Utilization of vesicular–arbuscular mycorrhizal fungi in agriculture

J. A. MENGE
Department of Plant Pathology, University of California, Riverside, CA, U.S.A. 92521
Received April 1, 1982

MENGE, J. A. 1983. Utilization of vesicular–arbuscular mycorrhizal fungi in agriculture. Can. J. Bot. **61**: 1015–1024.

Commercial use of vesicular–arbuscular mycorrhizae (VAM) may be an alternative to rising agricultural energy and fertilizer costs. Vesicular–arbuscular mycorrhizae may be able to increase crop yields while reducing fertilizer and energy inputs. Since mycorrhizal fungi are naturally present in most soils, their unique fertilizer abilities are already being utilized by most crop plants. Commercial uses of VA mycorrhizal fungi are therefore currently restricted to situations where the natural populations of VAM fungi have been destroyed or damaged such as in fumigated or chemically treated areas, greenhouses, and disturbed areas such as coal spoils, strip mines, waste areas, or road beds. Commercial production of VAM inoculum is presently being attempted at several locations in the U.S. Vesicular– arbuscular mycorrhizal inoculum is produced by growing VAM fungi on the roots of suitable host plants under aseptic greenhouse conditions The inoculum consists of the host-plant growth medium and host roots associated with VAM hyphae and spores which have been ground and dried. Most large-scale uses of VAM involve the establishment of the mycorrhizae on seedlings which will be transplanted to the field. Large-scale methods for direct inoculation with VAM have not yet been devised, but in small trials, layering, banding, broadcasting, and pelleting seed with VAM inoculum have proved effective. Methods for determining what soils are most likely to benefit from applications of VAM fungi are available. The potential for employing VAM fungi on a wide scale in agriculture is dependent on the development of crop growth-promoting strains of VAM which are superior to native soil populations of VAM fungi.

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L'utilisation commerciale des mycorhizes à vésicules–arbuscules (MVA) pourrait être une solution aux coûts croissants de l'énergie et des fertilisants dans le domaine agricole. Les MVA pourraient augmenter les rendements des cultures tout en diminuant les besoins de fertilisants et d'énergie. Puisque les champignons mycorhiziens sont présents naturellement dans la plupart des sols, leurs capacités fertilisantes uniques sont déjà utilisées par la plupart des cultures. L'utilisation commerciale des champignons à MVA est par conséquent restreinte actuellement aux situations où les populations naturelles de champignons à MVA ont été détruites ou endommagées, par exemple les sites fumigés ou traités par des composés chimiques, les serres et les endroits perturbés comme les terris de charbon, les mines à ciel ouvert, les terrains vagues et les abords routiers. La production commerciale d'inoculums de MVA est couramment à l'essai à plusieurs endroits aux États-Unis. Les inoculums de MVA sont produits en faisant croître des champignons à MVA sur les racines de plantes hôtes adéquates, dans des conditions aseptiques en serre. L'inoculum consiste en une préparation broyée et séchée comprenant le milieu de croissance de la plante hôte, les racines de l'hôte associées aux hyphes de MVA et les spores. La plupart des utilisations de MVA sur une grande échelle comportent l'établissement des mycorhizes sur des plantules qui seront ensuite transplantées sur le terrain. Des méthodes de grande envergure de procéder à une inoculation directe des MVA n'ont pas encore été élaborées mais, dans des essais limités, la stratification, l'enrobage et l'ensemencement des graines avec un inoculum de MVA se sont avérés efficaces. Il existe des méthodes de déterminer quels sols ont le plus de chance de profiter d'une application de champignons à MVA. Le potentiel agricole de l'utilisation des champignons à MVA sur une grande échelle est lié au développement de souches de MVA qui favorisent la croissance des cultures plus que les populations naturelles de ces champignons dans les sols.

[Traduit par le journal]

Introduction

As seen from previous papers at this conference, mycorrhizal fungi are beneficial symbiotic microorganisms that increase growth and yield of most crop plants through increased nutrient uptake, resistance to drought and salinity, and increased tolerance to pathogens. However, harnessing these beneficial effects for commercial utilization has proven difficult. There is still a need to optimize the activities of these fungi to benefit agriculture.

