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Title: STUDIES ON THE VESICULAR-ARBUSCULAR MYCORRHIZAE OF EASTER LILY IN THE PACIFIC NORTHWEST

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A study was conducted to characterize the vesicular-arbuscular (VA) mycorrhizal fungi of commercially grown Easter lily. Monthly field soil and root samples were collected from March through September, 1975, from five fields in the coastal area of southern Oregon and northern California. Soil sievings were inoculated onto clover, onion and lily to increase mycorrhizal spore numbers and to facilitate identification. Four different VA mycorrhizal species were found: Acaulospora elegans, A. trappei, Glomus fasciculatus, and G. monosporus. All four VA species infected Easter lily, clover, and onion. A. trappei and G. fasciculatus were the most frequently isolated species from all five fields. Two of the five fields under study contained only two mycorrhizal species, and three fields contained all four species.

Mycorrhizal infections in roots of field grown lilies were young

and sparse in March and gradually increased until September when bulbs were harvested. Root systems became over 75% infected with mycorrhizae in fields with four species, while in fields with two mycorrhizal species, usually 50% or less of the root stystems became mycorrhizal. High infection levels were reached more rapidly in fields with four VA species present.

Lilies were inoculated in the greenhouse with roots and spores from onion, lily, and clover trap plants. Two levels of mycorrhizal inoculum and three fertilizer rates were tested for their effects on lily growth. Controls were either non-inoculated or inoculated with a solution from the mycorrhizal inoculum which had passed through a 38 μm sieve to remove mycorrhizal spores. Plants given either the high or low level of inoculum did not grow as well as controls. These results were apparently attributable to root rot caused by Fusarium oxysporum which had increased along with the mycorrhizae on trap plants, and was subsequently inoculated onto lilies. More F. oxysporum was recovered from roots inoculated with mycorrhizae than from control plants inoculated with a sieving solution. None was recovered from the non-inoculated plants. The high fertilizer level reduced mycorrhizal infection and enhanced root disease incidence. However, there was more mycorrhizal infection in roots given high fertilizer than no fertilizer. The most mycorrhizae formed in plants given the low fertilizer rate.

A Rhizoctonia-like fungus was found to infect field grown lilies. No apparent adverse or beneficial effects on lily by this fungus were observed under any of the same three fertilizer levels used in the mycorrhizal inoculations.

Another experiment was conducted in order to test the effects of a single mycorrhizal species on Easter lily growth in the absence of pathogens. Lily seedlings were inoculated with A. trappei in the form of spores and infected root fragments from an A. trappei-red clover pot culture. Controls were given a sieving solution made from the mycorrhizal inoculum. Plants inoculated with A. trappei grew significantly better than the controls (fresh weight). Mycorrhizal plants also had a higher level of N, P, K, Ca, and Mg than non-mycorrhizal controls. If the benefits shown in this greenhouse study also occur on field grown plants, then mycorrhizae may have practical application in Easter lily bulb production.

Studies on the Vesicular-Arbuscular Mycorrhizae of Easter Lily in the Pacific Northwest

by

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TO MY WIFE HARRIET

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STUDIES ON THE VESICULAR-ARBUSCULAR MYCORRHIZAE OF EASTER LILY IN THE PACIFIC NORTHWEST

I. INTRODUCTION AND PURPOSE OF THE RESEARCH

Vesicular-arbuscular (VA) mycorrhizal fungi are extremely common, and can be found in most soils (Gerdemann, 1968, 1969; Mosse, 1973b). These phycomycetous fungi belong to the family Endogonaceae (Gerdemann & Trappe, 1974) and have been found to colonize the roots of a large number of agricultural crops (Gerdemann, 1968, 1969). They are more numerous and diverse in cultivated soils than non-cultivated (Mosse and Bowen, 1968b; Mosse, 1973b). These fungi benefit the host by sending hyphae out into the soil from colonized roots, exploiting nutrient sources, and translocating absorbed nutrients to the host (Sanders and Tinker, 1971; Rhodes and Gerdemann, 1975). Mycorrhizal plants are generally healthier than non-mycorrhizal plants in soils that are below the minimum agricultural standard of fertility (Baylis, 1967). Infected plants take up more phosphate than non-infected plants from soils with little available phosphate (Mosse, 1973b). Small additions of nutrients to very nutrient deficient soils can increase mycorrhizal infection and plant growth (Mosse, 1973b), but differences between mycorrhizal and non-mycorrhizal plants are less striking in high nutrient soils (Harley, 1969). Greenhouse experiments usually show

adverse effects of high nitrogen and phosphorus levels on VA mycorrhizal root colonization (Hayman, 1975). These effects have also been shown in field studies (Gerdemann, 1968; Mosse, 1973b; Hayman, 1975).

It has been suggested that VA mycorrhizal fungi can act as direct pathogens (Truscott, 1934; Hildebrand and Koch, 1936), but the amount of literature showing the beneficial effects of mycorrhizae is much greater. Several good reviews dealing with the biology of VA mycorrhizae have been published (Gerdemann, 1968; Harley, 1969; Mosse, 1973b). Some of the current research on these fungi has been directed toward their practical applications in horticulture and agriculture. Progress was slowed by the fact that VA mycorrhizal fungi are obligate symbionts and can not be grown on artificial media. But once researchers by-passed this obstacle by growing inoculum in 'pot cultures', great strides have been made toward a greater understanding of VA mycorrhizae.

The purpose of this research was to investigate the effects of vesicular-arbuscular mycorrhizae on Easter lily (Lilium longiflorum Thunb.). No previous studies have been conducted on the VA mycorrhizae occurring in lily fields or on the effects of fertilizer on the mycorrhizal lily plant. The research was conducted in two phases. Phase one was a field study to determine which mycorrhizal fungi occurred in lily fields, how they were distributed, and how the

infections progressed through the growing season. Phase two was conducted in the greenhouse to determine how the lily field isolates of VA mycorrhizae affected lily growth at different nutrient levels.

II. CHARACTERIZATION OF VA MYCORRHIZAE IN LILY FIELDS

A. Materials and Methods

Area of Study

Plant and soil samples used in this study came from the lily-growing area along the coast of southern Oregon and northern California. About 75% of the Easter lily bulbs grown in the United States for greenhouse forcing of potted plants are produced in this area (Rees, 1972). The five fields used in this study are located along U. S. Highway 101, between Brookings, Oregon and Smith River, California. Individual fields will be referred to only as A, B, C, D, and E.

Field Collection and Observation of Mycorrhizae

Monthly soil and root samples were collected from each of the five fields during the 1975 growing season, beginning in March and ending in September. The monthly sample from each field consisted of ten adjacent plants in a single row. The roots were cleared and stained by a modification of the technique of Phillips and Hayman (1970) to observe the presence of vesicles and arbuscules (Ames and Linderman, 1976b). The soil collected from directly around the roots of all ten plants was combined, mixed, and pre-screened to remove

large rocks and plant debris. Small 50 cc subsamples were wet-sieved using a method similar to that of Gerdemann and Nicolson (1963), to look for VA spore types.

Increasing Spore Numbers for Species Identification

In order to determine exactly which VA fungi infected field grown lilies, whole plants were removed from each field in March and September, 1976. The plants were washed and replanted in the greenhouse in a pasteurized soil mix to allow spores to form in the soil from the infected roots. This method has been used by Daft and Nicolson (1974).

Few spores from soil sievings are perfect specimens that can be readily identified. Mosse and Bowen (1968a) claim that "the only confirmative evidence therefore is the reproduction of a uniform and distinctive spore population in the rhizosphere of inoculated test plants." In order to do this, trap plants were planted so the roots would pass through a layer of inoculum placed in a small tubular plastic growing container. This method was similar to Gerdemann's (1955) funnel technique in that the roots are directed down through a narrow area where they come into contact with the mycorrhizal inoculum. These small tubes measured 3 × 16 cm. The growing medium was washed river sand which was autoclaved for one hour and stored until needed. Inoculum was collected by mixing a 100 cc

soil sample in tap water, allowing a one minute settling time, and decanting through screens with the following μm openings: 355, 250, 125, 90, 63, and 45. Figure 1 illustrates this procedure.

After placing a paper plug in the bottom of each tube, 20 cc of autoclaved sand was added. The soil inoculum caught in each of the six screens was placed in six respective tubes. This procedure was repeated six times for each field, giving a total of 36 trap tubes per field, each month (Figures 1 and 2A).

Three types of test plants were placed in the tubes: red clover (Trifolium pratense L.), onion (Allium cepa L.), and lily (L. longiflorum). Twelve tubes were planted with each host plant from the 36 tubes inoculated each month from all the fields. Seed was used for clover and onion and bulblets were used for lilies. Small lily bulblets were obtained from surface sterilized (10% Clorox for ten minutes) scales from mature 'Ace' bulbs in moist vermiculite maintained in the dark for two months. One bulblet was placed in each of the 12 monthly tubes from each field. Thirty non-inoculated tubes, ten for each trap plant species, were used for controls each month. Controls were placed among the trap tubes from all fields.

