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THE AUTHOR

Barbara Mosse was Soil Microbiologist, Rothamsted Experimental Station, Harpenden, Herts, England. She was consultant, Consortium on Soils of the Tropics, University of Hawaii, when she prepared this report.

FOREWORD

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On the Cover: Yellow-vacuolate spore (*Glomus mosseae*) excised from a sporocarp and stained in cotton blue.

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Dr. D. J. Bagyaraj, University of Agricultural Sciences, GKVK Campus, Allalasandra, Bangalore, 560-065, India.

B. K. Bakshi, Director, Div. of Mycology & Plant Path. Indian Agric. Res. Inst., New Delhi, India.

Dr. S. H. Iqbal, Dept. of Botany, New Univ. Campus, Lahore, Pakistan.

Dr. A. G. Khan, Science Dept. Goulburn Coll. of Advanced Education, McDermott Drive, Goulburn, N.S.W. 2580, Australia.

Dr. Hormozd Kianmehr, Biology Dept., Ferdowsi University, Mashhad, Iran.

Miss P. Nadarajah, Botany Dept., University of Malaya, Kuala Lumpur, Malaysia.

Miss B. Parveen, 2, Liaquat Park, Beadon Road, Lahore, India.

Dr. S. K. Saif, Institut für Tropischen and Subtropischen Pflanzenbau, Universität Göttingen, Griesebachstrasse 6, 3400, Göttingen, West Germany.

Mr. M. N. Shamsuddin, UPM, Serdang, Selangor, Malaysia.

Dr. K. Swaminathan, Central Potato Research Institute, Simla, 171001.

Dr. Mahmud Hj Abd Wahab, Soils and Crop Management Div., Rubber Research Institute of Malaysia, P.O. Box 150, Kuala Lumpur, Malaysia.

Dr. U. P. De S. Waidyanatha, Research Laboratories, Dartonfield, Agalawatta, Sri Lanka.

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Dr. D. H. Marx, Institute for Mycorrhizal Research and Development, U.S.D.A. Forest Service, Athens, Georgia, U.S.A.

Dr. J. A. Menge, University of California, Riverside, California 92521, U.S.A.

Dr. M. Metcalf, Dept. of Soil Biochemistry & Microbiology, University of California, Berkeley, California 94720, U.S.A.

Dr. C. Ll. Powell, Ruakura Agricultural Research Centre, Hamilton, New Zealand.

E. St. John, Instituto Nacional de Pesquisas da Amazonia, Estrada do Eleixo 1756, Manaus, Brazil.

Dr. D. Shaw, Plant Pathology, Department of Primary Industries, Papua, New Guinea.

Dr. D. H. Lambert, Dept. of Plant Pathology, 211, Buckhout Laboratory, Pennsylvania State University, University Park, Penn. 16802, U.S.A.

Mr. G. W. Smith, College of Sciences, Dept. of Microbiology, Clemson, South Carolina 29631, U.S.A.

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Vesicular-Arbuscular Mycorrhiza Research for Tropical Agriculture

Barbara Mosse

SYNOPSIS

The roots of most plants form vesicular-arbuscular (VA) mycorrhizal associations with a group of phycomycetous soil fungi belonging to the Endogonaceae. The fungi cannot be cultured on synthetic media, but they form morphologically distinct resting spores in the soil and can be multiplied in association with a host plant. Such spores generally range from 100 to 600 μm and can be recovered from soils by a variety of sieving techniques. They can be surface sterilized and will produce typical VA infections in axenic seedlings or root organ cultures. The infections are confined to the primary cortex and do not cause visible tissue damage in the invaded root. Infection is both inter- and intracellular; the intracellular haustorial structures (arbuscules) are short-lived and collapse after 2 to 3 weeks.

The nutritionally significant function of VA mycorrhiza depends on soil exploration by hyphae that grow from the root and act as extensions of the root-absorbing surface beyond the zone explored by the root hairs. Hyphae have a very large surface-to-volume ratio and are therefore an economical way of producing an extra, well-distributed absorbing surface. This is particularly important for phosphorus (P) uptake by the plant because the phosphate ion is readily sorbed on clay complexes and diffuses slowly in soils, so that a depletion zone quickly develops around the actively absorbing rootlet. Hyphae can explore the soil beyond the depletion zone and transport the phosphate back into the root. Once taken up by the hyphae, the phosphate ion is protected against further sorption by the soil. Phosphate is translocated into the mycelium in the root and is there released and utilized by the plant for root and shoot growth. Zinc uptake is similarly improved, and mycorrhiza may also increase the uptake of copper and sulfur.

Mycorrhizal roots utilize the same sources of soil phosphate as nonmycorrhizal roots and do not appear to mobilize insoluble soil phosphate to any considerable extent. In some instances they seem to deplete the soil-solution P more than nonmycorrhizal roots, and this could lead to a slow mobilization of insoluble soil phosphate by purely chemical means as the soil-solution P falls below the solubility product of the insoluble soil phosphate. This process could be important in the natural ecosystem but would contribute little to plant growth in agricultural situations. There the chief benefit of mycorrhiza probably lies in the better utilization of applied phosphate fertilizers, particularly in soils subject to rapid fixation or where fertilizers of

moderate-to-low phosphate availability are used.

Some plant species are efficient users of soil phosphate, while others are almost entirely dependent on mycorrhizal uptake. The latter include citrus, sweet gum, grapevine, *Coprosma*, onion, and some other plant species with thick, fleshy roots and few, short root hairs. Because of their different P requirements and foraging abilities, plants vary in their responses to inoculation with VA endophytes, and their different reactions may influence the balance of species in P-deficient environments. The extent to which plants require mycorrhiza also depends on levels of available soil phosphate. Mycorrhizal infection has particular value for legumes because (1) nodulation and symbiotic nitrogen fixation by rhizobia require an adequate P supply and (2) the relatively restricted root system of legumes makes them, compared to grasses, rather poor competitors for soil phosphate.

The extent to which mycorrhizal infection can improve plant growth also depends on the level of infection and the particular fungal species involved. In very P-deficient soils mycorrhizal infection can be increased by P additions, but in very fertile soils infection decreases. Eventually, high internal concentratons of nitrogen (N) and P make plants immune to infection. Fungal development in the soil is affected by environmental conditions (pH, aeration, temperature, and other factors), and the fungal species differ in adaptability to particular conditions. Agricultural practices, therefore, can alter endophyte populations both qualitatively and quantitatively; it may then become desirable to introduce endophyte species better adapted to the changed soil conditions. This appears to be possible both in pots in a glasshouse and under field conditions. Such improvement through introduction of better species forms the basis of one possible application of VA mycorrhizal research. In addition, since infectivity is low in some soils, and many annual crops (for example, cotton) require an adequate P supply during the early stages of growth, a possible increase in soil infectivity can be beneficial.

VA mycorrhiza may have particular significance for tropical agriculture because P, even more than N, is often the nutrient most limiting growth in tropical soils. In the undisturbed ecosystem, plant roots are normally mycorrhizal, and this may be an important factor in the tight nutrient cycle known to operate in this environment. Local rock phosphates, often of relatively low solubility, could be used to improve crop production at relatively low cost if their utilization by the plant could be improved.

Mycorrhizal fungi appear to have outstanding effects on soil aggregation and may be important as a means of erosion control. They may also have a function as an aid to plant establishment in degraded sites. Many tropical trees of agronomic importance have VA mycorrhiza, e.g., citrus, coffee, tea, cocoa, rubber, papaya, and oil palm. Where these trees are raised in nurseries in sterilized soil, inoculation may greatly improve establishment and early growth after transplanting to the permanent site.

This report discusses some technical aspects of work with VA mycorrhiza, including methods of establishing pot cultures of different endophyte species, methods of inoculation and types of inoculum, and methods of evaluating soil infectivity and degree of mycorrhizal infection. Some practical suggestions for the advancement of VA mycorrhizal research in tropical soils are also discussed.

INTRODUCTION

Most plant roots form mycorrhizal associations of one kind or another with fungi in the soil. Harley's (1969) book, The Biology of Mycorrhiza, gives an excellent account of the different kinds of mycorrhiza, their structure, and their functions. Although it is well documented, the widespread occurrence of mycorrhizal associations in natural ecosystems and agricultural crops has been largely ignored, except perhaps in the field of forestry. Vesicular-arbuscular (VA) mycorrhiza, the subject of this report, are by far the most common form; they occur in nearly all the important crop plants, including many tropical trees, and have been well described in various monographs. Nevertheless, virtually no standard botanical or agronomic textbook even contains a description. The present heightened interest in VA mycorrhiza, shown also by the sharp increase in the number of research papers, reviews, and meetings (*see* Appendix A), stems from three separate developments:

1. During the last 25 years, the study of VA mycorrhiza has passed from a largely descriptive to an experimental phase. This has demonstrated the importance of VA mycorrhiza in phosphorus (P) uptake by the plant.
2. The greatly increased cost of P fertilizers has led to a search for possible ways of economizing in their use and of utilizing new P sources—mainly less-soluble rock phosphates.
3. An increased awareness of the natural ecosystem and of the factors contributing to its stability has led to detailed studies of nutrient cycling, and a reassessment of some modern agronomic practices, including the increased use of pesticides and the breeding of new, high-yielding varieties with high fertilizer requirements. In addition, pressure on land has led to erosion, and industrial development has led to pollution of many sites. Mycorrhiza are an important and responsive part of the environment, and the question is being asked how far new agricultural practices are affecting them and to what extent it is possible or desirable to adapt agricultural practices to make full use of the mycorrhizal potential.

It is not the intention of this report to give a comprehensive review of the literature. The subject has been well reviewed, both in general (Nicolson, 1967; Gerdemann, 1968, 1975; Khan, 1972*b*; Mosse, 1973*a*; Hayman, 1978*a*) and with special reference to plant nutrition (Tinker, 1975*a*; Mosse and Tinker, 1980), to legumes (Mosse, 1977*b*; Munns and Mosse, 1980) and to general plant ecology (Mosse, 1978). It is the objective here to give an outline of the subject in relation to agriculture and ecology, to note research trends, and, in particular, to consider the application of VA mycorrhizal research to tropical soils and conditions.