In the past 20 years the use of agricultural fertilizers throughout the world has more than doubled. Crop yields have risen dramatically as a result. However, because of shortages in some fertilizer supplies and the current cost of energy which is used to produce some fertilizers, the cost of fertilizers, both in terms of dollars and energy, has risen tremendously and will continue to rise. Agricultural economists indicate that as energy costs rise, the most responsive agricultural input is the fertilizer input. That is, as energy costs rise, fertilizer use will decrease. Since chemical fertilizers are said to account for one third to one half of the current U.S. agricultural output (39), this response would be a dangerous one, unless alternative fertilizer sources can be found or fertilization efficiency can be improved. Mosse (49) maintains that 75% of all phosphorus (P) applied to crops is not used during the 1st year and reverts to forms unavailable to plants. In soils high in pH

or high in aluminum or calcium carbonate, nearly 100% of the P fertilizer can be immobilized to nonusable forms via chemical soil reactions. Tropical oxisols and ultisols are notorious for their capacity to immobilize P.

Estimates indicate that agriculture consumes between 2.6 and 4.4% of all U.S. energy (39). Fertilizers and their application comprise 30–45% of the total agricultural energy use. Nitrogen is the main energy user, with P and K accounting for only 15% of the fertilizer energy use (39). It has become apparent that we must maximize fertilizer efficiency to conserve energy and material resources and reduce food production costs.

Most mycorrhizal researchers agree that the increase in effective nutrient-absorbing surface provided by vesicular–arbuscular mycorrhizal (VAM) fungi is primarily responsible for the increase in uptake of soil nutrients by mycorrhizal plants. Hyphae from mycorrhizal plant roots can extend up to 8 cm into the surrounding soil and transport nutrients this distance back to the roots (68). Bieleski (3) has calculated that VAM fungi may increase the effective absorbing surface of a host root by as much as 10 times. Nutrient ions such as P, zinc (Zn), and copper (Cu) do not diffuse readily through soil. Because of this poor diffusion, roots deplete these immobile soil nutrients from a zone immediately surrounding the root. Mycorrhizal hyphae extend into the soil past the zone of nutrient depletion and can increase the effectiveness of absorption of immobile elements by as much as 60 times (3). Because mycorrhizal fungi increase the efficiency of fertilizer use, they can be thought of as "biotic fertilizers" and can indeed substitute for substantial amounts of some fertilizers (47, 46).

The concept of mycorrhizae as substitutes for fertilizers

Theoretically, the most efficient level of fertilization for a plant is that level which provides concentrations of mineral elements in the tissue which are just above the "critical concentration" necessary for optimal growth. Additional fertilizer may be consumed, but it is "luxury" fertilizer and adds little to yield. It appears that many plants without mycorrhizae are incapable of absorbing adequate P, Zn, and Cu and perhaps other nutrients from normally fertile agricultural soils. Nutrient concentrations of nonmycorrhizal plants frequently fall below the "critical concentration." When this situation occurs, mycorrhizal fungi are usually able to improve fertilizer absorption significantly and increase elemental concentrations above the "critical concentration" without addition of fertilizer. To reach similar "critical concentrations" in tissues of nonmycorrhizal plants requires the addition of more fertilizer. Menge *et al.* (46) compared mycorrhizal citrus seedlings with nonmycorrhizal seedlings which received various amounts of fertilizer (Figs. 1 and 2). Brazilian sour orange was far more dependent upon mycorrhizal fungi for nutrient absorption than