The tubes were held in racks which were placed in a growth chamber in a large tray. When watering was necessary, the tray was filled with water so only the bottom 2-3 cm of the tubes were submerged. After 24 hours, the tray was drained. The growth chamber

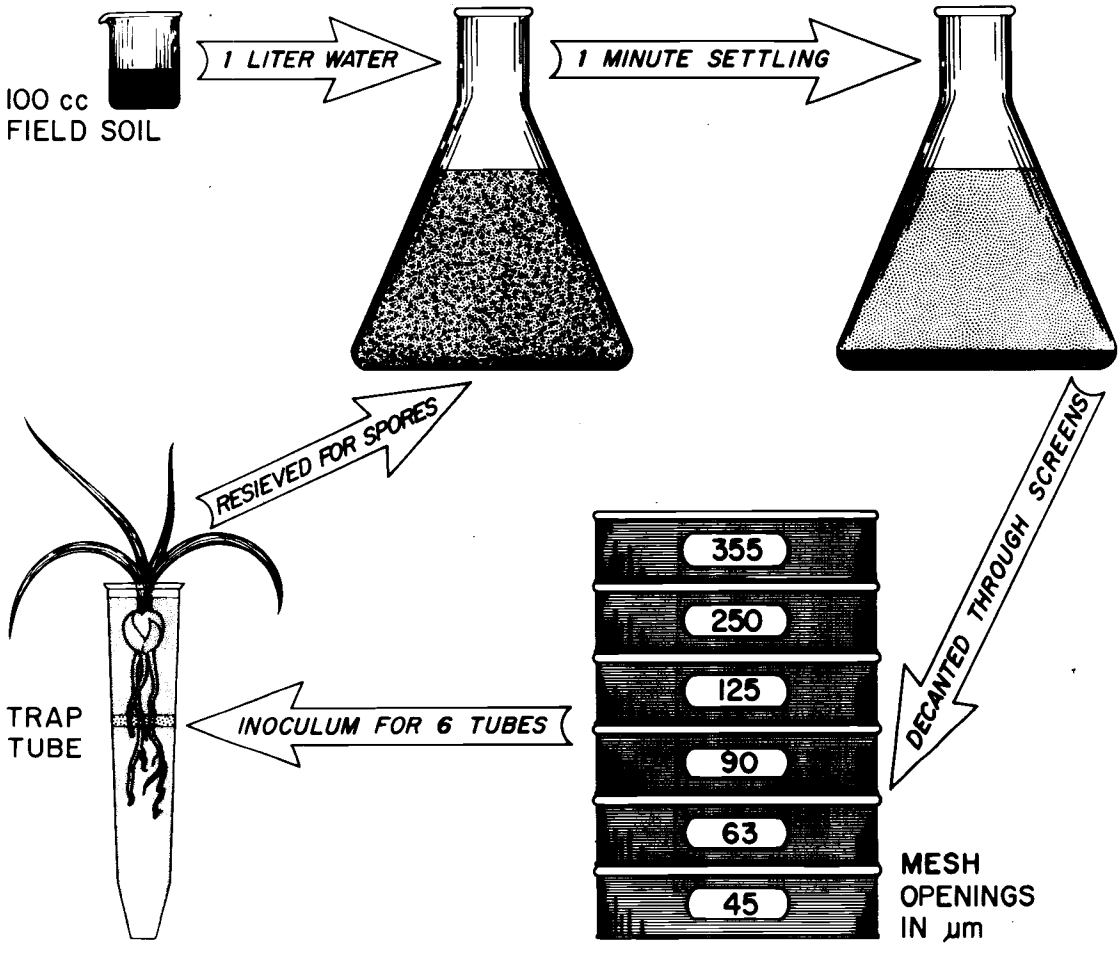

Figure 1. Methods used to collect mycorrhizal inoculum from field soil and increase spores in trap tubes for identification.

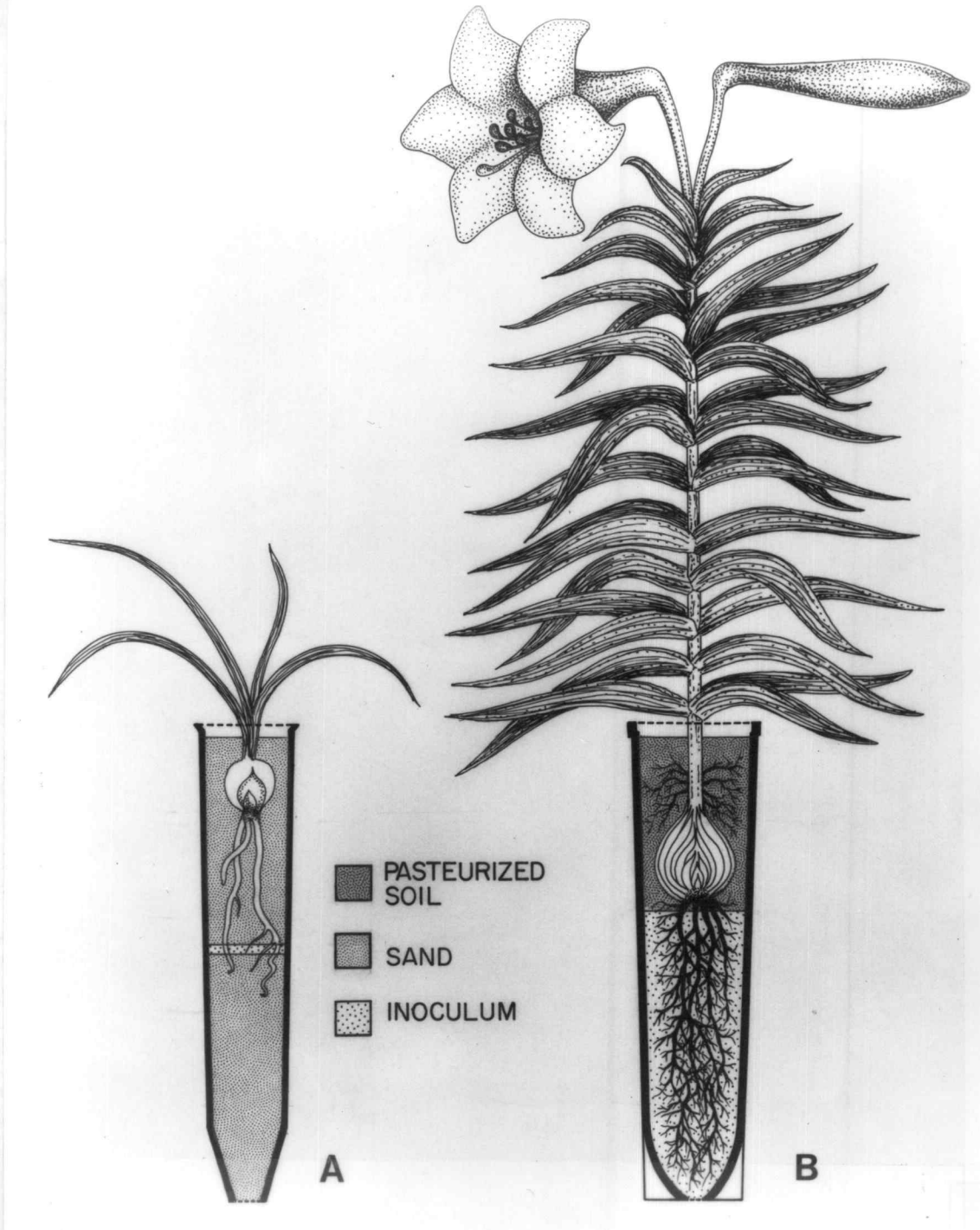

Figure 2. Diagram of inoculum placement in a trap tube (A) and 'Dee-Pot' (B).

was set for a 14 hour photoperiod with a day temperature of 23° C (75° F) and a night temperature of 18° C (65° F). Plants were given about 5 ml of 1/2 strength Hoagland's solution once a month. After four to five months, trap tubes were checked for mycorrhizal development. One-half of the total number of trap tubes were sieved to recover the newly formed spores. The whole root system from each tube was cleared and stained to reveal the presence of mycorrhizal infection. The remaining half of the tubes were left for later experiments.

B. Results and Discussion

Mycorrhizal Species Found in Lily Fields

Four different VA mycorrhizal species were identified (Ames et al., 1976a) according to the system of Gerdemann and Trappe (1974). One of the species had not been previously found and has now been described as *Acaulospora trappei* Ames & Linderman (Ames & Linderman, 1976b). Another species which was identified was *Glomus monosporus* Gerdemann & Trappe which occurred in three fields, A, B, and D. *Glomus fasciculatus* (Thaxter sensu Gerdemann) Gerdemann & Trappe was identified from all five fields. *Acaulospora elegans* Trappe & Gerdemann was found in fields A, B, and D. *A. trappei* was isolated from all five fields. The spore types listed were not found in every field from each monthly soil sample. All four VA

species infected the roots of onion, lily, and clover. None of the control plants became mycorrhizal. The four spore types are shown in Figure 3.

Whole plants removed from the field failed to produce any spores after transferring to the greenhouse. A. trappei and G. fasciculatus were the most frequently isolated species from all five field sites. It is presumed, therefore, that these are the main species that infect lilies in the field.