THE VA MYCORRHIZAL SYSTEM

General Structure

VA mycorrhiza result from the colonization of fine absorbing roots of plants by soil fungi belonging to the family Endogonaceae. The fungi invade only the primary cortex; vascular tissue, the secondary cortex, and the thick fleshy roots that develop into the main

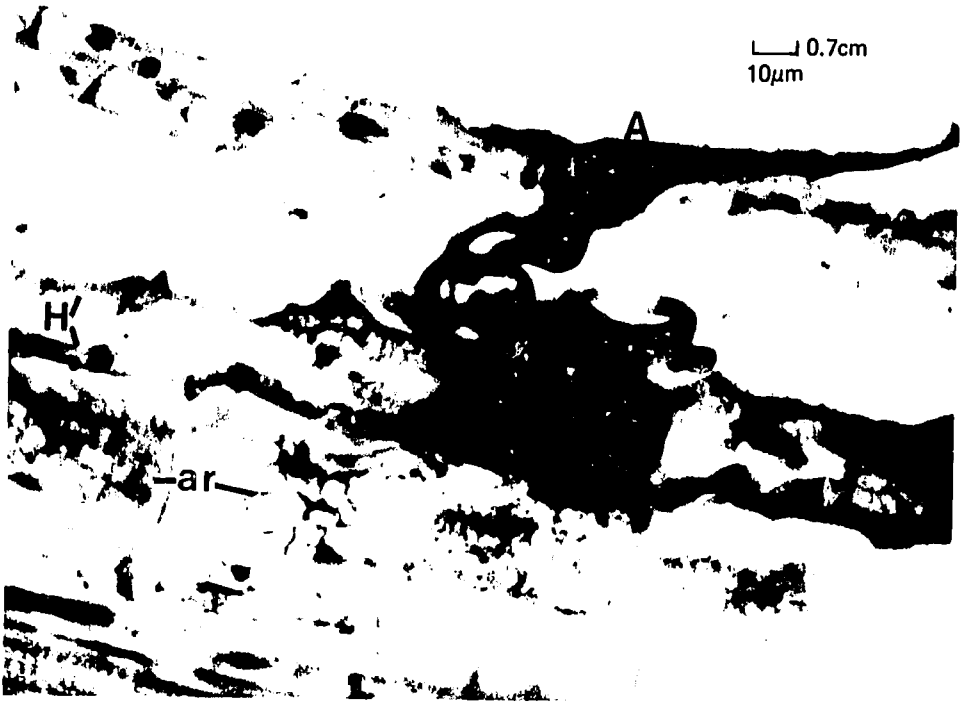

Fig. 1. Section of a mycorrhizal apple rootlet showing appressorium (A), distributing hyphae (H), and arbuscles (ar).

structural roots of perennial plants are not infected. Essentially, therefore, VA infections only involve temporary structures with a limited functional life. In this respect, they differ from more pathogenic infections by other fungi that cause lesions, distortion, and discoloration of the invaded tissue and often spread into permanent tissues of the stele and beyond. Each rootlet that becomes mycorrhizal is infected from a fungal propagule in the soil.

After entry into the rootlet, which is often preceded by formation of an appressorium on the root surface, the fungus usually traverses the outer cortex and proliferates in the inner cortical layers (Fig. 1). Spread is largely by the growth of intercellular hyphae along the root. The root tip remains uninfected, and the fungus does not interfere with normal root growth, although there may be a slight overall swelling and increased branching of the fine roots. Mycorrhizal roots cannot be distinguished from nonmycorrhizal roots by macroscopic observation, although in some plant species (e.g., onions and corn), heavily infected regions of the root develop a characteristic yellowish tinge. To see the infection clearly, roots must be cleared to render them more transparent and stained to show the fungal tissue. The method of Philips and

Hayman (1970) is widely used, although other methods have been described. Sections of roots cut on a freezing microtome or of roots fixed and embedded in wax allow more detailed observation. Scanning and transmission electronmicroscopy have also been employed, particularly to study the intracellular phase of infection (Kaspari, 1973, 1975; Cox and Sanders, 1974; Cox, et al., 1975; Kinden and Brown, 1975*a–c*, 1976; Scannerini, et al., 1975; Cox and Tinker, 1976; Holley and Peterson, 1979; Mosse, unpubl.).

Arbuscules

The main distinguishing features of VA infection are the arbuscules and vesicles. Arbuscules are intracellular, haustoria-like structures that arise by repeated dichotomous branching of one, rarely two or three, hyphal branches that penetrate into the host cell (Figs. 1, 2). The ultimate size of these fine branches is comparable to that of host mitochondria and beyond the resolution of the light microscope. The arbuscules are short-lived; estimates of their life vary from only 1

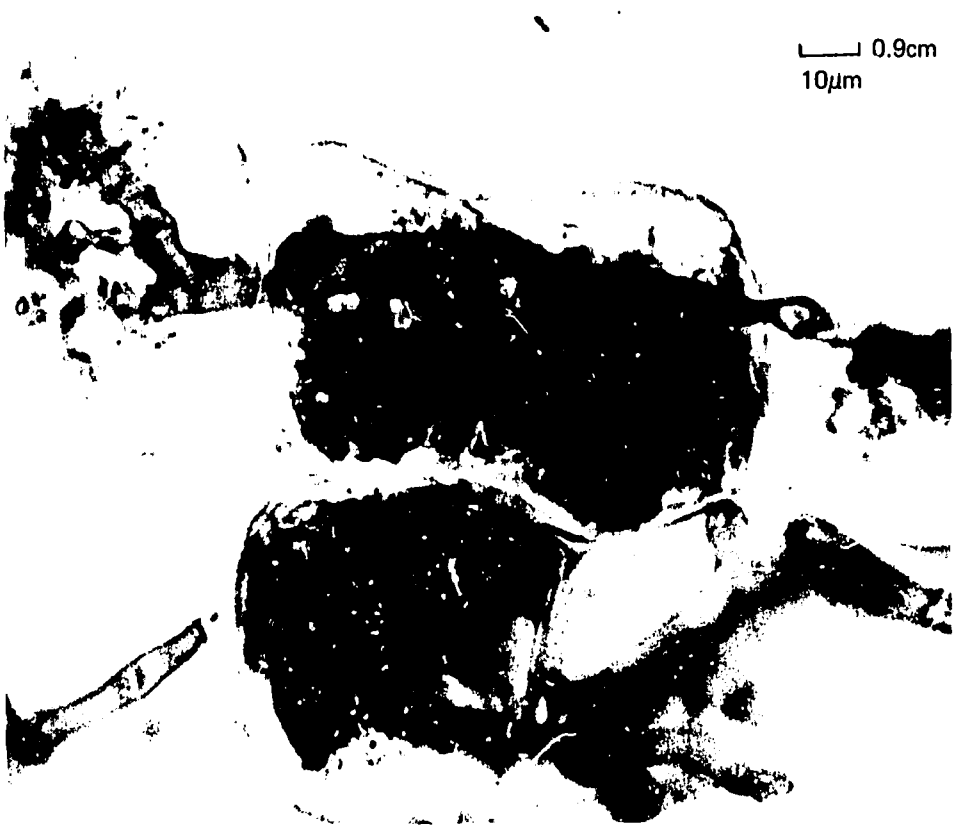

Fig. 2. Detail of arbuscles in the root of ash.

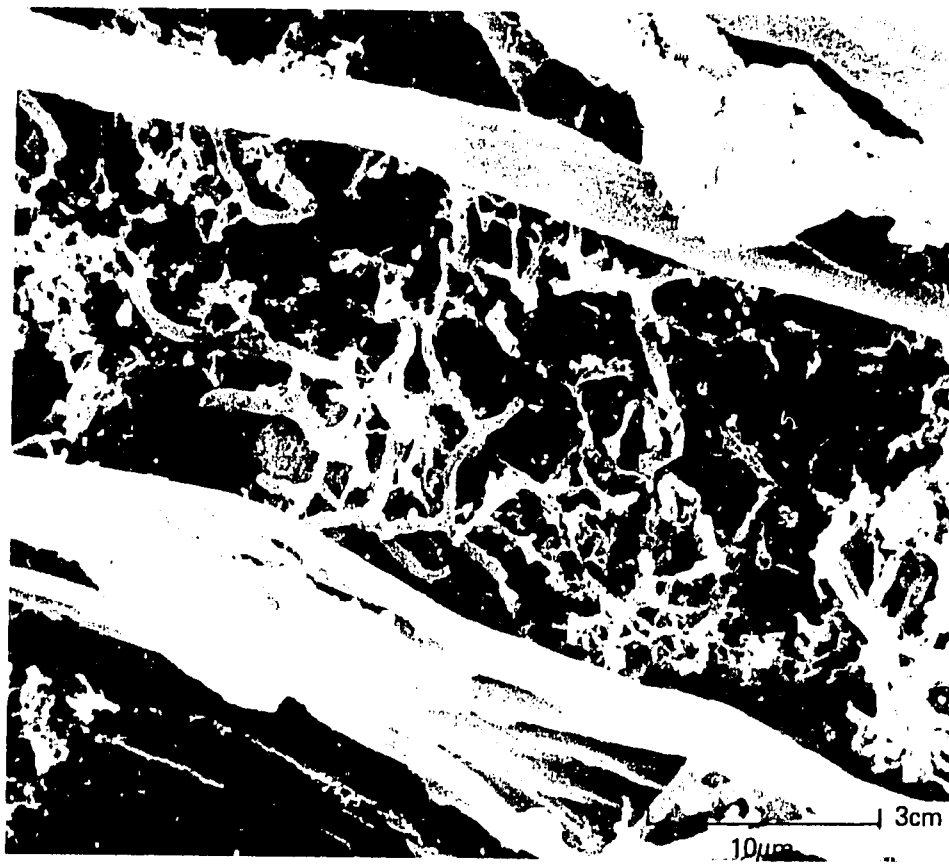

Fig. 3. Stereoscan picture of an arbuscle after treatment to remove the host cytoplasm (onion). (*Courtesy C. M. Hepper*)

to 3 weeks; thereafter, the walls collapse inward. Electronmicrographs suggest that some of the cytoplasm may be recycled to other parts of the hyphal system, but there is also some disintegration, and some constituents of the fungal cytoplasm, especially lipids and autolysis vesicles, can be found as recognizable entities in the host cytoplasm. Throughout its development and breakdown, the arbuscule remains surrounded by the host-cell plasma membrane.

Invasion of the host cell is preceded and accompanied by (1) a marked stimulation of cytoplasmic activity, (2) formation of new organelles (mitochondria, endoplasmic reticulum, ribonucleic acid, and others), (3) swelling of the nucleus (its diameter may increase two- to threefold), (4) mobilization of starch reserves (starch grains disappear from invaded cells), and (5) increased respiration and enzyme activity. A detailed study of arbuscule development and host

reaction in corn roots was made by Joseph (1977). Similar host reactions also occur in response to invasion by pathogenic fungi, but in VA infection the host cytoplasm remains intact and functional after the arbuscule has collapsed. The nucleus reverts to its original size and very occasionally the cell may be reinvaded a second time. The exact sequence and details of arbuscule development and collapse vary with the fungal species causing the infection.