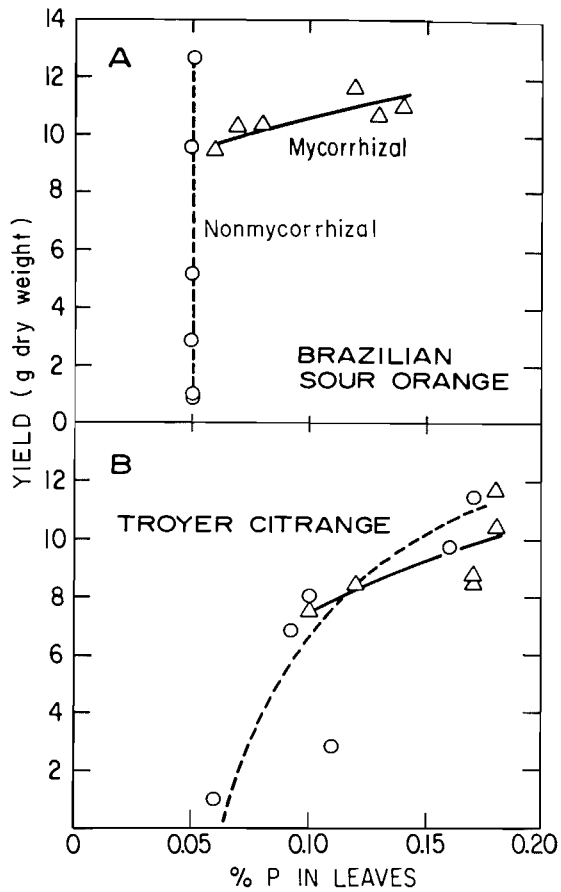

FIG. 1. Interaction between mycorrhizae, P content of leaves, and growth of Brazilian sour orange and Troyer citrange seedlings.

Troyer citrange. It appears that for sour orange the "critical concentration" of P in leaves was approximately 0.06% (Fig. 1). Therefore, in this experiment it appears that all nonmycorrhizal seedlings of sour orange fell into the P-deficient range, while all mycorrhizal sour orange fall into the "luxury P-consumption" range. For citrange, maximum growth may not have been reached, so a calculation of a critical concentration was not made; however, it appears that all mycorrhizal citrange seedlings contained concentrations of P adequate for good growth, while some of the nonmycorrhizal plants did not. It appears that in sterile soils, mycorrhizal fungi can partially substitute for fertilizer.

Mycorrhizal Troyer citrange plants which received no fertilizer P were equal in size to nonmycorrhizal Troyer citrange plants which received 112 kg P/ha (Fig. 2). Similarly, mycorrhizal Brazilian sour orange plants which received no fertilizer P were equal in size to nonmycorrhizal plants which received 560 kg P/ha. It appears that mycorrhizal fungi in this study could be

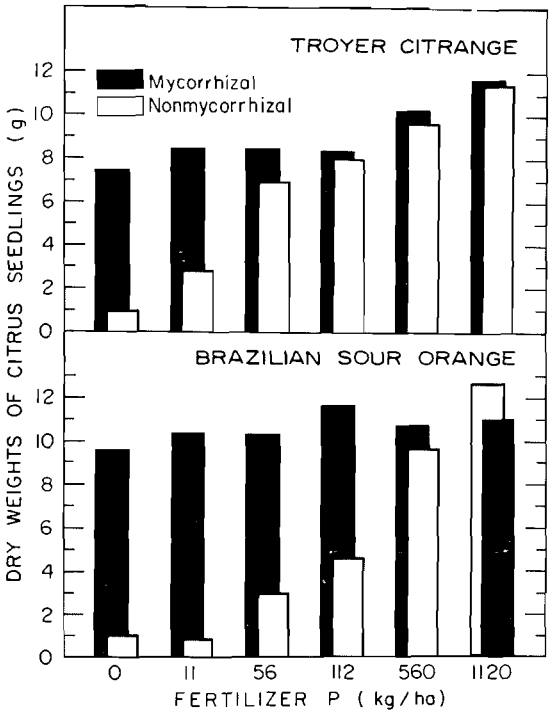

FIG. 2. Dry weights of mycorrhizal and nonmycorrhizal Brazilian sour orange and Troyer citrange seedlings fertilized with different amounts of phosphorus.

substituted for between 112 and 556 kg/ha P in the culture of citrus. In one California citrus nursery, it was found that inoculation with mycorrhizal fungi could reduce P fertilization by two thirds. Similar savings in P fertilizers have been shown by Schultz *et al.* (74) in fumigated forest nurseries in the production of sweetgum, by Csinos (11) in the growth of tobacco in fumigated seedbeds, and by Ross (70) in the growth of soybeans in fumigated soil.

It must be emphasized that VAM fungi do not manufacture fertilizer and some fertilizer nutrients must be available for them to absorb. Secondly, VAM fungi can be substituted for fertilizer only in sterilized soils. Since mycorrhizal fungi are present in most soils, their unique fertilizer-absorbing abilities are normally already being utilized by most crop plants. If mycorrhizal fungi are removed or damaged in any way, the amount of fertilizer required by a crop increases enormously. This is demonstrated effectively by Menge *et al.* (46), who reported that citrus grown in fumigated soil or in hydroponic solutions often require massive P applications for adequate growth compared with field-grown citrus. Chapman and Rayner (6) reported that citrus under nonsterile field conditions can absorb P from P-deficient soils more efficiently than can either corn or tomatoes, and citrus orchards do not normally require P fertilization. Differences in P absorption by citrus grown in fumigated soil and citrus grown in nonfumigated soils can be reconciled if mycorrhizal fungi, which are present in nearly all citrus orchards (43), are the equivalent of 112–556 kg P/ha.