The original purpose of sieving the field soil was to separate and increase numbers of each spore type by size classes. Only the largest spores, A. elegans and G. monosporus, were consistently separated out in the larger meshes. A. trappei inoculum was sieved out at all meshes either in the form of spores attached to plant debris or as hyphal inoculum or spores within small root fragments. Individual A. trappei spores either with or without the attached vesicle were usually caught in the 63 or 45 μm screens when no debris was attached. G. fasciculatus was found as individual spores, but occurred most often in clusters of variable size, so it too was found in all meshes.

No spores were found from tubes in which the trap plant did not become mycorrhizal. Mycorrhizal colonization of the trap plants was more frequent and diverse from soil samples taken towards the end of the growing season. These findings are in agreement with Mason's

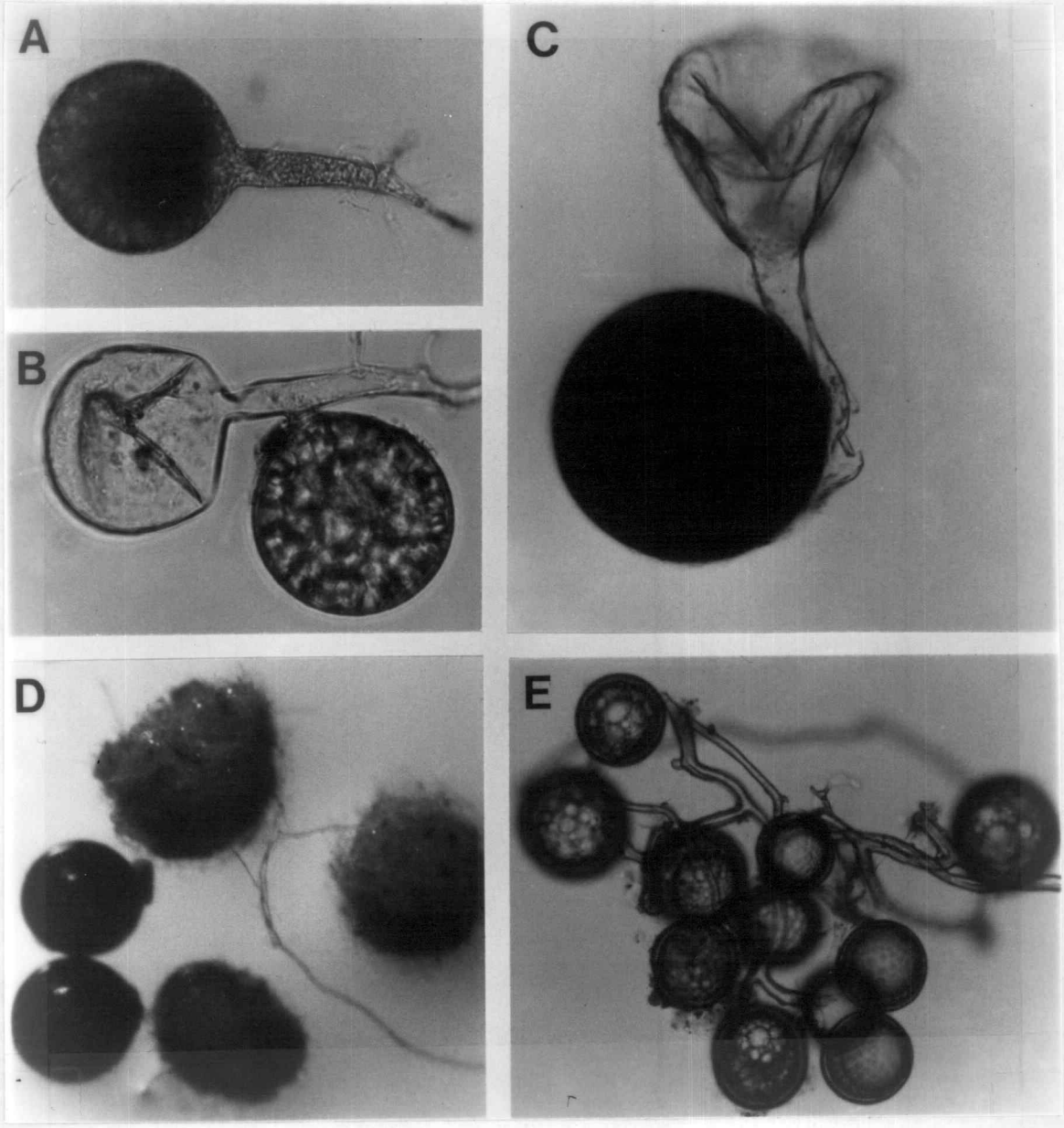

Figure 3. Species of VA mycorrhizal fungi found in Easter lily fields. (A-B) Acaulospora trappei X 250. (A) Young vesicle prior to spore formation. (B) Mature spore with empty vesicle attached. (C) Acaulospora elegans with empty vesicle attached X 125. (D) Glomus monosporus showing spores with and without hyphal mantle X 31. 2. (E) Glomus fasciculatus spore cluster X 125.

(1964) work on soil from fields cropped with barley, raspberry, and strawberry. He found spore numbers to decrease with the production of new roots, and increase with cessation of root growth and the onset of senescence.

Gerdemann (personal communication) suggested that the one minute settling time allowed after mixing the field soil with water may have been too long. Other workers have allowed as much as two minutes and found that 20-70% of the spores from a given sample were less than 100 μm in diameter (Sutton and Barron, 1972). It is quite reasonable that longer settling times will select for the smaller, more buoyant spore types. Although A. trappei is among the smallest spore types of the Endogonaceae and remains suspended in water for a long time, larger, less buoyant species such as G. monosporus and A. elegans were also recovered.

Many workers fail to screen for mycorrhizal spores below the 100 μm mesh screen (Mosse, 1968b; Hayman, 1970; Khan, 1971; Daft and Nicolson, 1974). Many new species may have been overlooked, especially in studies as extensive as the one conducted by Mosse (1968b). Nemec (1974) made this same observation and sieved soil down to 45 μm. Gerdemann (1961) sieved soil down to 44 μm, but neither he nor Nemec encountered A. trappei. Vozzo (1969) failed to find many spores unless meshes below 100 μm were used for wet sieving.

Analysis of field soils for the presence of VA mycorrhizal species has sometimes uncovered only one or two species (Mosse, 1968b; Hayman, 1970; Schenck and Hinson, 1971; Khan, 1971). More frequently, however, three or four are found (Gerdemann, 1961; Hayman, 1970; Daft and Nicolson, 1974; Schenck and Kinloch, 1974), and occasionally five (Mosse, 1968b; Khan, 1971). The number of species in any field will be determined by its agricultural uses and many other factors (Gerdemann, 1968; Mosse, 1973b, 1975).

The cleared and stained roots of trap plants did not reveal any unusual structures. All mycorrhizal species produced vesicles and arbuscules in each infected host. Some interesting observations were made, however, concerning root infection by A. trappei. Spores with the vesicle still attached were frequently observed inside the roots of trap plants. Because of the method in which A. trappei spores are formed, it is relatively easy to distinguish between a spore and an internally produced vesicle in a stained root. With other VA species, especially of the genus Glomus, this is more difficult or impossible. Another interesting observation made was of the formation of A. trappei spores inside clover root nodules. The nutrient stress under which these plants grew may have had an influence on where the spores were formed. No arbuscules were ever observed in clover nodules. Bevege (1975) suggested that infection of legume nodules by VA mycorrhizal fungi may occur only "with difficulty."

Progress of Field Root Infections

Monthly root samples from each field were cleared and stained to evaluate the progress of VA mycorrhizal root colonization. Hyphae entered lily roots primarily through root hairs. This method of root entry is common (Gerdemann, 1968; Daft and Nicolson, 1974). Vesicles and arbuscules were found to be abundant in stem roots and basal roots, but not in the large contractile roots of field grown plants (Ames et al., 1976a). Contractile roots of seedlings were observed in other experiments to become infected but only for a short time. This colonization disappears when root compression begins. Vanderploeg (1972) observed few infections of stem roots and occasional infections of contractile roots of lily seedlings grown in the greenhouse.

Only young, very restricted infections were found in March. As the season progressed, the total percentage of VA root colonization increased until September when the bulbs were harvested. Hayman (1970) found similar results in wheat where infections were sparse in May and steadily increased to a peak in September. In fields with four VA species, the percentage of root colonization exceeded 75% of the total root system, while fields with only two species rarely reached more than 50%. VA mycorrhizal infection of roots progressed slower in fields C and E where only two species were found.

Cultural Practices and Their Possible Effects on Mycorrhizae

Roberts et al. (1964) studied lily growth in the Oregon-California area. They stated that management of the soil is similar in all fields, but that use of fertilizer varies considerably. The adverse effects of high levels of fertilizer on VA mycorrhizae are well known. This may have been one selective factor influencing which VA mycorrhizal species occurred in each field. Roberts et al. (1964) also stated that large differences in bulb yields have been observed, even though none of the fields had nutrient deficiencies. Mycorrhizae may have influenced these yield differences.