Arbuscules can form 2 to 3 days after the root becomes infected. They are, however, the most labile part of VA infection, strongly dependent on host metabolism and influenced by nutrient supply (Mosse, 1973*b*), light (Hayman, 1974), stage of host development (Greny, 1973; Sutton, 1973; Saif and Khan, 1975) and other factors affecting the host. Cox and Tinker (1976) estimated that the area of host plasmalemma might increase two- to threefold in a cell with an arbuscule and by 20% in the cortex as a whole in a moderately infected onion root. A stereoscan picture of an arbuscule (Fig. 3) shows its large surface area. The intracellular infection is the phase of most intimate contact between the fungus and its host, and, therefore, it may be presumed to have special significance in transfer processes between the two. Nevertheless, mycorrhiza exist with very few arbuscules.

Vesicles

The vesicles are sack-like, usually terminal, swellings at the tip of hyphae (Fig. 4). They contain many lipid droplets and are primarily

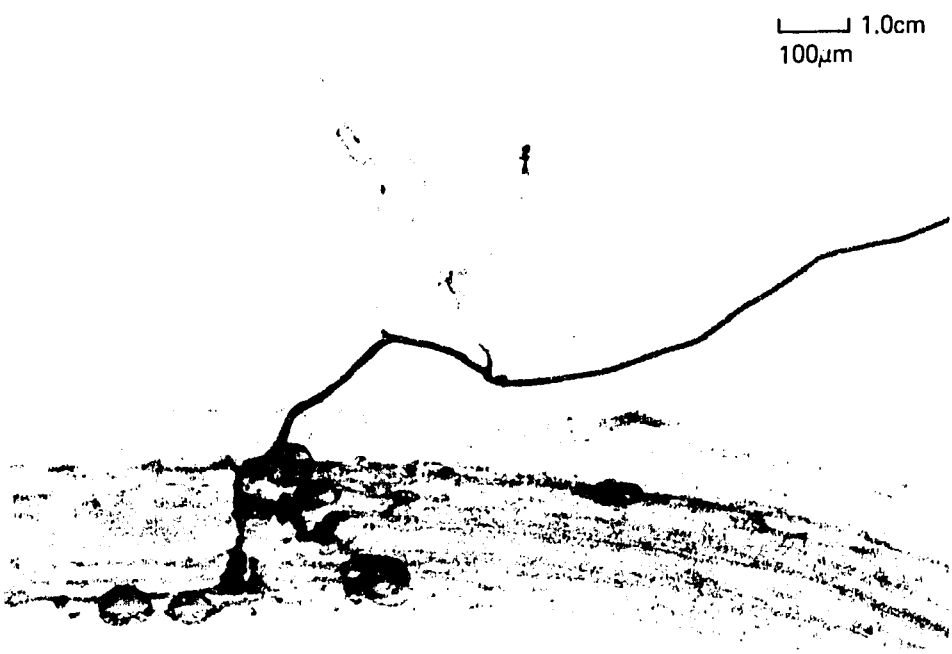

Fig. 4. Detail of an infection in a clover root grown in agar culture. Note the fine absorbing branches of the external mycelium and the vesicles in the root near the point of entry.

Fig. 5. Section of apple rootlets showing attached external mycelium carefully soaked out of the soil. Note the exploration of the area between the roots by the endophyte mycelium.

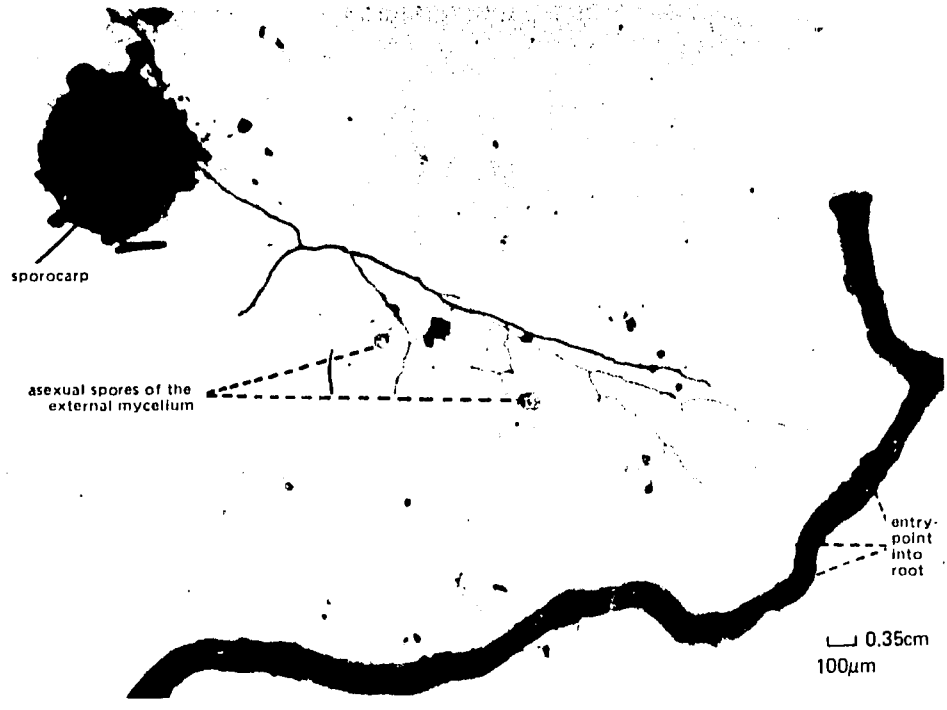

Fig. 6. Section of a strawberry rootlet showing attached external mycelium bearing vegetative spores and the fructification (sporocarp) of an endophyte.

storage organs of the fungus. As the primary cortex is sloughed, a few vesicles may emerge from the root tissue into the soil, where they may germinate and act as infective propagules. Normally, vesicles form after arbuscules. Usually they become more numerous late in the season as plants mature. They also increase following heavy mineral fertilization. Production of many vesicles is often characteristic of individual rootlets rather than the whole root system (Redhead, 1975). Vesicle shape, wall structure, content, and number differ according to the fungal species forming the mycorrhiza.

External Mycelium

An important part of the mycorrhizal system is the mycelium outside the root. It constitutes a strategically placed network of an additional absorbing surface that enables the plant to tap soil P not otherwise accessible to the unaided root (Figs. 5, 6).

The soil mycelium is dimorphic (Nicolson, 1959; Mosse, 1959) and essentially nonseptate. It consists of the main, dichotomously branched, coarse hyphae, usually 8–12 μm but sometimes up to 20 μm in diameter, and tufts of much finer, repeatedly branched,

thin-walled, and ephemeral absorbing hyphae (*see* Fig. 4). The main hyphae have characteristic, one-sided, angular projections (Butler, 1939) from which the rhizoid-like absorbing branches arise when a suitable substrate is encountered. Particles of organic matter and peat are often permeated by these fine hyphae. When the substrate is exhausted, the cytoplasm is withdrawn into the main hyphae, septa are formed, and the absorbing branches wither. Anastomoses frequently occur in the main hyphae, which also have a characteristic method of wound healing (Gerdemann, 1955*b*). With some experience the researcher can recognize the external mycelium of VA mycorrhiza by its morphological characteristics. In carefully collected material, some part of the mycelium can usually be traced back into the root.

The amount of external mycelium has been estimated as 80 cm/cm root length in onions (Sanders and Tinker, 1973), 1% of total root weight in subterranean clover (Bevege, et al., 1975), and 5% of root weight of very heavily infected apple rootlets (Mosse, 1956). In agar cultures, the ratio of internal infection to external mycelium was constant at different rates of infection when $CaHPO_4$ was used as a source of P, but relatively more external mycelium developed when the medium contained calcium phytate, inositol, or glycerol (Mosse and Phillips, 1971). In soil, also, there was a strong correlation between amount of infected root and amount of external mycelium (Tinker, 1975*a*). Development of the external mycelium is affected by soil conditions, particularly aeration, and in some soils the mycelium spreads little from the root surface (Hayman and Mosse, 1971; Mosse, 1977*a*). Spore germination is very sensitive to heavy metals (Hepper and Smith, 1976), and high aluminum and manganese levels in the soil may also affect mycelial growth.

Spores may survive in the soil for months and perhaps even years, but it has been widely believed that the fungus does not spread unless it has a base in a living root. More careful, recent experiments indicate a limited saprophytic spread from detached inoculum (Warner and Mosse, 1980; Ocampo and Hayman, 1980), and more extensive saprophytic activity may occur in soils when the mycelium is attached to a living host.

Occurrence

VA infections are extremely widespread. They occur in most plant families with the exception of Cruciferae, Chenopodiaceae, Cyperaceae, and a few others containing plants of little economic importance. Also excluded are those families that are exclusively ectomycorrhizal, such as Pinaceae and Cupuliferae, or are mainly so, such as Eucalyptus, or have other specialized associations, such as the Ericales and Orchidaceae. Gerdemann (1975) discusses the occurrence of VA mycorrhiza at greater length. Papers reporting growth responses to VA mycorrhiza in important crop plants and their presence in a range of tropical plants are listed in Appendixes B and C. The prevalence of VA mycorrhiza in tropical tree species is often not fully realized (Redhead, 1968; Thapar and Khan, 1973; Tupas and Sajise, 1976; St. John, 1977). Among the temperate crop plants, many cereals (including corn), potatoes, most legumes, many vegetables, herbaceous and tree fruits, and vines form VA mycorrhiza.

It has long been accepted that most roots are mycorrhizal in undisturbed ecosystems, but that mycorrhiza are rare in fertile garden

soils. Recent studies of individual crop plants indicate that certain plant species may regularly attain infection levels never reached by others. Pineapple roots growing in Hawaii were virtually 100% infected with scarcely a single uninfected cell. Some tropical legumes, such as *Centrosema pubescens* and *Stylosanthes guyanensis,* attain similarly high infection rates. In other plants, however, a stationary phase of infection develops, and beyond this percentage, infection does not increase (Sutton, 1973; Saif and Khan, 1975). In cotton, this stage was reached after 20 days, and for the next 100 days infection remained at 60% (Rich and Bird, 1974). Powell and Sithamparanathan (1977) report a mean infection rate of 67% in three legumes inoculated with three separate endophytes, but only 30% infection developed in three similarly inoculated grass species. Grasses in a perennial turf rarely had more than 50% infection (Sparling and Tinker, 1978*a*). Even varieties within a species can have different infection levels (Crush, 1978; Hall, 1978; Khanaqua, 1980).