Current commercial utilization of mycorrhizal fungi

Although nearly all plants require mycorrhizal fungi to achieve maximum growth in nutrient-poor soils, the widespread occurrence of these fungi in nearly all soils limits the immediate need for inoculation with mycorrhizal fungi. Commercial use of mycorrhizal fungi is probably economically feasible at the present time in only three major agricultural areas: (*1*) disturbed sites, (*2*) fumigated soils, and (*3*) greenhouses.

Disturbed sites

Mycorrhizal fungi have been conclusively shown to improve revegetation of coal spoils, strip mines, waste areas, road sites, and other disturbed areas (2, 12, 13, 14, 15, 16, 33, 38, 67). In these disturbed sites, populations of VAM fungi are usually greatly reduced or are lacking. Adding VAM fungi provides a nutritional advantage to associated plants in addition to providing possible resistance to low pH, heavy metal toxicants, and high temperature. Growers whose nurseries and greenhouses provide plants for revegetation of disturbed sites are well aware of mycorrhizae and the benefits they provide. The production of mycorrhizal plants for use in revegetation at such sites is a reality in some areas.

Fumigated or chemically treated sites

Application of many soil fungicides may reduce or delay mycorrhizal infections, but they rarely eliminate them. These chemicals include botran (58), dichlofluanid (29), lanstan (58), maneb (57), PCNB (58), benomyl (5), ethirimol (29), chloraniformethan (29), tridemorph (29), triforine (29), thiabendazole (29), thiophanate (5), and triademifon (29).

Fumigation with chloropicrin (59), formaldehyde (57), mylone (58), methyl bromide (59), vapam (58), or vorlex (58) frequently eliminates root infection by VAM fungi. Fumigation with these biocides to remove soilborne pests is required by regulation for the production of many nursery crops and is also regularly used in many field agricultural situations. Methyl bromide and chloropicrin appear to be especially toxic to mycorrhizal fungi and most field fumigations with these chemicals are sufficient to destroy native mycorrhizal inoculum.

Stunting of crops following fumigation is common and is due to the destruction of VAM fungi. The stunting syndrome is characterized by poor growth and small chlorotic leaves, which may become necrotic at the edges. Older leaves abscise prematurely and concentrations of P, Cu, and Zn in the plant tissue are frequently reduced to deficiency levels (34, 35, 41, 76). Although fewer than 60 000 ha are treated annually in the U.S.,

stunting following fumigation has been reported in the U.S., Africa, Spain, Peru, Venezuela, and many other countries (47). Stunting after fumigation has been reported with avocado, citrus, cotton, peach, soybean, white clover, and hardwood tree species (47). Other crops which are routinely grown in fumigated soils include strawberries, tomatoes, tobacco, nursery crops, tree crop replants, and some vegetable crops. The addition of VAM fungi to fumigated sites has repeatedly eliminated stunting following fumigation and reduced the need for additional fertilizer applications (8, 34, 35, 36, 46, 47).

Currently, the cost for commercial mycorrhizal inoculum per hectare is similar to that of P; however, mycorrhizal inoculum can provide additional benefits to crops besides improved P nutrition. For nursery plants growing in fumigated soil, inoculation with mycorrhizal fungi is imperative for the following reasons: (*i*) the plants grow better (prevents stunting following fumigation); (*ii*) there is a decreased need for fertilization, specifically P, Zn, and Cu, resulting in decreased fertilizer cost and energy conservation; (*iii*) there is less potential for water stress and, therefore, reduced transplant injury (42); (*iv*) the plants survive better, especially if transplanted to fumigated, poorly fertilized, or disturbed soils; (*v*) the plants will be inoculated with effective mycorrhizal fungi and, therefore, infection is not left to chance; and (*vi*) the plants may be more resistant or tolerant to some plant diseases (73).