Lilies may be plagued by many pathogens. Treatments to control pathogens may also affect lily mycorrhizae. Nematodes are usually controlled by nematicides. This practice has been shown to enhance mycorrhizal activity (Bird et al., 1974; Rich and Bird, 1974). Fungicides such as Terraclor (PCNB) are used as a bulb treatment to inhibit some fungal pathogens. This fungicide was shown to be the most harmful of those tested on mycorrhizal development of corn (Nesheim and Linn, 1969). Menge et al. (1976) has shown that PCNB can reduce spore production of Glomus fasciculatus from 70-90% depending on the time of fungicide application. PCNB can also reduce phosphorus accumulation by mycorrhizal onion plants (Gray and Gerdemann, 1969). Other fungicides, especially

those used against phycomycetous species, may also kill mycorrhizal fungi. Pfleger and Stewart (1976) stated that the fungicides Banrot and Pyroxychlor significantly reduced chlamydospore production by Glomus mosseae (Nicol. & Gerd.) Gerdemann & Trappe, but not G. fasciculatus.

It is possible that VA fungi can be carried from field to field in roots of planting stock. However, no mycorrhizae were observed in root fragments remaining on untreated bulbs after harvest. These roots consist mainly of portions of large, non-mycorrhizal, contractile roots. As a further test, 20 untreated bulbs, with typically fragmented roots attached, were removed from a storage crate after cold treatment. They were planted in a pasteurized soil mix and grown in the greenhouse for four months. The entire root system of each plant was cleared and stained. No mycorrhizal infection was found in any of the root systems.

The selection of cover crops may influence the levels of mycorrhizae prior to lily planting. Kruckelmann (1975) reported that different crops greatly influenced the total population of mycorrhizal spores. Some crops may not become heavily infected and therefore would not produce many spores. Fields A, B, and D, with periods of two or three years between lily plantings maintained a more diverse spore population, and better VA root infections than fields C and E with one and five years of rotation time (Table 1). Kruckelmann (1975) stated

that crop rotation "had no effect on the frequency of spore types in the soil." Many other factors may have influenced the relative amounts of mycorrhizae in addition to rotation period in these fields, however.

Table 1. Mycorrhizae in relation to cultural practices in the five lily fields studied.

Field	No. of VA species	Most common species[a]	Fertilizer (N-P-K)	Yrs. rotation		Over 75% VA colonization[b]
				cover	lily	
A	4	At	6-20-20	2	1	*
B	4	At	12-12-12	3	2	*
C	2	Gf	6-20-20	1	1	
D	4	At, Gf	6-20-20	2	1	*
E	2	At	7-26-26	5	1	

[a] At = Acaulospora trappei, Gf = Glomus fasciculatus

[b] More than 75% of the root systems of field-grown plants became mycorrhizal.

A Rhizoctonia sp. Infecting Lily Roots

While observing mycorrhizae in lily roots, another fungus was frequently encountered on field material. This fungus is apparently an unnamed species of Rhizoctonia. Figure 4 shows the structures this fungus forms in soil, agar, and in lily roots. The fungus was also observed to infect test plants of onion, clover, wheat, and lily when inoculated with 'spore' clusters sieved from soil. None of these hosts showed any apparent pathogenic effects. It was readily cultured on potato dextrose agar, corn meal agar, V8 agar, and it grew slowly on water agar. Branched chains of cells are formed in culture, in the

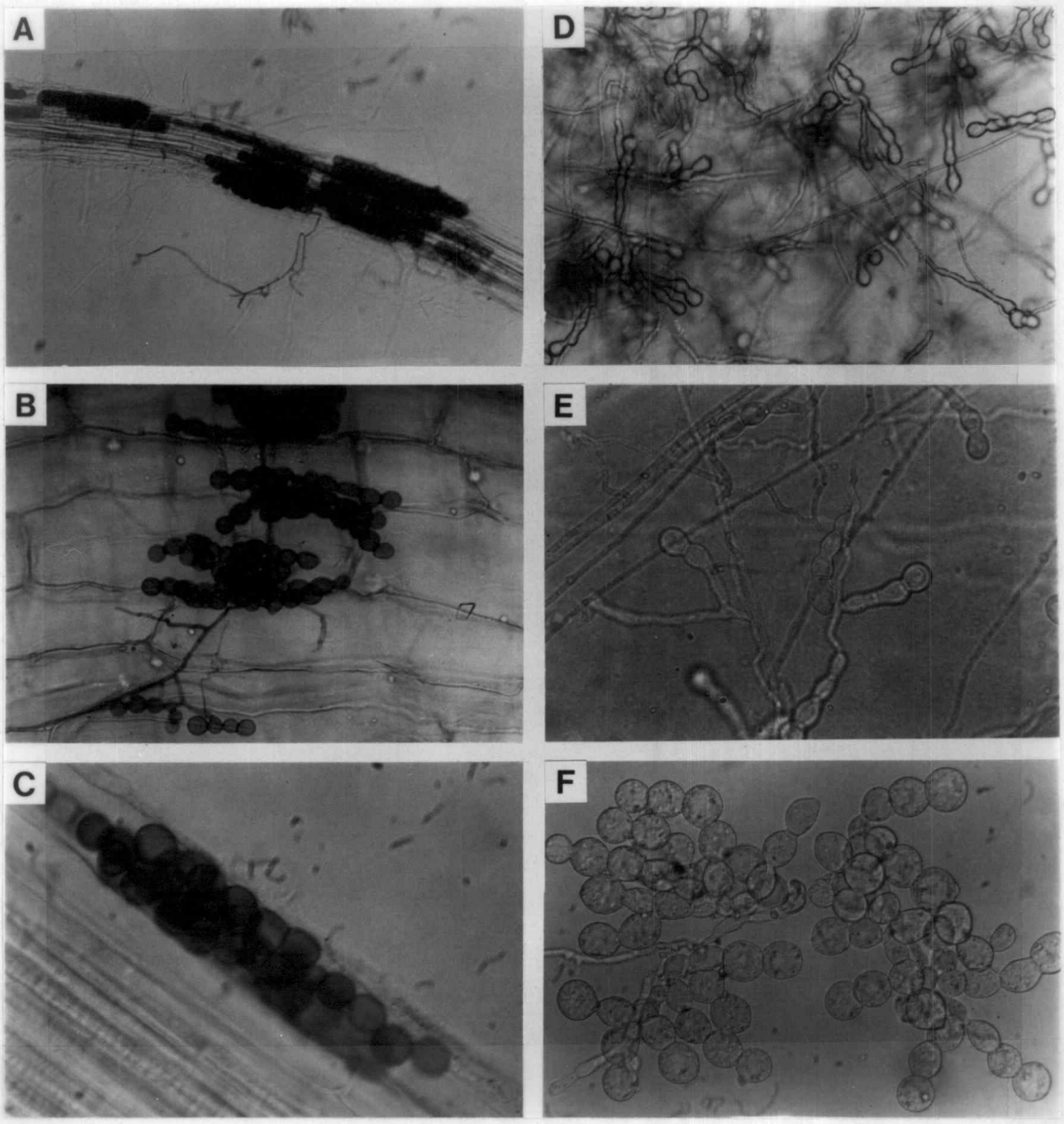

Figure 4. Spore-like structures of a Rhizoctonia sp. found infecting lily roots in the field. (A-C) In cleared and stained roots. (A) Heavily infected root X 100. (B) On root surface X 200. (C) In root cortical cell X 400. (D-E) Fungus grown on PDA. (D) X 200. (E) X 400. (F) Spore-like cluster sieved from soil X 400.

soil, and in root cells. These structures often completely fill root cortical cells and infection is usually restricted to the outermost cells. Hyphae are irregularly septate 3.5 to 8.1 μm in diameter. The usual septations near hyphal branches formed by many Rhizoctonia species do not occur with this fungus. Spore-like cells measuring 6.0-18.4 × 11.5-23.0 μm can be detached from the chain. Warcup (personal communication) suggests that this fungus is very likely a Rhizoctonia sp.

Peyronel (1923) observed a very similar fungus. Rayner (1926) summarized the findings of Peyronel, stating that it was observed frequently in plants belonging to 37 different families. Both this fungus and VA mycorrhizal fungi were observed in the same root system of many plants. Peyronel also reported that the Rhizoctonia-like fungus "behaves rather as a quasi-parasite or saprophyte than as a true symbiont..." Truscott (1934) has photographed and described a very similar fungus causing a root rot on strawberry. Hildebrand (1934) described a Rhizoctonia from strawberry which he called an "orchid type" and which formed "monilioid chains resembling chains of conidia." Koch (1935) reports on an "orchid type" Rhizoctonia which causes root necrosis on tobacco. Spores were reported as forming groups which sometimes fill cortical cells. Hildebrand and Koch (1936) photographed and described an orchid type Rhizoctonia which resembles the fungus found on lilies. They

stated that the orchid type did not belong to the Rhizoctonia solani group, and was apparently not pathogenic. Even in heavily infected roots, the orchid type of Rhizoctonia caused very little discoloration or disorganization of tissue.

More recently, Nicolson (1959) encountered the same Rhizoctonia-like fungus while studying the VA mycorrhizae in the Gramineae. He (personal communication) suggested that the fungus observed in the lily study may be Rhizoctonia fragariae Husain & McKeen. Black and Sangawongse (1969) thought R. fragariae might be a mycorrhizal fungus. Husain and McKeen (1963) and Riberiro and Black (1971) have shown R. fragariae to be a pathogen on strawberry. Under certain conditions, however, it may be non-pathogenic or mycorrhizal (Ribeiro and Black, 1971). It was necessary, therefore, to determine if the fungus isolated from lily was R. fragariae and if it could function as a beneficial root endophyte. A culture of R. fragariae was kindly provided by Dr. W. E. McKeen. After a thorough microscopic and cultural comparison of the lily isolate and R. fragariae, it was determined that they were not the same fungus. Husain and McKeen (1963) listed several Rhizoctonia species which differed only in spore size from R. fragariae. It is possible that the Rhizoctonia sp. found infecting lilies and other hosts in this study is an undescribed species. Due to the unsettled state of Rhizoctonia identification and lack of dependable distinguishing characteristics

of many of these fungi, a species name was not attached.