The Fungi

VA endophytes belong to the Endogonaceae, a family in the Mucorales. They are obligate symbionts and cannot be grown on synthetic media in the absence of a host plant. Because of overall anatomical similarities in a wide range of hosts, it was widely assumed that all VA infections were caused by one, or at most a few, closely related species. This has proved to be wrong.

Progress has come with the discovery that fungal fructifications (sporocarps, *see* Fig. 6) and large, distinctive resting spores found near or attached to mycorrhizal roots in the soil could produce on inoculation typical VA infections in seedlings grown in sterilized soil (Mosse, 1953; Gerdemann, 1955*a*) and in axenic culture (Mosse, 1962). A range of such resting spores, differing in morphological characteristics and life histories, has now been recovered from soils; their relationship to the infected root is shown diagrammatically in Fig. 7. The spores can be multiplied in the presence of a host plant and reproduce, within 4 to 6 months, thousands of new spores of the same kind. This makes it possible to consider them as distinct species, although the normal criteria of species identification by growth and reproduction in monoaxenic culture cannot be applied. Life histories of spore development and range of variability within a progeny can be studied in open-pot cultures containing a living host plant. Ideally the progeny from single-spore inoculations should be examined in this way before accepting or naming a new species, but the success rate of single-spore inoculations is low (Kruckelmann, 1973), and this procedure is rarely followed.

Classification

Endogone resting spores in the soil usually range from about 100 to 600 μm and are some of the largest known fungal spores. This makes it possible to retrieve them from soils by some technique of wet-sieving that separates the lighter organic matter (containing the spores) from the heavier mineral fraction. The spores are borne singly on the soil mycelium or aggregated into more or less well-defined structures called sporocarps. Spores differ in shape and structure of the subtending hyphae, wall structure, cytoplasmic content, color and size, method of spore germination, morphology of secondary spores, presence or absence of sporocarps,

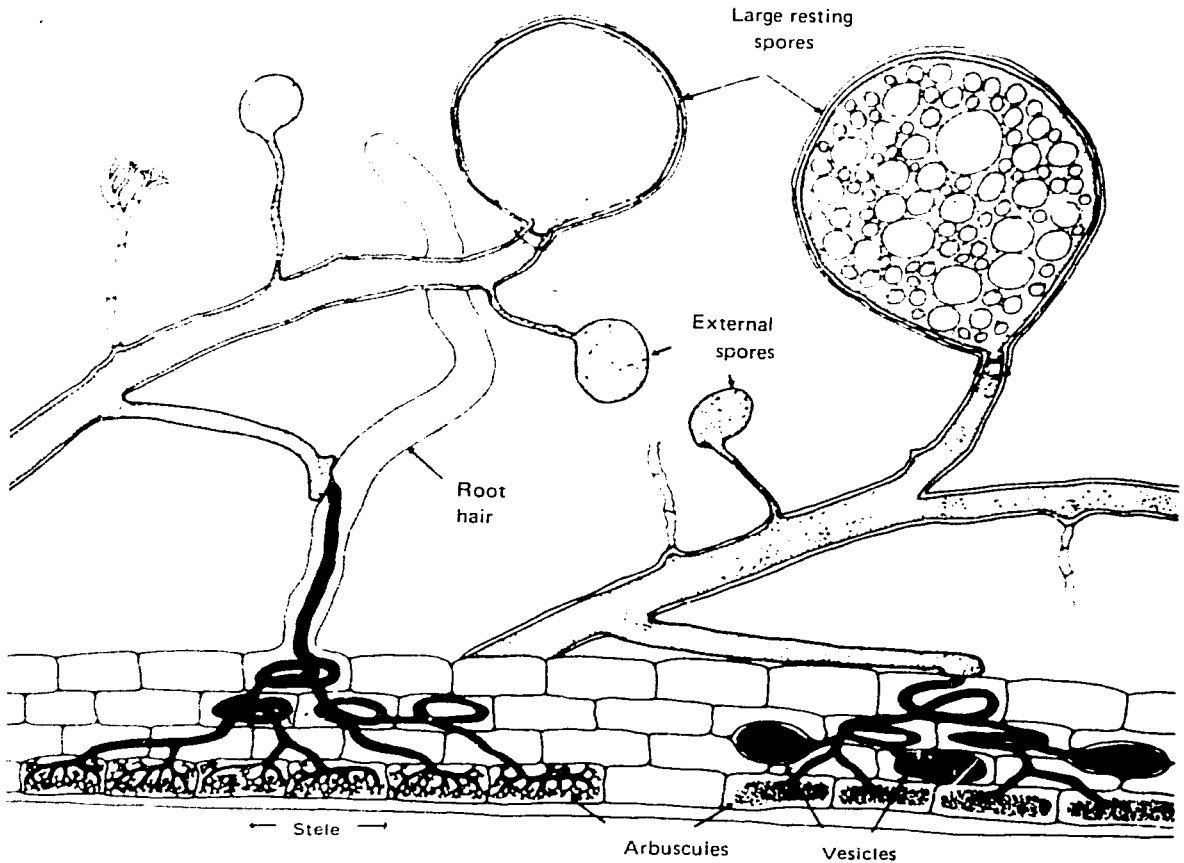

Fig. 7. Diagram of resting spores and soil mycelium and their relationship to a mycorrhizal root. (*Courtesy T. H. Nicolson, from Nicolson, 1967*)

and details of spore arrangement within them. Gerdemann and Trappe's (1974) classification, based more or less arbitrarily on these characteristics, contains four genera that form VA infections; namely, *Glomus*, *Gigaspora*, *Acaulospora*, and *Sclerocystis*. A fifth genus, *Endogone*, is zygosporic and does not form VA mycorrhiza. Within these genera are placed 17 species that form VA mycorrhiza, but this number has already been increased by naming of additional species and even genera. There is also a group of endophytes characterized by a fine mycelium, usually less than 3 μm in diameter, that does not produce recoverable spores in the soil. This fungus was described under the name *Rhizophagus tenuis* (Greenall, 1963) and may represent one or several species.

A reliable species identification of spores obtained by wet-sieving from natural soils is by no means easy, because relatively few spores are recovered in sufficiently good condition. It is usually possible, however, to assign them to the appropriate genus. Beyond this, spore classification is a specialized subject of no particular relevance to the present report. The fact, however, that different endophytes exist—with their different pH requirements (Hayman and Mosse, 1971; Mosse, 1972*a*, 1972*b*; Green et al., 1976; Graw, 1979), different temperature tolerances (Furlan and Fortin, 1973; Schenck and Schroder, 1974; Schenck, et al., 1975), and different reactions to added fertilizer (Mosse, Powell, and Hayman, 1976; Mosse, 1977*a*; Powell and Daniel, 1978*b*) and other unknown factors of the soil environment—has considerable practical significance because it affects their symbiotic function. More detailed study of the anatomy of infections caused by different endophytes has also shown small but diagnostically reliable differences, notably in vesicle structure and growth habit of the fungus (Abbott and Robson, 1978; Mosse, et al. 1980; Warner, 1980).

Stock Plants

Maintenance of stock cultures of endophytes is an important part of present VA mycorrhizal research, but there is no central clearinghouse for information or exchange of material and no manual of techniques. For the many research workers now entering this field, such a manual, describing methods and recording experiences of suitable hosts and soils for optimum multiplication of particular spore types, would be very valuable.

Procedures used for retrieving, collecting, and handling spores are more similar to those used by nematologists than to normal mycological techniques. Indeed, most nematologists are quite used to seeing *Endogone* spores in their preparations, although they may not always recognize them as such. The structures described as nematode microcysts are very likely *Endogone* spores. Various modifications of the wet-sieving technique first used by Gerdemann (1955*a*) to recover *Endogone* spores from soil have been described. All these procedures depend on the fact that the specific gravity of spores is somewhat less than that of soil particles, and therefore the spores float. Gradient centrifugation in a sucrose suspension (Ohms, 1957), sedimentation in high-viscosity liquids, especially gelatin solutions (Mosse and Jones, 1968) or glycerol (Furlan and Fortin, 1975), a flotation-adhesion technique of collecting spores on the side of a glass funnel (Sutton and Barron, 1972), and an adaptation of a fluidizing column (Trudgill, et al., 1972) designed for the extraction of *Heterodera* nematode

females have all been used. Plasmolysis of spores is a danger in many high-viscosity liquids, and immersion times have to be kept to a minimum. If it is desired, spores can be surface sterilized in 2% Chloramine T + 200 ppm Streptomycin (Mosse, 1962), but this is really only necessary for starting axenic cultures. Usually 30 to 50 spores are used as inoculum; fewer are possible, but infection will be slower (Daft and Nicolson, 1969; Ross and Harper, 1970).

For endophytes that do not form resting spores, other inocula have to be used. The commonest are well-washed, infected roots. Sometimes spore formation can be induced or inoculum multiplied by using a baiting technique. A seedling is planted in infested soil, left there for the minimum length of time needed to develop mycorrhiza, then washed well and transplanted into a sterilized soil. Infection will multiply and spores may develop.

Various inoculation procedures can be used, but it must be remembered that the inoculum has very limited growth potential and will not spread much more than 2 to 3 mm without a living root base. It is essential, therefore, that the roots make contact with or grow toward the inoculum.

The growth medium for the host plant can be soil, sand, vermiculite, peat, or a mixture of these. It has to be partially sterilized to remove the indigenous VA infection (*see* section on Distribution that follows). Gamma irradiation (0.8 Mrad), steam, or fumigation can be used for this. The soil should be well aerated and sufficiently fertile to allow reasonable plant growth for at least 6 months, and preferably for 1 year. Occasional feeding with mineral or organic fertilizers may be desirable. The feed has to be adapted to the host plant, its growth rate, whether or not it fixes N, and other special requirements. If the host plant is starved and growing poorly, spore formation will also be poor; but if it is too well fed, the plant will become immune to infection. Particular combinations of host plant and soil have been found to induce optimum spore production of particular endophytes (Mosse, unpubl.; Ross and Ruttencutter, 1977). These interactions are matters of trial and error and are not predictable at present. Soil pH, which is likely to change as pot cultures age, may be important.

Keeping stock plants free from contamination by soil from other stock plants, wind-blown soil particles containing fungal propagules, or insects carrying them (McIlveen and Cole, 1976) requires special precautions. Control of fungal diseases and eelworms also presents problems as fungicides and nematicides are also likely to affect the endophytes. In pot cultures, it is important to keep soil temperatures at or below the acceptable limit of 30°C, but this may be higher for endophytes from tropical soils. Spore production is usually optimum during the first year, declines in the second, and virtually ceases thereafter. When this happens, the stock culture becomes useless, as it can no longer be checked for purity and freedom from contamination. It is therefore necessary to remake stock plants every year.