For many crops growing in fumigated soils, the addition of mycorrhizal fungi is not only recommended, it is necessary to achieve maximum growth. Several citrus and avocado nurseries in southern California which practice methyl bromide fumigation are currently utilizing commercial mycorrhizal inoculum and are producing VAM-inoculated stock.

Greenhouses

Greenhouse culture utilizes growth media such as pine bark, vermiculite, perlite, builders sand, and peat moss, which are devoid of mycorrhizal fungi. In addition, most nurserymen steam, pasteurize, or chemically treat their mixes to eradicate harmful pathogens. Nurserymen have compensated for the absence of mycorrhizal fungi by applying luxury amounts of fertilizer and water to achieve desired growth. This heavy fertilizer application is not only wasteful and expensive but, in many areas, runoff water is being monitored for nitrate and other fertilizer nutrients by environmental regulatory groups.

Growth responses due to inoculation with VAM fungi under nursery or greenhouse conditions have been demonstrated for woody ornamentals such as *Viburnum*, *Podocarpus*, *Pittosporum* (9), and magnolia (40). However, an extensive study with rapidly growing foliage ornamentals at three nutrient regimes indicated that *Diffenbachia*, *Nephthytis*, and *Brassia* could easily be inoculated with mycorrhizal fungi under nursery conditions, but growth was not significantly enhanced by several species of VAM fungi (unpublished data). Several reports have expressed the desirability and practicality of utilizing VAM fungi in greenhouse and containerized nursery conditions (7, 30, 37). Johnson and Menge (30) indicated that P fertilizer could be reduced by approximately 70% and micronutrients reduced by 30–40% under current greenhouse practices. However, fertilization constitutes only 2–4% of a nurseryman's expense and many are reluctant to reduce fertilization in favor of VAM fungi.

Commercial production of VAM inoculum

Commercial production of mycorrhizal inoculum for use in disturbed, sterilized, or fumigated soil is presently being attempted at several locations in the U.S. Currently, the only way to produce suitable quantities of a mycorrhizal inoculum is on roots of susceptible host plants. The possibility of pathogenic organisms contaminating mycorrhizal inoculum is an extremely serious problem when growing VAM inoculum in semisterile cultures in the greenhouse. For this reason, many scientists will consider mass production of VAM fungi only if it is done axenically. Realistically, however, not only must these obligate biotrophs be grown *in vitro*, but they must produce large quantities of spores in culture which will survive under soil conditions and infect plants in nature. Information gained from the culture of other formerly obligate biotrophs suggests that the possibility of realizing this goal in the near future is unlikely. Even if mycorrhizal fungi are cultured axenically, mycorrhizal inoculum for field use will probably be produced on the roots of suitable host plants.

It is proposed that, with proper safeguards, mycorrhizal inoculum that is free of plant pathogens can be produced on plants in the greenhouse. Figure 3 illustrates a proposed scheme for producing mycorrhizal inoculum. Vesicular–arbuscular mycorrhizal fungi can be isolated by using bits of roots or soil from the field to inoculate roots of "trap plants" growing in sterilized soil in the greenhouse. Sudan grass (*Sorghum vulgare* Pers.) is frequently used, but other plants such as peanut, tomato, soybean, corn, and safflower may be equally suitable. The soil used throughout is a low-nutrient sand fertilized once a week with one half the standard Hoagland's solution minus P. After production of VAM spores in the "pot cultures," the spores can be removed by wet-sieving (22), elutriation (19), or centrifugation (71). These spores must be surface disinfested with substances such as chloramine T or sodium hypochlorite and streptomycin to insure that pathogens do not accompany the spores (56). These surface-disinfested