It was still necessary to determine what effects this fungal endophyte has on lily growth. The results of an artificial inoculation are reported in the following sections.

III. GREENHOUSE GROWTH EXPERIMENTS

A. Introductory Remarks

Mosse et al. (1969) showed that onions inoculated with VA mycorrhizae grew better than non-inoculated plants in unsterilized soil. Vozzo (1969) claims that natural soil inoculum containing both mycorrhizal and non-mycorrhizal fungal species benefit plant growth more than the isolated mycorrhizal fungi. Two experiments were conducted to test the effects of lily field isolates of VA mycorrhizae on the growth of Easter lily. Experiment #1 used a mixed inoculum of four mycorrhizal species and many other pathogenic and non-pathogenic organisms that might be found in lily fields. Experiment #2 tested the effects of a single mycorrhizal species on lily seedling growth in the absence of other pathogenic organisms.

High levels of fertilizer inhibit VA mycorrhizal infection (Hayman, 1975), but small amounts of nutrients added to very nutrient deficient soils can increase mycorrhizal infection (Mosse, 1973b). Three fertilizer levels (high, low and no additional fertilizer) were applied to the plants in experiment #1 to test their effects on lily growth and mycorrhizal infection.

B. Materials and Methods

Experiment #1: A Lily Growth Experiment Using a Mixed Inoculum

The sand from half of the trap tubes from the trap tube experiment was combined after most of the roots were removed. This sand contained VA mycorrhizal spores, some root fragments, and other unknown fungi and bacteria which might have infested the field soils from which the original inoculum was collected. The sand inoculum was diluted 1:2 with a pasteurized mix of sand, soil, and hemlock bark (3:1:1). After thorough mixing, the inoculum was divided into two portions. The roots from the trap tube plants were cut into segments about 2.5 cm long and blended into one of the inoculum portions. This gave a high level of mycorrhizal inoculum with root segments, and a low level without roots. Each pot given mycorrhizae received 400 cc of inoculum. This amount of the low level of inoculum contained about 200-300 spores of A. trappei, approximately eight of A. elegans, 28-48 of G. fasciculatus, and about eight to ten spores of G. monosporus. The high level of inoculum contained this same approximate number of spores with the addition of any spores and fungal hyphae that were inside the 3-4 gm fresh weight of added root material.

Several mycorrhizal species often occur together in cultivated fields (Mosse, 1968b; Gerdemann, 1961; Hayman, 1970; Khan, 1971),

yet most growth response experiments use only one species. Powell (1975) found no significant differences in ^{32}P uptake with onion or clover using seven different mycorrhizal species. Mosse (1973b, 1975) states that some VA species may benefit a host more than others. It was not determined which, if any, of the species found in lily fields affect Easter lily growth the most. Since three of the five fields contained four VA mycorrhizal species, they were all included in the mycorrhizal inoculum.

Control plants were inoculated with a solution obtained by sieving the mycorrhizal inoculum to remove all VA mycorrhizae spores. This was prepared by mixing 1000 cc of inoculum in 5 liters of distilled water and passing the solution twice through a 38 μm mesh screen. A 100 ml volume of this solution was poured over the 400 cc of pasteurized soil mix in each control pot. The reason for inoculating the controls with a sieving solution was to add the same microbial complex (except mycorrhizae) in the controls as that found in the plants inoculated with VA mycorrhizal inoculum. The 38 μm mesh screen did not sieve out bacteria or the spores of other non-mycorrhizal fungal species. Bowen and Rovira (1966) showed that non-sterile tomato and clover plants had a higher total uptake of phosphorus in roots and tops than sterile grown plants. Harley (1969) lists several types of inocula used for controls in mycorrhizae studies. Gerdemann (1964, 1965), Marx et al. (1971), and Rhodes and Gerdemann (1975)

used similar sieving solutions to inoculate control plants.

The Rhizoctonia-like endophyte was included in this experiment to determine its effects on lilies. Inoculum was made by growing the fungus for two weeks on V8 agar in petri plates. Three discs of agar were cut with a #5 cork borer from the edge of each colony, and were pressed into the 400 cc of pasteurized soil about 2 cm below the lily bulb.

Yearling 'Ace' bulbs were harvested from field A in September, 1975. They were placed in the cold room at 5° C until April, 1976. The 180 bulbs used in this experiment were scaled down to a 17-25 gm fresh weight and surface sterilized in 10% Clorox for 15 minutes. Each bulb was numbered and its weight recorded.

The pots used in this experiment were 'Dee-Pots' (7.0×25.5 cm), available from the Crown-Zellerbach Co., Aurora, Oregon. Racks were constructed to hold the pots so that the plants would be 10 cm apart. Inoculum and bulbs were placed in the pots as follows (Figure 1B); 400 cc of soil mix infected with mycorrhizal inoculum (or pasteurized soil mix for the Rhizoctonia tests and all controls) was placed in each pot. The bulb was placed on the 400 cc of base soil (inoculated or not), and then covered over with pasteurized soil so the bulb was about 5 cm below the surface. All plants were given a number to correspond with the bulb weight, inoculum type, and fertilizer level. The plants were completely randomized on the

greenhouse bench (Figure 5) and randomized again half-way through the experiment. There were ten replications each of the high, low and no fertilizer applications for each of the inoculum groups. The five groups were: 1) high VA mycorrhizae-inoculated, 2) low VA mycorrhizae-inoculated, 3) sieving solution inoculated controls, 4) non-inoculated controls, and 5) Rhizoctonia sp.-inoculated. Extra plants were grown for each type of treatment as replacements for plants that failed to emerge.

Rockwell et al. (1961) suggested the use of a 5-10-5 NPK fertilizer on greenhouse grown lilies. Mohr (1973) used a 20-20-20 or 15-30-15 NPK formulation with good results. In this study, a 20-20-20 soluble fertilizer was applied at rates above and below the suggested dosage for greenhouse potted plants. The high fertilizer level was applied at the rate of 1 1/2 tablespoons/gallon water. The low level application was at 1/2 tablespoon/gallon water. The remaining ten plants from each group received only water. When plants were about 2.0 cm above the soil surface, they were given three weekly fertilizer applications. After that, the applications were biweekly for two months. Nutrient solution was applied until it drained through to prevent salt build-up. The leached solution from several plants was checked after each fertilizer application with a Myron L. Delux Dissolved Solids Meter, Model 532.

This experiment was started in April, 1976, and ended in

Figure 5. Lily growth experiment #1 showing placement of plants in the greenhouse.

August, 1976. Greenhouse temperatures varied from 18° C (65° F) to 32° C (90° F). Supplemental lighting with high pressure sodium vapor lamps was supplied at intensities of 12,000 lux each day for 12 hours from 6:00 AM to 6:00 PM. Occasional sprays were applied as needed to control aphids.

Growth Parameters Measured in Experiment #1

The surface area of the 15 uppermost leaves, the increase in bulb fresh weight, and the root volume of each plant was measured to determine plant growth. Leaf surface area was measured by a Lambda Li-Cor Portable Area Meter, Model LI-3000. The remaining leaves for each treatment were bulked for tissue analysis. The leaf tissue analysis was conducted by the Plant Tissue Analysis Laboratory, Department of Horticulture, Oregon State University. The final bulb fresh weight was taken after roots and stems were removed. The volume of the entire root system of each plant was measured by water displacement. Safir et al. (1972) also used this method to compare root growth. The whole root system was cleared and stained to observe mycorrhizal and Rhizoctonia sp. infections. The percentage of mycorrhizal infection was estimated visually by observing the entire root system under a dissecting microscope at 7.5X. Rhizoctonia-inoculated and control plant roots were assessed qualitatively for relative amounts of infection. Other methods have

been used to assess the amount of mycorrhizal infection by the amount of yellow pigmentation present in roots. This is not practical with Easter lily since a yellow pigment is not associated with the presence of mycorrhizae. Another method, counting the numbers of spores produced in each pot, would have been extremely difficult, especially since four mycorrhizal spore types were present in the inoculum. A method was developed, however, to count the number of A. trappei spores in a soil sample. If the soil sample is mixed in about three times its volume of lactophenol, and allowed to stand for a few hours, all the A. trappei spores will turn clear and gather at the meniscus. The soil and plant debris will sink to the bottom of the container.

Isolation of Fungal Root Pathogens

Isolations were made from root systems of extra experimental plants on plates of potato dextrose agar (PDA). Roots of plants given high and low fertilizer from all treatments except the low mycorrhizae level were used. No additional plants were available from this treatment. The root systems were washed and surface sterilized in 10% Clorox for ten minutes. Forty randomly selected root segments, 0.5-1.5 cm long, were cut from each root system and eight segments were placed in each of five petri plates of PDA. The cultures were stored at room temperature and checked frequently. Hyphal tips were removed from near each root segment as soon as

they were observed and transferred onto separate PDA plates.

