and Hacskaylo (23) found that mycorrhizal red maple plants grown in anthracite soil contained more Mg than nonmycorrhizal plants, no reports of such effects with maize could be found. Mycorrhizal fungi extend the root absorbing surface area and, in doing so, explore a larger volume of soil than nonmycorrhizal roots (50, 121, 131). The observed increase in Mg and Mn uptake by plants may result directly from this phenomenon.

Percent leaf Mn of apple seedlings grown in Willamette soil but inoculated with different VA mycorrhizal fungi was not significantly different from that of nonmycorrhizal plants. However, mycorrhizal apple seedlings grown in a soil with low P (Parkdale soil) had lower percent leaf Mn than nonmycorrhizal plants (this thesis). These differences could not be compared because of the differences between plants, fungi and soils involved.

Increased soil phosphate reduced percentage of root colonization (Table 15). This is in agreement with many reported findings (87, 125, 145). Mosse (88) observed a decline in onion root colonization with P added to soil, and colonization did not occur when 1500 ppm monocalcium phosphate was added. Increasing plant P by applying phosphorus to one part of the root system (P_1M_0-P_0M_1) did not reduce percent colonization on the other part. This differs from Sanders' (130) results in which onion P was increased by leaf injection. Possibly P forced into plants alters their physiology such that they are less susceptible to mycorrhizal colonization as opposed to when they take up P through the normal pathway, i.e., roots. Moreover, different plants perhaps respond differently.

Table 12. Soil analysis[1] for Willamette silty loam soil[2].

P (ppm)	K (ppm)	Ca (meq/100g)	Mg (meq/100g)	PH
117	264	8.7	1.2	6.2

[1]Means pooled over 4 replications.

[2]Pachic Ultic Argixeralls, fine, silty, mixed, mesic.

Table 13. Effects of P and VA mycorrhizal fungi treatments on height, shoot fresh weight, and the concentration of P, Mg and Mn in the leaves of maize grown in Willamette soil in a greenhouse split root experiment.

Split Root Treatment[1]	Shoot Ht. (cm)	Shoot Wt. (g)	P % Dry Wt.	Mg % Dry Wt.	Mn (ppm)
P_0M_0-P_0M_0	107.33	48.61	0.18	0.10	91
P_0M_1-P_0M_1	133.89**	69.56**	0.36**	0.19**	123*
P_1M_0-P_1M_0	117.33**	54.39**	0.31**	0.10	117
P_1M_1-P_1M_1	121.22**	59.06**	0.38**	0.14*	148**
P_1M_0-P_0M_1	127.33**	64.61**	0.36**	0.16**	155**

[1] P_0 = no phosphorus, P_1 = 50 ppm P_2O_5, M_0 = no VA mycorrhizae and M_1 = VA mycorrhizae applied.

* and ** indicate data different from control at P = .05 and P = 0.01 respectively.

Table 14. Effects of VA mycorrhizal and P treatments on the concentration of N, K, Ca, Fe, Cu, B, Zn and Al in leaves of maize grown in Willamette soil in a greenhouse split root experiment.

Split Root Treatment[1]	% dry wt.			ppm				
	N	K	Ca	Fe	Cu	B	Zn	Al
P_0M_0-P_0M_0	2.11	2.71	.59	123	23	25	36	55
P_0M_1-P_0M_1	2.09	2.78	.56	131	29	27	40	55
P_1M_0-P_1M_0	2.16	2.96	.49	126	26	28	41	53
P_1M_1-P_1M_1	2.05	2.91	.58	126	27	31	43	48
P_1M_0-P_0M_1	2.12	2.85	.58	129	26	32	41	48

[1]P_0 = no phosphorus, P_1 = 50 ppm P_2O_5, M_0 = no VA mycorrhizae and M_1 = VA mycorrhizae applied.

Data in the same column are not significantly different.

Table 15. Mean level of root colonization by VA mycorrhizal fungi in maize grown in Willamette soil in a greenhouse split root experiment.

Treatment[1]	P_0M_0-P_0M_0	P_0M_1-P_0M_1	P_1M_0-P_1M_0	P_1M_1-P_1M_1	P_1M_0-P_0M_1
Percent Root Colonization	0-0	76-80	0-0	53-55	0-79

[1] P_0 = no phosphorus and P_1 = 50 ppm P_2O_5, M_0 = no VA mycorrhizae and M_1 = VA mycorrhizae applied.

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