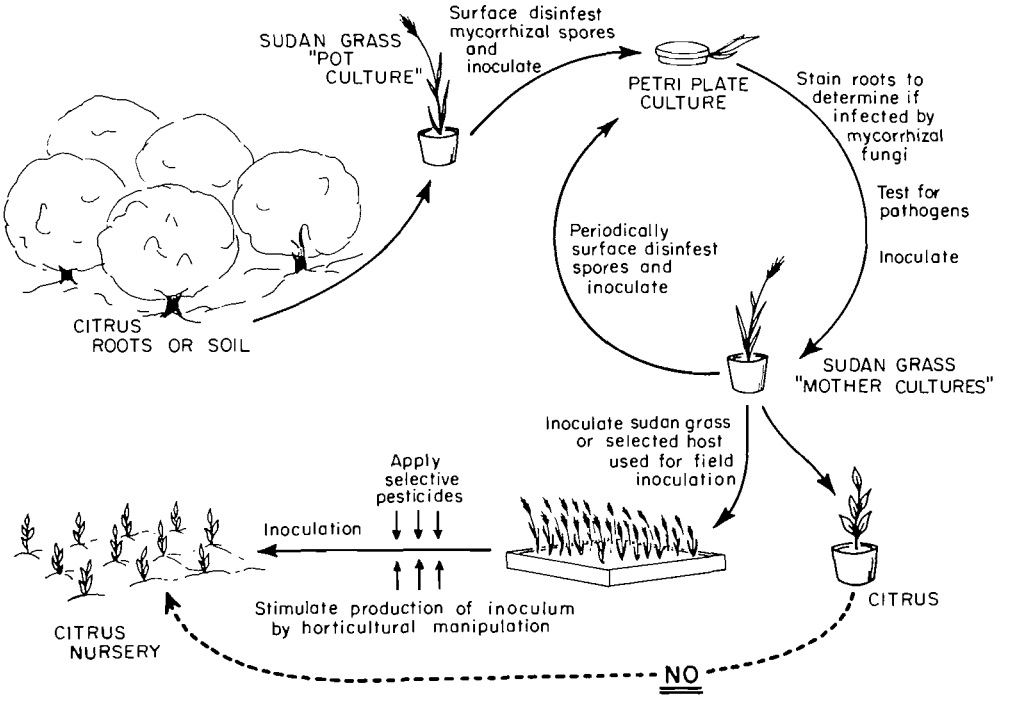

FIG. 3. Proposed scheme for commercial production of mycorrhizal inoculum.

spores are used to inoculate the roots of plants which were germinated and grown under aseptic conditions in growth chambers. The containers illustrated are made from plastic petri plates (Fig. 3) and filled with the low-nutrient sand. After 1–4 weeks, when the mycorrhizal fungi have colonized roots grown under aseptic conditions, root pieces can be removed and stained (60) to observe infection, and other root pieces can be carefully removed and used to infect suitable host plants grown in sterilized soil in the greenhouse. Similar root pieces can be removed, examined, and plated on agar to observe pathogenic organisms. If no pathogens are observed, the greenhouse "pot culture" may be used as a "mother culture" to produce inoculum which will be used in the field. Inoculum should be produced on selected hosts which have no root diseases in common with the host plant for which the inoculum is intended. For instance, inoculum for citrus could be produced on Sudan grass but never on citrus. In this way the wide host range of most VAM fungi can be utilized.

As another precaution against propagating pathogens along with mycorrhizal inoculum, the field inoculum should be drenched several times with pesticides chosen to eliminate pathogens known to infect the host for which the inoculum is intended. Mycorrhizal inoculum intended for citrus should be drenched with a nematicide to control the citrus nematode and fungicides to control *Phytophthora* and *Rhizoctonia* spp. Suggested fungicides which are not harmful to VAM fungi are ethazole, captan, chloroneb, sodium azide, alliet, and ridomil (45, 57). Some of these fungicides can actually increase VAM spore production (45). Horticultural practices could also be used at this point to maximize VAM spore production. Large containers and supplemental light have been shown to increase spore production (18). Eliminating fertilization and slowly reducing the water may also be effective in increasing spore production. When spores are mature, plant tops are removed and roots, soil, and spores can be ground up and partially dried (7–20% moisture content) and stored at 4°C until used. If concentrated spore suspensions are desired, spores can be concentrated by wet-sieving (22), elutriation (19), or centrifugation (71) before storage. Vesicular–arbuscular mycorrhizal inoculum can be freeze- or L-dried if desired (10, 75). Inoculum produced in this manner should be consistently infective and yet pathogen free.

By using the method described above, the estimated costs for producing mycorrhizal inoculum have been calculated by Johnson and Menge (30). These figures are derived from production costs of a foliage plant greenhouse and could be reduced considerably, since mycorrhizal inoculum quality is of importance and not plant quality. A reasonably generous estimate of the cost of mycorrhizal production, including technical labor and quality control, together with a small margin of

profit, indicates that consumers may pay about 0.19 cents/g of VAM inoculum. Such a cost could easily be borne by consumers.