Experiment #2: A Lily Growth Experiment Using A. trappei

Ten flats (14.5×14.5×6 cm) were filled 2/3 full with a pasteurized mix of 3 sand: 1 soil: 1 hemlock bark. Five flats were inoculated with A. trappei and five with a sieving solution. The A. trappei inoculum contained about 300 spores, root fragments, and soil in a 50 gm fresh weight amount that went into each mycorrhizae inoculated flat. This inoculum was mixed into the soil of each test flat with a glass rod. The A. trappei inoculum was removed from a six month old pot culture of red clover. A sieving solution was made by thoroughly mixing about 100 cc of mycorrhizal inoculum in 1 liter of distilled water and passing this suspension through a 38 μm mesh screen twice to remove A. trappei spores. A 50 ml aliquot of the sieving solution was poured over the surface of the five control flats.

Seed of Easter lily 'Ace' × 'Nellie White' which had been previously collected and stored at 5° C, was used in this study. The soil surface in each flat was covered to a depth of about 0.5 cm with autoclaved peat moss. Lily seed was scattered on this and covered over with another 0.5 cm layer of peat moss. The flats were placed under a mist system until the seeds germinated (about one month). The flats were then randomized on a greenhouse bench, given supplemental

lighting for 12 hours daily, and grown for three and one-half more months. All plants were fertilized with a solution of 20-20-20 NPK soluble fertilizer (1/2 tablespoon/gallon water) every other week. Occasional sprays were applied to control aphids.

At the end of the experiment, ten plants of uniform size were selected from each flat (50 plants per treatment). The root systems of all plants were examined under the dissecting microscope for the presence of mycorrhizae. Some of the controls had become contaminated with VA mycorrhizae and were replaced with non-mycorrhizal control plants. Each plant was washed, blotted dry and the fresh weight of the whole plant, the root system alone, and the top was recorded. The top weight consisted of the leaves and the small bulblet.

An analysis of variance was performed on the data from experiments one and two, and differences were compared with the appropriate LSDs. All root systems were cleared and stained to reveal the presence of mycorrhizae.

C. Results

High vs. Low Mycorrhizal Inoculum (Experiment #1)

Based on a percentage estimation of the degree of mycorrhizal infection in the root systems, the high level of inoculum gave a

significantly larger (P=. 01) amount of infection than the low level (Table 2). This difference was observed only at the high and low level of fertilizer. The differences were not significant (P=. 05) when no fertilizer was applied. Fertilizer greatly influenced root infection by mycorrhizal fungi (Figure 6). The amount of infection averaged 63% in plants given the low fertilizer level, 13% in plants given the high fertilizer level, and 3. 3% in those plants given no fertilizer. These differences were significant at the . 1% level.

Table 2. Percent of VA mycorrhizal colonization in lily roots.[a]

	High fertilizer	Low fertilizer	No fertilizer
High inoculum	21. 7**[b]	70. 0*	5. 5 ns
Low inoculum	4. 3	56. 0	1. 2

[a]Percent of the total length of the plant's root system which is micorrhizal.

[b]Means of ten plants are not significantly (ns) different, significantly different at the 5% level (*), or 1% level (**), from plants given the low level of mycorrhizal inoculum.

Mycorrhizal Plants vs. Controls (Experiment #1)

All of the mycorrhizae-inoculated plants became infected. None of the sieving solution inoculated controls became mycorrhizal. Control plants generally had a larger root volume than the mycorrhizal plants, but differences were significant (P=. 01) only with the high level of inoculum under high and low fertilizer, and the low inoculum

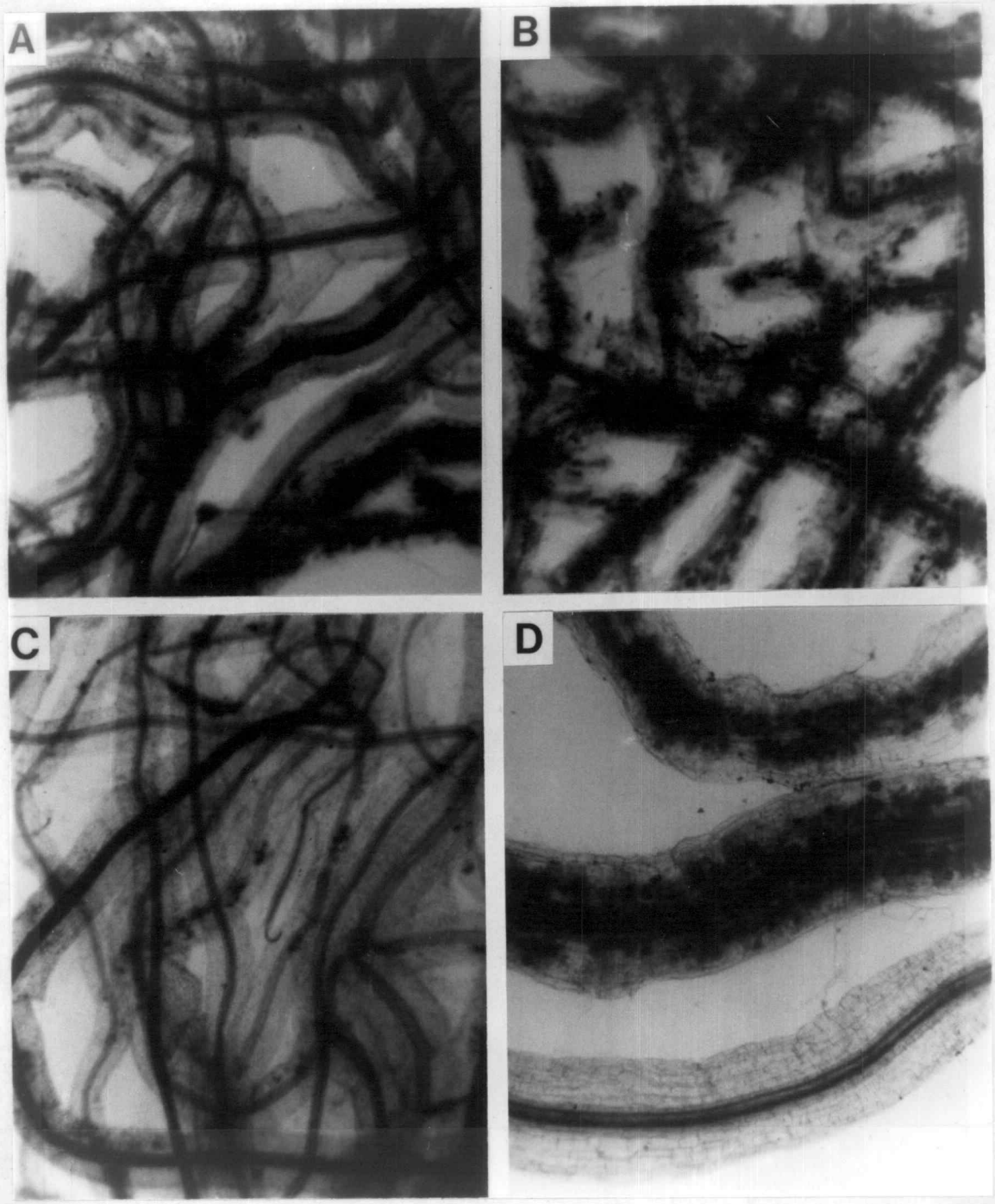

Figure 6. Cleared and stained lily roots showing effects of fertilizer on mycorrhizal infection. (A-C) X 15. (A) High fert. (B) Low fert. (C) No fert. (D) Mycorrhizal (top) and non-mycorrhizal (bottom) roots X 32.5.

level with high fertilizer (Table 3). Root volumes were somewhat larger with the low level of mycorrhizal inoculum than the high level. Plants given the low fertilizer rate had the largest root volumes. The high fertilizer rate apparently was toxic to the root systems and these plants had a lower root volume than the plants given no fertilizer (Figure 7).

Increases in bulb fresh weight were larger in the controls than with mycorrhizae inoculated plants. Weight differences were not significant ($P=.05$) with low fertilizer and low inoculum. There were no significant differences ($P=.05$) in bulb weights between the low and high inoculum levels. Bulb weights were larger ($P=.001$) when plants were given the lower fertilizer rate.

For the most part, there were no significant differences in leaf area between the controls and the high and low inoculum levels. There was no significant difference ($P=.05$) in the leaf area of plants given high or low fertilizer rates. However, plants not given any fertilizer had a much reduced ($P=.001$) leaf area.

Fertilizer rate had the largest effect on plant growth. Plants given the low fertilizer rate grew better than those given large amounts or no fertilizer. There were no large differences in the nutrient level of plant tissue other than that caused by fertilizer level. Plants given the high fertilizer rate showed leaf scorch symptoms. The root systems of these plants were small and lacking in fine feeder

Table 3. Lily growth response to a mixed inoculum of mycorrhizae and other organisms.