Distribution of Endophyte Species

Most endophytes appear to have a worldwide distribution, though some may predominate in certain areas. Surveys have been made in the Pacific Northwest (Gerdemann and Trappe, 1974), Florida (Schenck and Kinloch, 1974; Nicolson and Schenck, 1979), and Canada (Sutton, 1973; Koske, et al., 1975); in Scotland (Gerdemann and Nicolson

1963), England (Hayman, 1975), France (Stelz, 1968), Germany (Kruckelmann, 1973), and Spain (Hayman, Barea, and Azcon, 1976); in Nigeria (Redhead, 1973; Sanders, 1976), Tanzania (Mbaga, 1977), and Libya (El-Giahmi, et al., 1976); in Pakistan (Khan, 1971, 1974; Saif, 1975; Saif and Iffat, 1976; Saif and Parveen, 1976; Saif, Ali, and Zaidi, 1977) and India (Thapar and Khan, 1973; Bakshi, 1974), and in Australia (Mosse and Bowen, 1968; Koske, 1975; Hayman and Stovold, 1979); New Zealand (Hayman, 1977; Johnson, 1977), and New Guinea (Shaw, priv. comm.). Others are underway in Brazil, Sri Lanka, Malaya, Cuba, and the Philippines. Most of these surveys have covered limited areas. No relationship has been found between soil types and particular endophyte species. Some endophyte species are pH dependent. For instance *Glomus mosseae* will not generally colonize soils below pH 5.6, whereas *Acaulospora laevis* does not usually occur in neutral or alkaline soils.

In spite of their widespread, general distribution, particular spore types are often localized within quite small areas. For instance, a spore type occurring exclusively in one location at Rothamsted (England) did not occur in a nearby field that contained five other types. Although soils and previous cropping histories are known, it is not possible to explain this distribution. Relatively few fields contain one spore type only; three or four different types are often found together. Nothing is known about microhabitats, whether many spores are formed in a particular soil niche, or whether they are more evenly distributed. Soil adhering to the roots usually contains most spores. Up to 800 spores/g dry soil have been reported (Nemec, 1974). There is much speculation about the evolution of the different endophytes and their distribution, which seems to be both erratic and extremely widespread. Whether human activities could be partly responsible for the erratic distribution is debatable; VA endophytes have no airborne spores and without human agency can move only in drainage water, with animals in whose stomachs they have been found (Dowding, 1955; Bakerspigel, 1956; McIlveen and Cole, 1976), or in windblown soil particles.

Although all susceptible plant species seem able to form VA mycorrhiza with any of the endophyte species, there may be some degree of preferential association (Graw, et al., 1979). Some spore types may multiply better when associated with certain plant species (Bevege, 1971; Fox and Spasoff, 1972; Porter and Beute, 1972; Schenck and Kinloch, 1976; Ross and Ruttencutter, 1977), but the evidence is inconsistent. It is clear, however, that spore numbers can be affected by crop rotation: after 16 years of monoculture, wheat plots contained 130 spores/50 g soil, and potato plots contained less than 10 (Kruckelmann, 1975). Even much shorter rotations affect spore numbers: after 1 year's fallow, numbers dropped from 29 to 18 spores/ml soil, and after a second year's fallow, to 4/ml (Black and Tinker, 1977). Soil growing wheat, sugar beet, and potato for 1 year after oats were grown contained 70, 50, and 5 spores, respectively, per 50 g soil (Kruckelmann, 1975), although potato is a host and sugar beet is a nonhost plant. Similarly, rutabaga (swede), although a nonhost plant, reduced spore numbers very little in a three-course rotation (Hayman, Johnson, and Ruddlesdin, 1975). Spore populations can change qualitatively as a result of fertilizer treatments. In a mixed population containing four spore types, one was selectively de-

creased by N and another selectively increased by farmyard manure (Hayman, 1970, 1975). Introduced endophytes may be more tolerant to added fertilizers than indigenous ones adapted to stress conditions (Mosse, 1977*a*; Powell and Daniel, 1978*b*; Clarke and Mosse, 1980). Sparling and Tinker (1978*b*) preferentially stimulated separate components of a mixed endophyte population by liming or by adding phosphate.

Assessment of Soil Infectivity

Very few natural soils are entirely free from VA endophytes, except those that have been inundated or waterlogged for long periods. To ensure nonmycorrhizal plants, soils must be sterilized. However, the infectivity of natural soils varies; it can be so low that test plants fail to become infected during the experimental period (Mosse, 1977*a*) and may die from P deficiency before infection occurs. Not only soil infectivity, but also soil exploration by roots of the test plant determines whether or not infection will occur (Barrow, et al., 1977). Root spread is genetically determined, but it is also affected by soil fertility.

Spore numbers recovered from agricultural soils are usually of the order of 0.1 to 5 spores/g soil. Using the flotation-adhesion method, by which more dead spores are collected, 20 to 70 spores/g soil were recovered (Sutton and Barron, 1972). Comparison of an adhesion-flotation technique, a wet-sieve sucrose-centrifugation method, differential sedimentation on gelatin columns, and a direct count of a soil suspension poured onto an agar plate gave, respectively, 14, 20, 14, and 74 spores/g of moist soil (Smith, priv. comm.). Clearly there is also some difference in the way a technique is applied. Spore frequency decreases in the deeper soil layers, usually quite markedly below 30 cm (Sutton and Barron, 1972; Saif, Sheikh, and Khan, 1975; Redhead, 1977). There are also marked seasonal variations, usually with a pronounced increase toward autumn (Mason, 1964; Hayman, 1970; Sutton and Barron, 1972). Spores increased from about 26/10 g of sand in a marine foredune to 275/10 g sand in the second dune (Koske, 1975).

The endophyte population of a soil can be assessed in four ways: (1) by direct observation of infection levels in the plant population; (2) by measuring the rate at which a test seedling becomes infected; (3) by determining the maximum dilution at which infection still occurs (Porter, 1979); and (4) by a count of spores in the soil. The purpose of the survey will affect the choice of method; (1) and (4) have been most commonly used and can provide immediate answers.

A direct assessment of root infection requires collection of a representative root sample and a method of assessing the extent of infection in the sample. There are two parameters of infection, namely, incidence and extent. The usual aim is to give a figure for the proportion of potentially infectable tissue (i.e., primary cortex) that is colonized by the fungus. This would exclude main roots. The entire sample can be spread out in a Petri dish and infections estimated visually, either overall or by averaging a number of randomly selected microscope fields. Or, presence or absence of infection can be recorded at points selected by a gridline intersect method (Marsh, 1971; Sparling and Tinker, 1975; Ambler and Young, 1977) based on a formula of Newman (1966). These adaptations can give estimates of both total root length and the proportion infected.

A good dissecting microscope is sufficient for such observations. Alternatively, more detailed observations can be made on randomly selected root pieces mounted on slides and viewed under a compound microscope. The advantage of this is that closer observation may give more information on anatomical details of infection and other fungi present, but the disadvantage is the much more restricted sample. In an evaluation of the visual, gridline intersect, and slide methods (Giovanetti and Mosse, 1980), the latter had the largest standard error. A method of evaluating total fungi weight by measuring chitin content has been described by Hepper (1977), and Becker and Gerdemann (1977) have assessed a yellow pigment produced in roots as a result of infection. Not all plant species develop the yellow pigment, however, and other chitin containing fungi and eelworms will be included in the chitin assay. The problem of assessing root infection is not pecular to mycorrhiza but applies equally to the study of fungal pathogens.

Spore counts have been used for two purposes: (1) to obtain a qualitative record of endophytes present and the effect of treatments on the composition of the population, and (2) to obtain a quantitive measure of soil infectivity. The correlation between spore number and root infection is usually positive in experimental situations involving a particular soil or a defined growth medium (Hayman, 1970; Daft and Nicolson, 1972) but is much less reliable for general surveys involving various soils, some of which may contain nonsporing endophytes (Mosse and Bowen, 1968; Hayman, Barea, and Azcon, 1976; Redhead, 1977; Hayman, 1978*b*). Correlation was also poor at low fertility levels in a survey of differentially manured field plots (Hayman, Johnson, and Ruddlesdin, 1975).

Assessments of soil infectivity based on soil dilution or serial harvest, to determine the onset of infection, are more exact but also require more time and space to grow the test plants. In addition, results can be affected by the choice of test plant.

EFFECTS OF VA MYCORRHIZA ON PLANT PHOSPHORUS UPTAKE AND GROWTH

General Principles

There is now much well-documented evidence that VA mycorrhiza have important effects on plant P uptake (*see* reviews in Introduction). Some typical effects of inoculation in sterilized soils are shown in Table 1. It is usual in such experiments to wash the inoculum and to add the filtered washing to the controls in order to reintroduce contaminants associated with the impure innocula. Sometimes the washings also have minor effects on plant growth (Mosse, 1972*b*). The extent of the growth improvement due to the mycorrhiza depends on the amount of available P in the soil and on the plant species. Manifold growth increases are quite frequently recorded, and a nearly fiftyfold increase occurred in grapevine seedlings and in sweet gum (*see* Table 1). Such large differences are real but contain an element of artificiality since the nonmycorrhizal plants are so P deficient that they remain stationary while the mycorrhizal plants grow steadily. The final size difference simply reflects the duration of the experiment.

Table 1. Growth of nonmycorrhizal (NM) and mycorrhizal (M) plants in sterilized soils

Host	Dry wt (g)/plant and P (%) in tissue (in parentheses)				Reference
	NM		M		
Liriodendron tulipifera (yellow poplar)	1.1		6.61[a]		Clark, 1969
Vitis vinifera (grapevine)	0.19		9.51		Possingham and Obbink, 1971
Liquidambar styraciflua (sweet gum)	0.4		21.9		Bryan and Kormanik, 1977
Zea mays (corn)	3.7		13.3[b]		Gerdemann, 1964
Manihot sp. (cassava)	1.2	(0.10)	11.9	(0.14)	Islam, 1977
Guizotia abyssinica (niger seed)	1.6	(0.61)	3.1	(1.10)	Nyabyenda, 1977
Sorghum bicolor (sorghum)	2.9	(0.47)	5.1	(0.74)	Nyabyenda, 1977
Trifolium repens (white clover)	0.08	(0.21)	0.14[c]	(0.29)	Mosse, Powell, and Hayman, 1976
Glycine max (soybean)					
plant wt/m^2	2567.0		3450.0[d]		
seed yield/m^2	812.0		1161.0		Ross and Harper, 1970
Oryza sativa (rice)					
plant wt	31.0	(0.09)	29.0	(0.35)	
grain wt	8.9		12.6		Sanni, 1976*b*

[a] Fresh weight in grams.
[b] Soil contained 30 lb/acre available acid-soluble phosphorus.
[c] Soil contained 16 ppm $NaHCO_3$-soluble phosphorus.
[d] Treatment = 444 kg/ha of 0:10:20.