A similar method to that outlined above has recently been patented in England and is being perfected for large-scale commercial use (27). In this method, plants are grown in peat blocks, which are standing in a shallow nutrient-flow culture. After VAM spores are produced in the peat blocks, they are ground up, roots and all, for inoculation. The finished product is not only excellent mycorrhizal inoculum but is light and easy to ship.

Commercial inoculation

Although many methods have been used to inoculate plants with VAM fungi in greenhouse trials, few inoculation methods are acceptable for large-scale commercial inoculation. Jackson *et al.* (28) studied several different methods to inoculate corn and found that layering inoculum under the seed was superior to seed inoculation or banding the inoculum. Menge *et al.* (47) found that layering inoculum below the seed and banding inoculum were superior to seed inoculations. Crush and Pattison (10) experimented with several means of inoculating seeds with VA mycorrhizal fungi, but again they found that sowing seed above pelleted mycorrhizal inoculum was the most effective method for obtaining mycorrhizal infection. Hall (24) developed a method for pelleting seed with mycorrhizal inoculum and determined that mycorrhizal fungi could survive up to 28 days under these conditions. Hattingh and Gerdemann (25) reported growth responses to citrus in a fumigated nursery after inoculating citrus seed with mycorrhizal inoculum. Gaunt (20) inoculated onion and tomato seeds with a VAM fungus and reported that seed-inoculated plants grew as well as plants that were inoculated by mixing VAM inoculum into the soil. Commercial applications of mycorrhizal inoculum using fertilizer banding and seeding machinery were successfully carried out in citrus nurseries in California (18).

Plants do not respond favorably to VAM inoculum in all soils. If soil nutrition is optimum, mycorrhizal fungi will not enhance growth of plants. A method for detecting which soils require mycorrhizae for maximum production of citrus was devised by Menge *et al.* (44). In soils with less than 34 ppm available P (Olson analysis), 12 ppm available Zn, 27 ppm available Mn, or 3% organic matter, citrus trees will probably require mycorrhizal fungi for maximum growth. Mycorrhizal inoculations are recommended for citrus only in soils with these characteristics. It is estimated that this includes approximately 85% of the southern California citrus soils. Similar studies could be done with other crops to determine which soils require mycorrhizal infestation.

Potential uses for mycorrhizal fungi

Because mycorrhizal fungi occur on most agronomic crop plants and improve the growth of these plants, the potential use of these fungi as commercial "biotic fertilizers" is enormous. Large-scale field inoculations with mycorrhizal fungi are rare because of limited inoculum, and natural field soils usually contain adequate populations of indigenous mycorrhizal fungi. Under these conditions, any growth benefit due to mycorrhizal inoculation would depend primarily upon the superiority and (or) placement of the mycorrhizal inoculum. Beneficial responses under these conditions would be predicted to be far less than the responses obtained in fumigated or partially sterilized soil. However, greenhouse and field experiments in which plants were inoculated with mycorrhizal fungi in nonfumigated soils have demonstrated that growth responses due to mycorrhizal fungi can occur under these circumstances.

In greenhouse experiments, utilizing untreated soil, Mosse and her colleagues (50, 51, 52, 54, 55) demonstrated that preinoculation with mycorrhizal fungi could provide the following growth increases: *Centrosema* sp., 34%; corn, 306%; *Melinis* sp., 41–60%; onions, 48–3155%; strawberries, 250%; *Stylosanthes* sp., 85–88%; sweetgum, 45%; and *Viola* sp., 527%. Other studies have noted similar growth increases in untreated soil: subterranean clover, 156% (1); corn, 14% (21); corn, 0–53% (28); mahogany, 151% (66); sudan grass, 0–18% (28); white clover, 80–100% (63); and ryegrass, 29–34% (64).

Field experiments in nonsterile soil are less common, but wheat preinoculated with a mycorrhizal fungus produced 220% more grain than nonmycorrhizal wheat (32). In a similar experiment (31), corn inoculated with a mycorrhizal fungus was 122% larger than nonmycorrhizal corn. Hayman (26) reported white clover growth increases in the field owing to inoculation with a mycorrhizal fungus. Black and Tinker (4), in an extremely well-documented field experiment, found that fallow field inoculation with a mycorrhizal fungus increased potato yield 20%.