A. Root Volume (ml)

	High fertilizer	Low fertilizer	No fertilizer
High VA level	14.60**[a]	18.65**	18.50 ns
Low VA level	13.95**	24.60 ns	19.30 ns
Control	18.90	26.80	18.60

B. Bulb Weight Gain (gm)

	High fertilizer	Low fertilizer	No fertilizer
High VA level	13.90**	18.20**	8.58*
Low VA level	16.20*	21.60 ns	8.44*
Control	21.10	23.90	12.70

C. Leaf Area (cm^2)

	High fertilizer	Low fertilizer	No fertilizer
High VA level	109.88 ns	88.97*	69.53 ns
Low VA level	108.88 ns	111.68 ns	66.30 ns
Control	111.35	109.34	67.99

[a]Means of ten plants are either not significantly (ns) different from controls, or significantly different at the .05 (*) or .01 (**) levels of probability using LSDs.

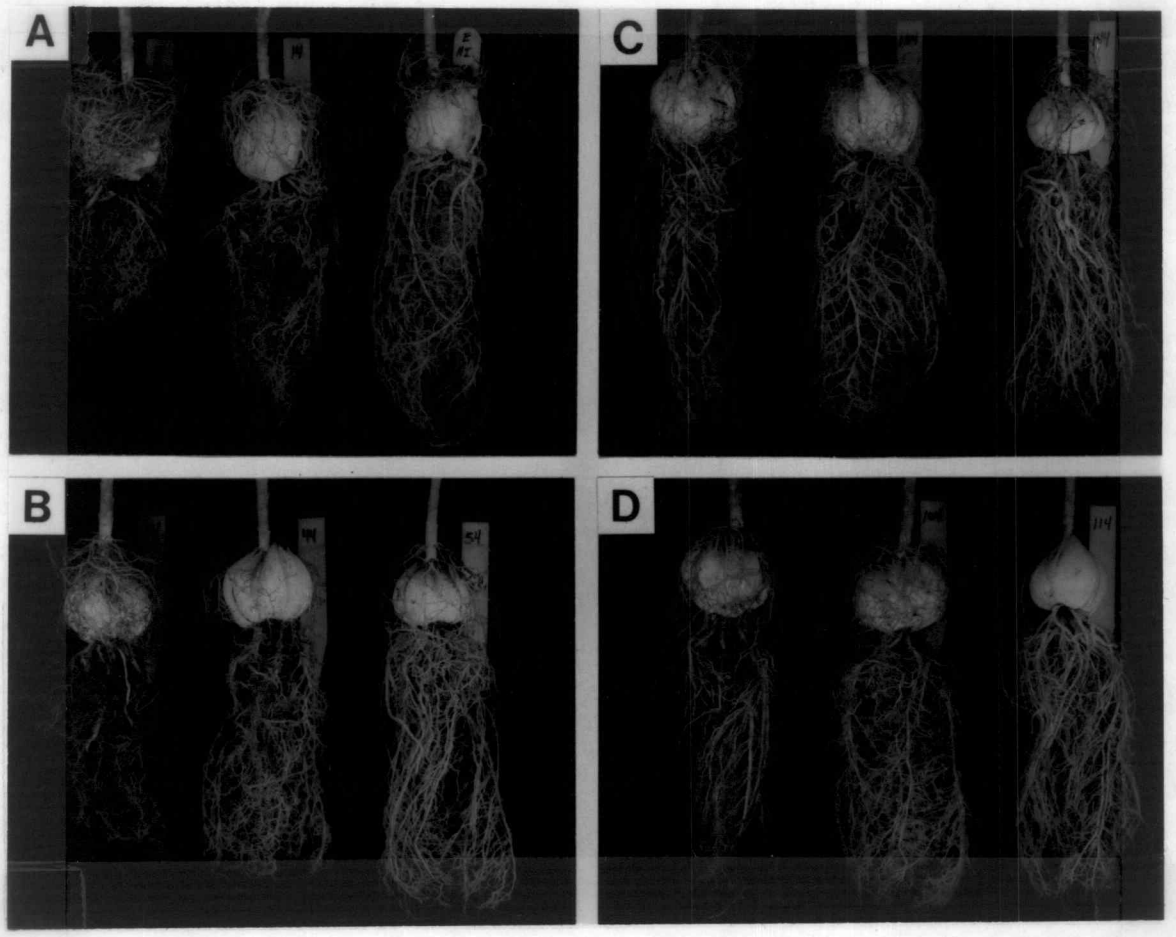

Figure 7. Bulbs and root systems from growth experiment #1. In each picture from left to right, plants were given the high fertilizer rate, low fert. rate, and no fert. (A) Plants given the high inoculum level. (B) Low inoculum level. (C) Sieving solution inoculated controls. (D) Non-inoculated controls.

roots. The root systems of plants given the mixed inoculum and high fertilizer developed several lesions which were apparently caused by pathogen attack.

Mycorrhizal Plants vs. Controls (Experiment #2)

Seedlings inoculated with A. trappei were significantly larger than the controls at the .1% level for all parameters measured (Table 4). Figure 8 shows examples of inoculated and control plant tops which were randomly selected from the 50 plants of each treatment. No pathogenic activity was observed. Some of the control plants had one or two small areas of mycorrhizal infection but this never amounted to more than 1% of the root system. All A. trappei-inoculated plants had over 75% of their root systems infected.

Table 4. Fresh weights (gm) of lily seedlings inoculated with A. trappei.

	Whole plants	Tops	Roots
Inoculated	.52[a]	.32[a]	.20[a]
Control	.38	.22	.16

[a]Inoculated seedlings were significantly greater than the controls at the .001 level of probability using calculated LSDs.

Nutrient analysis of the plant tops showed a slightly higher percentage of nitrogen, potassium, phosphorus, calcium, and

Figure 8. Lily seedlings from growth experiment #2. Plants inoculated with Acaulospora trappei (top) and controls (bottom).

magnesium in the mycorrhizal plants than in controls (Table 5). Vanderploeg (1972) reported higher levels of phosphorus, magnesium, potassium, and calcium in mycorrhizal over non-mycorrhizal lilies.

Table 5. Percent of nutrients in tops of control and A. trappei-inoculated lily seedlings.

	N	P	K	Ca	Mg
Inoculated	1.55	.42	3.20	.53	.44
Control	1.38	.37	2.68	.43	.34

Fungi Isolated from Lily Roots (Experiment #1)

Fusarium oxysporum Schlect was isolated from 40% of the root segments from the mycorrhiza-inoculated plants. Only 16% of the control plant root segments inoculated with the sieving solution were infected with F. oxysporum. No F. oxysporum was isolated from the non-inoculated or Rhizoctonia-inoculated plants. The Rhizoctonia sp. was not recovered on PDA but 'spore' clusters were observed in the soil sievings. A Trichoderma sp. was recovered from all treatments. An occasional colony of a Cylindrocarpon sp. was isolated from the mycorrhizae and sieving-solution inoculated root systems. No Pythium or Phytophthora species were isolated.

Rhizoctonia vs. Controls (Experiment #1)

Very little infection occurred in the Rhizoctonia sp. inoculated plants. Many of the control plants became infected with this fungus, but to a lesser extent than inoculated plants. Inoculated plants had a slightly larger root volume and bulb gain, and a smaller leaf area than controls. However, none of these differences were significant at the 5% level (Table 6). There were no significant differences ($P=.05$) between high and low fertilizer treatments in bulb weight gain or leaf area. Bulb weights and leaf area were significantly ($P = .001$) reduced when no fertilizer was applied. The root volume was larger ($P=.001$) at the low fertilizer level than those plants given high or no fertilizer. There were no differences in the nutrient analysis of the leaves due to inoculation.

D. Conclusions and Discussion

Effects of a Mixed Mycorrhizal Inoculum on Lily Growth

In experiment #1, lily plants inoculated with a mixture of mycorrhizal and non-mycorrhizal organisms did not grow as well as controls. Root volumes were significantly lower with the high level of inoculum. Safir et al. (1971, 1972) found no significant differences between the root volumes of mycorrhizal and non-mycorrhizal

Table 6. Effects of a Rhizoctonia sp. on lily growth.

A. Root Volume (ml)

	High fertilizer	Low fertilizer	No fertilizer
Rhizoctonia	21.0 ns[a]	31.2 ns	25.4 ns
Control	18.7	30.1	23.8

B. Bulb Weight Gain (gm)

	High fertilizer	Low fertilizer	No fertilizer
Rhizoctonia	22.4 ns	22.2 ns	11.1 ns
Control	22.0	22.7	10.4

C. Leaf Area (cm^2)

	High fertilizer	Low fertilizer	No fertilizer
Rhizoctonia	105.7 ns	115.0 ns	75.3 ns
Control	113.1	115.7	70.2

[a]Means of ten plants are not significantly (ns) different at the .05 level of probability.

soybean. Daft and Nicolson (1966) reported that growth benefits of mycorrhizal plants over non-mycorrhizal plants were highly significant when over 50% of the inoculated root systems were colonized. With the low rate of fertilizer, plants inoculated with the low level of inoculum had 56% of the root systems colonized, and an average of 70% with the high inoculum level, yet they did not grow as well as the controls. Growth depressions have been observed with up to 50% and occasionally 70-90% of the root system being mycorrhizal (Cooper, 1975). Cooper stated that these effects were often transitory, however. There are three possible explanations for the growth depression of lilies inoculated with VA mycorrhizae in experiment #1: 1) Mycorrhizae were pathogenic on lily. 2) Pathogens had increased on the trap plants along with the mycorrhizae and were transferred along with the mycorrhizal inoculum. 3) Mycorrhizae enhanced pathogen activity; the higher the level of mycorrhizae, the more severe the disease.