Two factors clearly indicate that the growth responses are due to an increased P uptake: (1) the P concentration of mycorrhizal plants is usually higher than that of nonmycorrhizal plants, and (2) mycorrhiza and added P have similar effects on growth (Table 2). When sufficient P is added, there is no longer any growth difference between mycorrhizal and nonmycorrhizal plants, although the mycorrhizal plants may have a higher percentage of P (Holevas, 1966; Ross, 1971; Abbott and Robson, 1977; Menge, Lembright, and Johnson, 1977). If the P additions are made in sufficiently small steps, both mycorrhizal and nonmycorrhizal plants will generally respond with growth increases (Ross, 1971; Mosse, 1973*b*; Menge, Lembright, and Johnson, 1977; Powell, 1977*c*; Roncadori and Hussey, 1977; Smith and Daft, 1977; Abbott and Robson, 1977). For the mycorrhizal plants, the response curve will generally be steeper and reach a plateau with less added P; that is, the critical point (95% of potential growth) is usually reached by the mycorrhizal plants at a considerably lower P input. Fig. 8 shows a series of hypothetical response curves for mycorrhizal and nonmycorrhizal plants. The literature contains examples of nonmycorrhizal plants reaching a final growth plateau above (NM_1), below (NM_3), or equal to (NM_2) that of mycorrhizal ones. A response curve for cassava (Fig. 9) shows that even 800 kg/ha of triplesuperphosphate (≈166 kg P) did not fully equal the effect of mycorrhiza on growth.

Some general principles can now be formulated from the results of many pot experiments with (1) different host plants, (2) soils of different P contents, and (3) increasing additions of phosphate.

1. Plants differ in the extent to which they depend on mycorrhizal uptake.
2. The extent to which a plant benefits from mycorrhizal association depends on the degree of P deficiency the nonmycorrhizal plant is experiencing in that environment and on the reserves of available soil P.
3. The extent of mycorrhizal development is affected by the plant nutrient level.

Plant Species

Some plant species, such as *Coprosma robusta, Liquidambar styraciflua, Leucaena leucocephala,* some *Citrus* spp., and others, are almost totally mycorrhiza-dependent, at least during the early seedling stage. Without mycorrhiza they respond little to even large additions of phosphate. In a soil containing 26 kg P/ha of extractable phosphate, even 1120 kg of a 10:10:10 fertilizer failed to induce growth in nonmycorrhizal sweet gum seedlings; many seedlings with only applied fertilizer died, and the remainder attained a maximum height of 5 cm, while mycorrhizal seedlings were 36 cm high (Kormanik, et al., 1977*a*). On the other hand, temperate grasses often depend little on mycorrhizal uptake (Sparling and Tinker, 1978*b*). *Nardus stricta,* for instance, grew equally well with or without mycorrhiza in a soil in which onions responded to mycorrhiza with a fivefold increase in dry weight (Mosse, unpubl.). In addition, sweet vernalgrass (*Anthoxanthum odoratum*) and orchardgrass (*Dactylis glomerata*) only responded to mycorrhiza in a soil containing 4 ppm Truog P (Crush, 1973*a*). Yost and Fox (1979) compared the growth of seven plant species in soils with different levels of available P with and without the indigenous mycorrhizal fungi. Increasing dependence on mycorrhiza was in the following order: soy-

Table 2. Growth effects of mycorrhiza and of added phosphate: yield (g) and phosphorus (%) (in parentheses) of plants without mycorrhiza (NM), with mycorrhiza (M), and with added phosphorus (P)

Host	Treatment								Amount of P added
	NM		NM + P		M		M + P		
Onion[1]									
dry wt/shoot	0.25	(0.09)	1.48	(0.11)	1.48	(0.10)			50 ppm
Strawberry[2]									
dry wt/shoot	6.7	(0.09)	18.8	(0.15)	16.0	(0.14)	17.4	(0.19)	64 ppm
Soybean[3]									
dry wt/1.5 m^2	1271	(0.10)	1752	(0.14)	2561	(0.21)	2492	(0.21)	44 kg/ha
grain yield/1.5 m^2	540		700		1202		1172		
dry wt/1.5 m^2			2282.00	(0.16)			2406	(0.22)	176 kg/ha
grain yield/1.5 m^2			940.00				1052		

References: 1. Mosse, 1973*b*; 2. Holevas, 1966; 3. Ross, 1971.

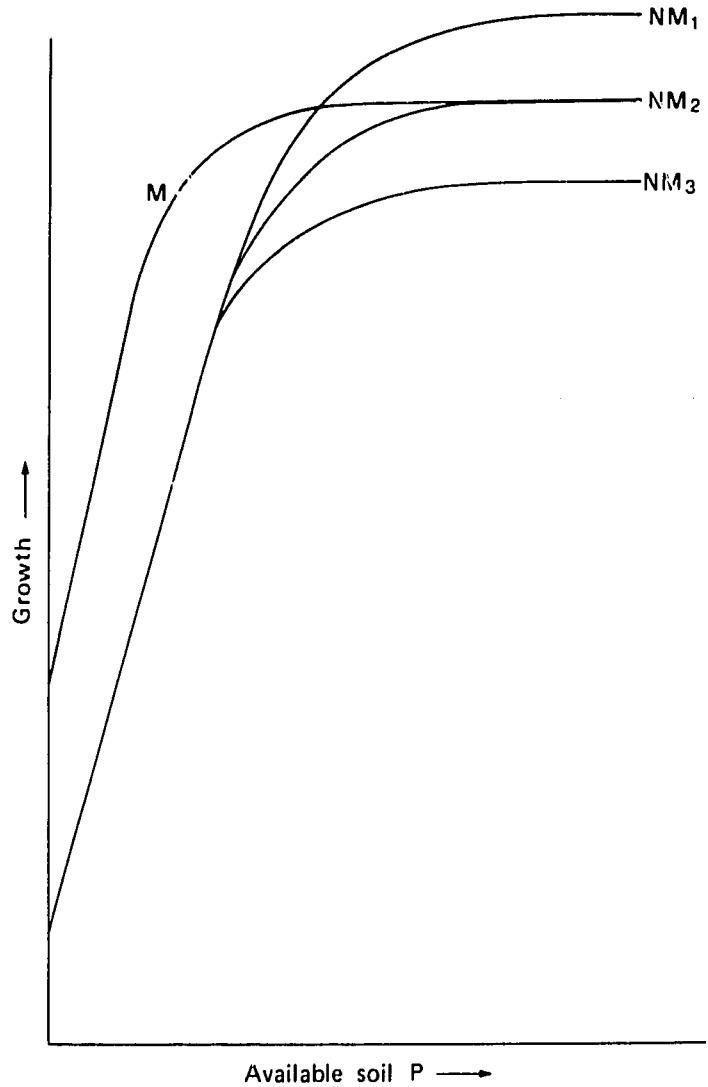

Fig. 8. Hypothetical curves showing response of mycorrhizal (M) and nonmycorrhizal (NM_1, NM_2, and NM_3) plants to increasing amounts of available soil phosphorus.

bean, cowpea, onion, *Leucaena*, *Stylosanthes*, and cassava.

Agronomists are well aware that plant species, and even varieties, differ in their ability to extract soil phosphate. The reasons are by no means fully understood, but root geometry (the amount and distribution of roots in soil) is an important factor (Nye and Tinker, 1977). Root length of grasses is twice that of legumes and 10 to 15 times greater

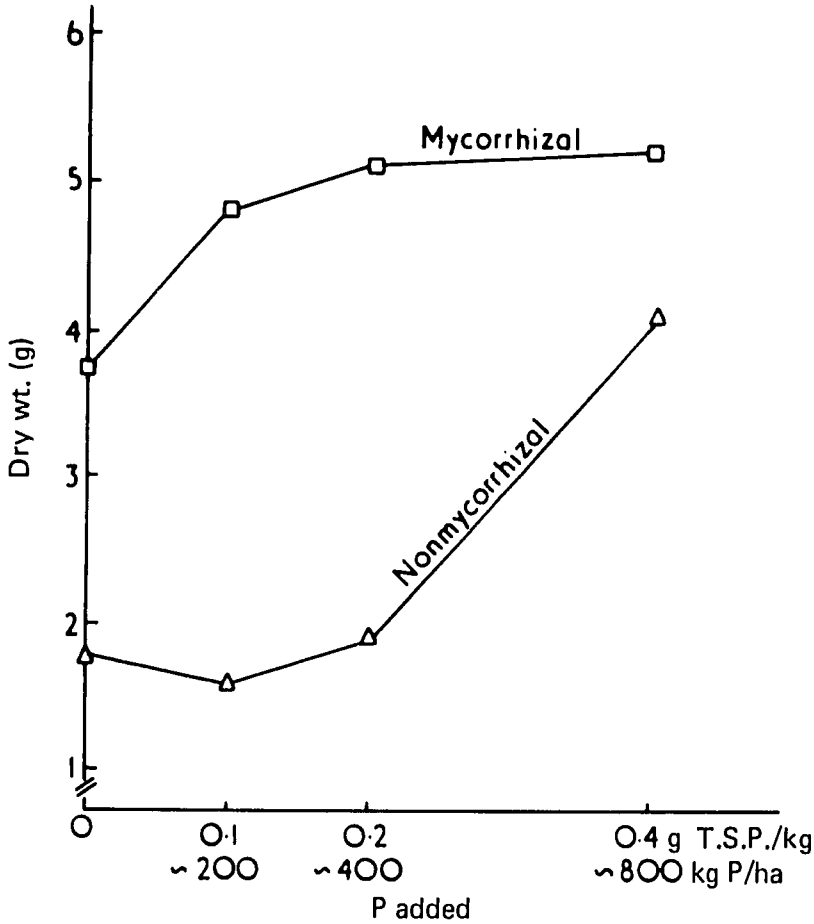

Fig. 9. Growth responses of mycorrhizal and nonmycorrhizal cassava in a sterilized soil to increasing additions of triplesuperphosphate. (*Courtesy F. E. Sanders*)

than that of woody plants (Barley, 1970). The seedlings of many woody plants are almost obligatorily mycorrhizal, and legumes are more dependent on mycorrhizal association (particularly for adequate nodulation) than grasses. Baylis (1975) suggested that plants with few or short root hairs tended to be more mycorrhiza-dependent than those with many long ones.