Not all mycorrhizal inoculations in nonsterile soil result in increased growth. Hayman (26) indicated that mycorrhizal fungi did not stimulate growth of white clover at several field locations. Powell (63) obtained significant growth increases of white clover after inoculation with mycorrhizal fungi in only three of nine sites. Jackson *et al.* (28) indicated that, with certain mycorrhizal inoculation methods, growth of corn, Sudan grass, and soybeans was not stimulated in nonsterile soil. Mosse (52) obtained significant growth responses of *Stylosanthes* sp. owing to mycorrhizae in 6 of 11 nonsterile soils. Ross and Harper (71) reported no growth stimulation of soybeans in nonsterile soil.

Vesicular–arbuscular mycorrhizal fungi are abundant

and extremely important ecologically in the tropics (17, 50). Huge expanses of tropical soils, such as the Brazilian Cerrado, are either deficient in P or immobolize P fertilizers. These marginal agricultural lands could be productive if mycorrhizal fungi, with the ability to utilize extremely small quantities of fertilizer, were developed and added to the soil. Inexpensive, rock phosphate could be added as the P source. This P source is a poor fertilizer but releases small quantities of P for long periods of time. It has been shown that some mycorrhizal fungi utilize rock phosphate much better than others and can tremendously improve growth of plants growing in poor soils fertilized with this material (53). The use of effective VAM fungi in the tropics on poor agricultural soils, which have been cut and burned or which have been flooded during rice production, may be a viable alternative to high-cost fertilizers.

The key to economically successful inoculations with VAM fungi in undisturbed or untreated agricultural soils is through the development or selection of highly efficient VAM fungi, which are capable of promoting plant response to a greater extent than indigenous VAM fungi. Powell and his colleagues have indicated that many indigenous VAM fungi are inefficient symbionts and that inoculation by more efficient strains will result in growth responses even in nonsterile soil which contains high populations of inefficient VAM fungi (62, 63, 64, 65). Mosse (52) agrees with this assessment and adds that the efficiency of the indigenous VAM fungi is the major determinant governing growth responses of plants to VAM fungi in nontreated soil.

The selection of efficient strains of VAM fungi is critical to the development of VAM fungi for use in agriculture. The factors which contribute to symbiont efficiency (Table 1), such as high inoculum density, placement of inoculum, dependable spore germination, rapid growth through soil, competitive abilities, survival mechanisms, and effective infection capabilities are all part of the inoculum potential of the VAM isolate. Other factors including spread through the root, amount of external hyphae, effectiveness of P uptake and transfer, and the amount of host carbon used are all part of the intrinsic efficiency of a VAM isolate. The intrinsic efficiency must always be separated from inoculum potential for any VAM isolate. Comparison of VAM isolates using crude inoculum or even specific spore numbers is not adequate simply because the inoculum is not comparable. Spores are of different sizes and germinability. Some isolates may be effective at high densities, while others are more effective at low densities. Spores of some isolates may be dormant at specific times and comparison of efficiencies using crude inoculum will not adequately measure intrinsic effectiveness if infection is reduced by a temporary dormancy of spores. Inoculum potential of isolates can easily be equated by the method of Porter (61) and the intrinsic efficiency of isolates should be compared only when infection levels are similar.

TABLE 1. Factors governing symbiont efficiency

Inoculum potential
Spore germination, maturity, dormancy (vernalization, scarification)
Inoculum density
Inoculum potential (infection potential)
Location of inoculum
Type of inoculum (hyphae, spores, vesicules, organic matter base)
Rate of growth to root
Infection ability
Rhizosphere effect (exudation from host)
Microbial interactions (stimulation, competition, antagonism)
Soil physical and chemical factors
Intrinsic efficiency
Spread along root
Rate of growth
Host resistence?
Arbuscule formation and longevity
Amount of external hyphae
Efficiency of P uptake and transfer
Carbon drain

It has been shown repeatedly that the amount of VAM infection is not always correlated with efficiency (48). Hyphal connections of VAM fungi to roots are also not well correlated to isolate efficiency (62). Rapid infection (69) as well as the position of inoculum (28, 52) may be prime factors governing the efficiency of isolates. However, evidence indicates that the amount and location of external VAM hyphae, which functionally absorb soil nutrients, may be the most critical factor contributing to isolate efficiency (23, 48, 72). Accurate determinations of the factors governing isolate efficiency, including resolving the importance of carbon drain to the symbiosis, must be made before we can realistically select superior VAM isolates for use in agriculture.

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