Mycorrhizal fungi have been reported to function as mild pathogens (Crush, 1973b), especially at high levels of available phosphate (Baylis, 1967). Baylis (1970) observed discolored and decayed roots of tea-tree after inoculation with VA mycorrhizae in a phosphorus deficient soil. The roots were estimated to be less than 10% colonized. No attempt was made to isolate pathogens from the root system. It seems unlikely that if VA mycorrhizae were pathogenic on lily, an

average of 56% root colonization would produce no significant differences from controls in root volume, bulb weight, and leaf area, while an additional 14% increase in mycorrhizae would give a highly significant ($P=.01$) decrease in all the growth parameters measured.

The root fragments in the high level of mycorrhizae inoculum contained a large amount of F. oxysporum infection. It is very likely that micorrhizae-inoculated plants did not grow as well as controls because of the presence of this organism in the inoculum. Sieving-solution inoculated control plants had a much lower level of F. oxysporum infection. Non-inoculated plants had significantly larger root systems than the sieving solution inoculated plants (Table 7). No F. oxysporum was isolated from the non-inoculated controls. Imle (1942) has shown F. oxysporum f. lilii to be pathogenic on Easter lily. This fungus has been found in all the fields where the initial soil inoculum was collected for this study. The pathogenicity of the Fusarium isolates cultured from lily roots is currently being tested on Easter lily seedlings. The results will not be reported here, but it is likely they are pathogenic since they were isolated from diseased roots.

There still remains the possibility that VA mycorrhizae can enhance pathogen attack on some hosts (Ross, 1972; Redding, 1973). Schenck and Kinloch (1974) did not observe any correlation between the numbers of mycorrhizae spores and the presence of F. oxysporum,

Table 7. Growth differences between non-inoculated plants and plants inoculated with a sieving solution.

A. Root Volume (ml)

	High fertilizer	Low fertilizer	No fertilizer
Sieving solution	18.9 ns[a]	26.7*	18.6**
Non-inoculated	18.7	30.1	23.8

B. Bulb Weight Gain (gm)

	High fertilizer	Low fertilizer	No fertilizer
Sieving solution	21.1 ns	23.9 ns	12.7 ns
Non-inoculated	22.0	22.7	10.4

C. Leaf Area (cm^2)

	High fertilizer	Low fertilizer	No fertilizer
Sieving solution	111.4 ns	109.3 ns	68.0 ns
Non-inoculated	113.1	115.7	70.2

[a]Means of ten plants are not significantly (ns) different, significantly different at the .05 (*) or .01 (**) levels of probability using calculated LSDs.

F. solani, or F. roseum associated with soybean roots. Further testing is needed with closer controls over the levels of Fusarium and mycorrhizae on lily.

Effects of Acaulospora trappei on Lily Seedling Growth

Evidence was given in experiment #2 for the increased growth of Easter lily seedlings due to mycorrhizal root infection. Vanderploeg (1972), using seed from two different lily species, was able to show marked increases in leaf area, bulb weights, size of root systems, and nutrient uptake in mycorrhizal over non-mycorrhizal plants. He obtained growth increases and mycorrhizal infection without the addition of phosphorus or potassium to the growing plants other than what occurred in the soil. The extent of mycorrhizal infection was not determined, however. Earlier in this report it was shown that infection in lily was repressed when no additional nutrients were applied. The levels of nutrient applied to A. trappei-inoculated seedlings appeared to encourage mycorrhizal infection.

Effects of Fertilizer on Lily Growth and Mycorrhizal Infection

Fertilizer had a larger influence on plant growth than did the type of inoculum. All plants given the high level of fertilizer showed signs of leaf scorch. Boodley (1967) has shown that high levels of

phosphorus and nitrogen are the probable causes of scorch. The soil of plants given the low fertilizer level contained 43 ppm available phosphorus near the end of the experiment. Plants given the high fertilizer rate had a soil phosphorus level of 103 ppm. Phosphorus levels of the lily field soils tested ranged from 46 to 136 ppm. Nutrients do not diffuse in potted soils as they do in the field, which may have accounted for the toxicity symptoms at phosphorus levels below those found in the field where scorch symptoms rarely are seen. The soil of plants given no fertilizer contained 7 ppm of available phosphorus.

High levels of phosphorus and nitrogen have been shown to inhibit mycorrhizal infection (Mosse, 1973a, 1973b). Crush (1973a) reported that most experiments with VA mycorrhizae have been carried out with soils that were very deficient in phosphorus and that plants grown under these conditions became so heavily colonized by mycorrhizae that a growth response was guaranteed. In experiment #1 there was a higher amount of VA root colonization in plants given the high fertilizer amount than those given no fertilizer, but the best infection occurred in plants given the low fertilizer level. Other workers have shown a variable response (Mosse, 1973b; Hayman, 1975) or no response (Holevas, 1966; Ramirez et al., 1975) of mycorrhizal plants under various nutrient levels. Mosse (1973b, 1975) states that some VA species may benefit a host more than others.

In contrast to this, some hosts may benefit more than others from infection by a particular VA mycorrhizal species. Thus a plant nutrient response will differ according to the plant type, VA mycorrhizal species, and the nutrient level in the soil. Some plants may be more dependent on mycorrhizae than others and therefore different responses to nutrients are expected. Gerdemann (1975) defines mycorrhiza dependency as "the degree to which a plant is dependent on the mycorrhizal condition to produce its maximum growth or yield, at a given level of soil fertility."

Effects of a Rhizoctonia sp. on Lily Growth

From the observations made on the Rhizoctonia sp., it appears to be non-pathogenic on Easter lily. Although many outer root cortical cells may become completely filled with the spore-like structures, no discoloration or root destruction has been associated with this fungus. Further testing is needed at lower temperatures and in the field.

IV. SUMMARY AND GENERAL DISCUSSION

Field grown Easter lilies become infected with VA mycorrhizal fungi. These infections occurred prior to March and steadily increased until September when bulbs were harvested. Four different VA mycorrhizal species have been found in commercial lily fields: Acaulospora trappei, A. elegans, Glomus fasciculatus, and G. monosporus. A. trappei and G. fasciculatus were the most frequently isolated species from the five fields studied. The basal root laterals and stem roots of lily become heavily infected in the greenhouse and in some fields. Lilies in fields with few mycorrhizal species and where excessive fertilizer is used do not become heavily infected with mycorrhizae. The type of cover crop and rotation period may also affect the extent of mycorrhizal infection in lilies.

Greenhouse experiments showed that VA mycorrhizal infection is reduced by high or no fertilizer applications, but increased at low fertilizer levels. Fusarium oxysporum was present in the mycorrhizal inoculum and was the probable cause of the growth reduction in mycorrhizae-inoculated plants in experiment #1. High fertilizer appeared to enhance root disease. The Rhizoctonia sp. is apparently not beneficial or harmful to lilies.

Older lily plants may not be too dependent on mycorrhizae because they have large nutrient reserves stored in their bulbs which

may be drawn upon in times of stress. Seedlings inoculated with A. trappei grew better than controls and had higher levels of N, P, K, Ca, and Mg. Lily seedlings may be more dependent on mycorrhizae for the accumulation of nutrients required for bulb and leaf formation. Heavy mycorrhizal infection early in the plant's growth, and continued infection in the field, may be reflected at bulb maturity in plant size, number of flowers, and size of daughter bulbs.

Many cultural practices need to be investigated to determine how good plant growth and high mycorrhizal populations can be maintained. For example, how necessary is the placement of superphosphate directly under the bulb at planting time? This practice will probably prevent early season mycorrhizal colonization, although it should not kill the fungal inoculum (Mosse, 1973a). Daft (1969) stated that mycorrhizae may not be important to agricultural crops when good levels of fertility are maintained. With the increasing costs of fertilizer, how expensive will it become to maintain good fertility? If field inoculation with VA mycorrhizae should become more practical (or necessary) then perhaps fertilizer costs can be lowered.

The questions of which mycorrhizal species should be used and how field inoculation could be performed are unanswered. Field inoculation with native and non-native VA mycorrhizal species has been reported to improve the growth of some crops (Mosse, 1973b,

1975; Mosse and Hayman, 1971; Mosse et al., 1976). Khan (1972, 1975) has shown that pre-inoculated corn and wheat will grow better after transplanting to the field than field-seeded plants. This method may work well with Easter lily seedlings, especially if they were transplanted to fumigated fields and ideal fertility levels were established. Not enough mycorrhizal inoculum is carried with planting stock to be effective. These bulbs must also be treated for pathogens; the treatment probably kills any mycorrhizal fungi in the attached roots.

In addition to fertilizer usage and field inoculation, the interactions of lily mycorrhizae and pathogens should be investigated both in the greenhouse and the field. Special attention should be given to root pathogens such as F. oxysporum.

Vesicular-arbuscular mycorrhizae are not expected to be the 'cure-all' for nutrient uptake by Easter lilies or any other ornamental or food crop. All growers should become aware of their presence, however, and take advantage of the mycorrhizal association whenever possible.

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