Interactions between Plant, Soil, and Mycorrhiza

Much information about the complex interactions between plant species, soil P level, extent of infection, and effect of mycorrhiza has come from the experiments of a group of workers in New Zealand (Baylis, 1971, 1975; Cooper, 1973, 1975; Crush, 1973*a*, 1973*b*, 1976; Hall, 1975; Johnson, 1976;

Powell, 1977*d*). Table 3 illustrates some of the complexities of these interactions.

Menge, Johnson, and Platt (1978) showed similar diversity of inoculation responses for six citrus cultivars at three nutrient levels. In general, response curves are like those shown in Fig. 8, but the point at which mycorrhizal and nonmycorrhizal curves meet and the rate at which critical-point P levels are reached depend on plant species. At this point, the percentage of P in plant dry matter is often higher in mycorrhizal than in nonmycorrhizal plants (Stribley, et al., 1980). In practice, such luxury uptake by mycorrhizal plants may not matter, and it may even have advantages in concentrating added fertilizer P in plant residues from which it may be subsequently be released, rather than being irreversibly sorbed in the soil.

The matter is further complicated by the effect of nutrient levels on the development of mycorrhizal infection. In very P-deficient plants, the percentage of infection is generally less than in those given some phosphate, but at very high P levels, mycorrhizal infections first become abnormal and then die out (*see* Table 3; Mosse, 1973*b*). Foliar feeding (Sanders, 1975), split-root (Menge, Steirle, et al., 1978), and transplantation experiments (Mosse, 1973*b*) suggest that plants become immune to infection when their internal P concentration becomes too high for fungal development. Reduced exudation and lower membrane permeability of P-sufficient plants may contribute to this effect (Ratnayake, et al., 1978).

It is doubtful whether actual growth increments are always directly related to total number or volume of mycorrhizal roots, but there is some overall relationship. For a proper evaluation of the amount of infection, root density and the percentage of infection have to be taken into account. Daft and Nicolson (1972) found that in mycorrhizal tobacco and maize at various phosphate levels, the percentage of infection did not correlate well with shoot weight unless the size of the root system was included in the calculations. Root density is not only plant-specific but also affected by soil fertility. In a split-root experiment, a beech seedling formed 90 times as many root tips in an infertile mor soil as in a fertile mull. As many as 80% of the roots in the mull were mycorrhizal as compared with 50% of the roots in the mor. The total number of mycorrhiza was 50 times greater on the side with the lower percentage of infection (Meyer, 1973). Root density and root/shoot ratios are normally lower in fertile soil where relatively small root systems apparently suffice for nutrient uptake. Mycorrhizal plants also generally have lower root/shoot ratios than nonmycorrhizal (Hayman and Mosse, 1971; Abbott and Robson, 1978), although exceptions are recorded. Mycorrhizal root systems may or may not be smaller in absolute terms, but rootlet decay was faster in mycorrhizal apple rootlets than in nonmycorrhizal ones growing in a sterilized soil (Mosse, 1956). This appears to be contrary to the greater longevity of roots with sheathing mycorrhiza.

The mycorrhizal association appears to be in some measure self regulating: when the association is no longer advantageous, the plant becomes immune to mycorrhiza. Growth depressions can occur in some plant species at this stage when infection levels are already dropping (*see* Table 3; Mosse, 1973*b*; Cooper, 1973, 1975). In soils containing 4 to 12 ppm Truog P, a *Histiopteris* species and a *Leptospermum* species reacted with growth depressions or improvements to added P and a complete-nutrient, minus-P solution, accord-

Table 3. Effects of inoculation on three plant species grown at four levels of soil phosphate without mycorrhiza (NM) and with mycorrhiza (M)

Host	Truog P (ppm)	Mean wt (mg)		P (%)		Infection (%)
		NM	M	NM	M	
Fuchsia	11	185	304	0.14	0.12	9
	14	659	478	0.11	0.14	34
	25	1451	432	0.12	0.15	12
	60	2838	2672	0.14	0.15	2
Coprosma	11	38	239	0.06	0.17	53
	14	143	463	0.08	0.16	67
	25	623	918	0.09	0.14	62
	60	2138	2068	0.15	0.15	16
Griselinia	11	35	58	0.03	0.11	39
	14	49	62	0.04	0.09	56
	25	76	69	0.06	0.09	52
	60	201	818	0.11	0.11	21

After Johnson, 1976.

ing to the original soil P and the amounts of P added (Cooper, 1975). In a *Lolium* species (ryegrass), no growth depressions occurred, although at high levels of P there was no longer a response to mycorrhiza. In two *Solanum* species, initial growth depressions due to mycorrhiza at high P levels changed to increases at the end of the experiment (Cooper, 1975). Experiments with four legumes, three *Trifolium* and one *Medicago* species (Crush, 1976), also illustrate the delicate balance between growth effects of mycorrhiza, soil P, and plant species and the general unpredictability of their interaction at higher P levels. Graw (1979) found that, with different kinds of added P, mycorrhizal plants grew better or worse than nonmycorrhizal, according to plant species and soil pH, although the mycorrhizal plants always took up more P. A frequently suggested explanation of such growth depressions is that mycorrhizal infection deprives the plant of photosynthate carbon, used either in fungal growth or increased root respiration (Stribley, et al., 1980). Another possibility is that the increased P uptake can sometimes lead to supra-optimal P concentrations in the plant (Mosse, 1973*b*). Tolerance levels would vary with plant species.

Temporary growth depressions lasting 2 to 3 weeks are not unusual in young seedlings immediately after inoculation.

The Special Case of Legumes

Symbiotic N fixation by rhizobia in legume nodules has a high P requirement. The percentage of P in nodules is two to three times greater than that of the roots on which they are borne, and compounds rich in P are energy sources for the fixation process. In addition, the root systems of legumes are relatively restricted. It is therefore not surprising that most legumes respond favorably to mycorrhizal infection. In many experiments in P-deficient soils, nodulation and symbiotic N fixation were markedly improved or were even contingent on mycorrhizal infection (Asai, 1944; Crush, 1974; Daft and El-Giahmi, 1974, 1975, 1976; Smith and Daft, 1977; Mosse, Powell, and Hayman, 1976; Mosse, 1977*a*; Islam, 1976, 1977; Abbott and Robson, 1977). An example is shown in Fig. 10. *Centrosema* seedlings only nodulated when they were either mycorrhizal or were given phosphate. Without either treatment, the plants made very little shoot growth, and, in spite of a reasonably well-developed root system, they bore no nodules.

Table 4 shows that, like other plant species, legumes differ in their dependence on mycorrhizal uptake and that this may be inversely related to their root-hair development. Lupins, although good colonizers of P-deficient soils, appear to be relatively independent of mycorrhizal infection and *Lupinus cosentinii* is virtually immune (Trinick, 1977; Morley and Mosse, 1976). On the other hand, *Stylosanthes guyanensis* grew very little and virtually did not nodulate in several tropical soils from Brazil and Belize, even with extra phosphate, unless the plants were mycorrhizal (Fig. 11). This effect persisted in subsequent plantings with *Trifolium repens* and *Centrosema pubescens* (Mosse, Powell, and Hayman, 1976). Even when given bone meal or fed with a nutrient solution containing soluble phosphate, mycorrhizal peanuts had more nodules than nonmycorrhizal, and, at all levels of added P, mycorrhizal peanuts had a higher percentage of N in the shoots (Daft and El-Giahmi, 1976). Mycorrhizal beans had 6% more total shoot protein (Daft and El-Giahmi, 1974), and mycorrhizal soybeans had 2%

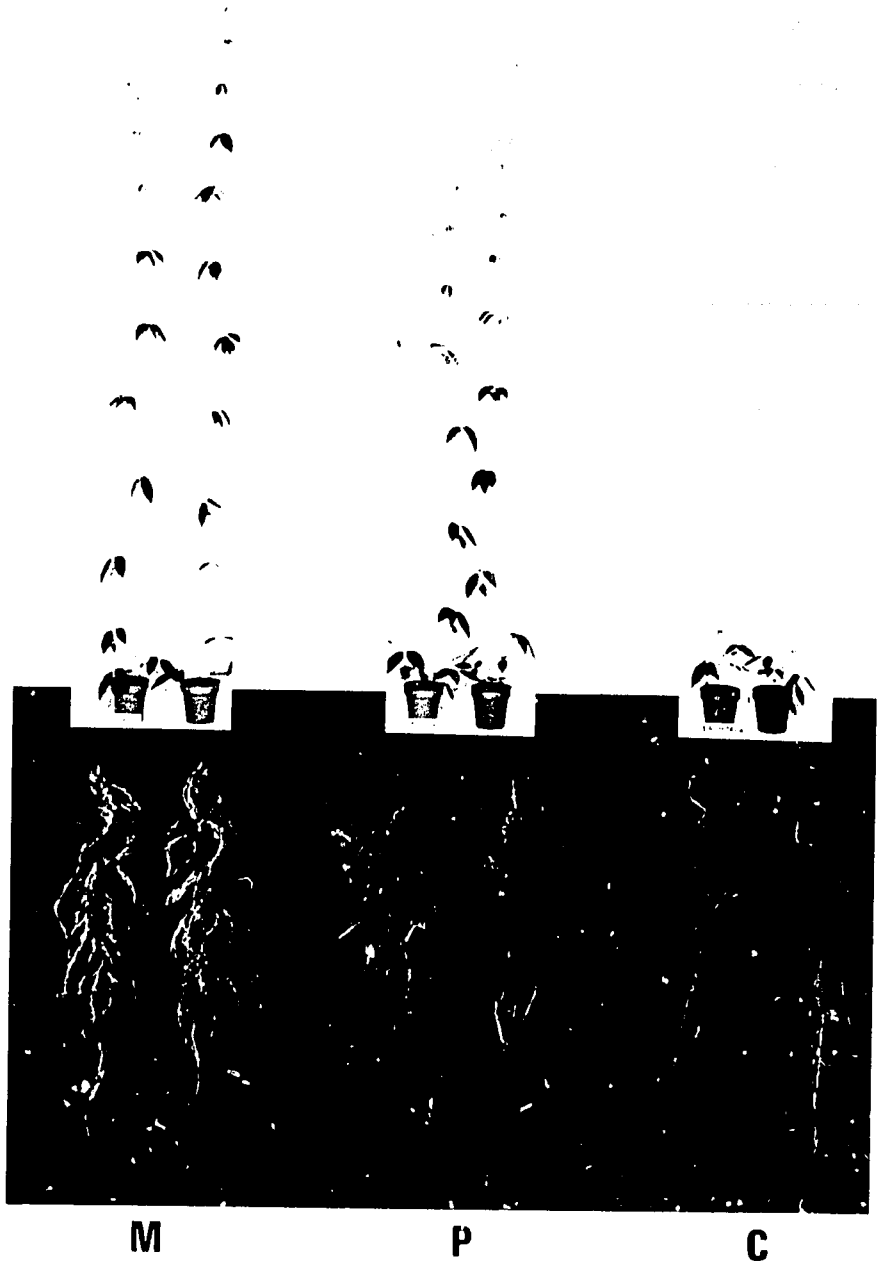

Fig. 10. Response of *Centrosema pubescens* to mycorrhiza (M) or added phosphate (P) at the rate of 275 kg P/ha. Note absence of nodules in control (C) without mycorrhiza or phosphate. All plants inoculated with *Rhizobium*. (*After Crush, 1974*)

Table 4. Effects of mycorrhiza and phosphate on growth and nodulation of four legumes

Host	NM (without mycorrhiza)		M (with mycorrhiza)		NM + P (with phosphate added)[b]		Length of root hairs (μm)
	Fresh wt (g)	Nodulation[a]	Fresh wt (g)	Nodulation[a]	Fresh wt (g)	Nodulation[a]	
Centrosema pubescens	1.7	1	3.9	5	4.9	5	106
Stylosanthes guyanensis	0.5	0	1.6	5	0.9	5	108
Trifolium repens	1.6	1	2.6	5	4.0	5	213
Lotus pedunculatus	2.5	4	2.0	4	3.9	5	809

After Crush, 1974.

[a]Nodulation category: 0 (no nodules) to 5 (abundant nodules).
[b]Treatment = 0.4 g monocalcium phosphate/kg soil.

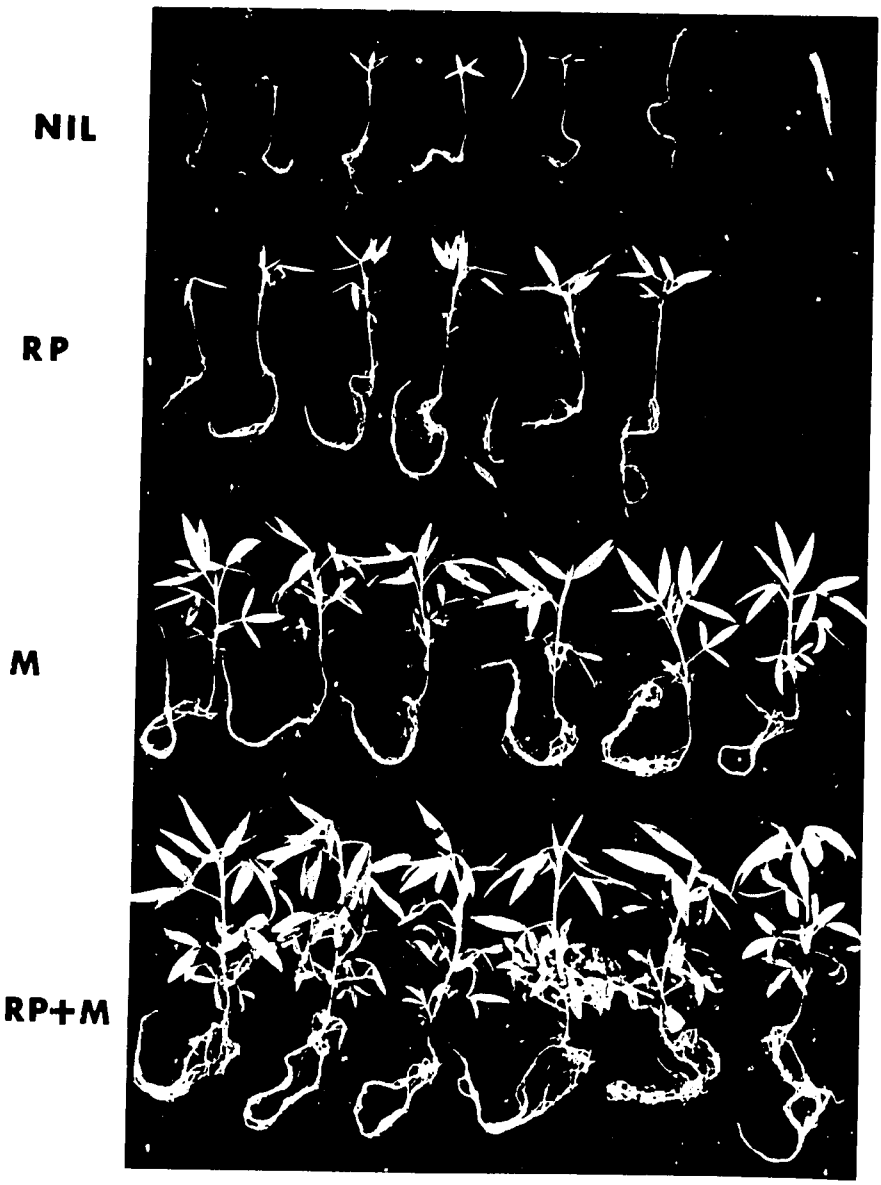

Fig. 11. Response of *Stylosanthes guyanensis* (a) without inoculation (NIL), (b) without inoculation but with added rock phosphate (RP), (c) to inoculation with mycorrhizal fungus (M), and (d) to inoculation *and* added rock phosphate (RP + M).

more seed proteins (Ross, 1971). Similarly, mycorrhizal alfalfa fed with either soluble or tricalcium phosphate had a higher percentage of N at all levels of added P (Smith and Daft, 1977). In field experiments, inoculating with mycorrhizal fungi increased the percentage of N in the shoots of soybeans (Bagyaraj, et al., 1979) but not in cowpeas (Islam, et al., 1980) or lucerne (Owusu-Bennoah and Mosse, 1979). Nevertheless, the possibility that not only dry-matter production but also protein content of legumes may be favorably affected by mycorrhizal infections should be further investigated.

Results of Smith and Daft (1977) indicate that the effect of VA mycorrhiza on nodulation and nitrogenase activity in alfalfa occurred 2 weeks after inoculation with VA endophytes, whereas increases in dry matter appeared only after 10 weeks. This suggests that nodules may have first call on extra phosphate taken up by mycorrhiza. Nodules are, of course, spatially very close to the mycorrhizal roots. Roots bearing nodules can be mycorrhizal, though the fungi hardly ever invade the nodules; the relative ontogeny of nodulation and mycorrhizal colonization of the root is not known.

In legumes with nodules and mycorrhiza, it is not always possible to separate the effects on total dry-matter production of the extra N produced by better nodulation and the extra P inflow due to mycorrhiza. No doubt the two symbiotic systems interact, as do N and P fertilizers. In an interesting trial with a nodulating and nonnodulating isoline of the soybean variety 'Hardee', Schenck and Hinson (1973) showed that only the nodulating line responded significantly with a 53% yield increase to mycorrhizal infection, and its seeds contained 0.6% more protein. These responses occurred in soil derived from phosphatic parent material containing high levels of available P.

Mechanisms of Mycorrhizal Uptake

As a P-uptake mechanism, the mycorrhizal system can be regarded as consisting of three components: the soil, the plant, and the fungus. Fig. 12 shows some of the relationships between them. The extent to which the mycorrhizal system increases plant P uptake is determined by (1) the plant species, its P requirement and inherent ability to extract soil P; (2) the P content of the soil; (3) the extent of mycorrhizal infection, which depends on plant nutrient level and fungal adaptation to soil and climatic environment; and (4) the efficiency of the endophyte species (discussed in Effect of Endophyte Species, which follows). Ultimately all P, whether taken up through the fungal symbiont or directly by plant roots, comes from the soil. This naturally occasions questions about the source of the extra phosphate and how it becomes available to the plant.

Utilization of Sparingly Soluble Phosphates

Experiments designed to see how mycorrhizal plants would grow when supplied with sparingly soluble phosphates, such as bone meal, rock phosphate, apatite, $FePO_4$, $AlPO_4$, and iron and calcium phytates, showed that phosphate was taken up more readily from all these sources when plants were mycorrhizal (Daft and Nicolson, 1966; Murdoch, et al., 1967; Hayman and Mosse, 1972*b*; Ross and Gilliam, 1973; Mosse, Powell, and Hayman, 1976; Boutros-Mikhail, 1976; Nyabyenda, 1977; Powell and Daniel, 1978*b*). Some typical results are shown in

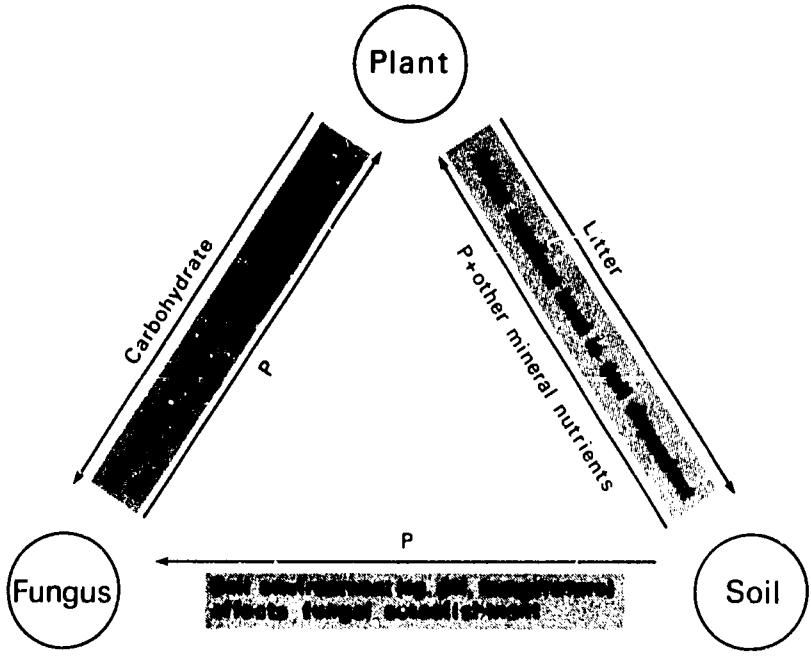

Fig. 12. Diagram showing some of the interactions determining the mycorrhizal contribution to plant phosphorus uptake.

Table 5. Only the utilization of rock phosphate in alkaline soils was not improved (Mosse, Powell, and Hayman, 1976). It was increased by a dual inoculation with mycorrhizal fungi and "phosphate solubilizing bacteria" (Azcon, Barea, and Hayman, 1976).

In particular, the utilization of $FePO_4$ seems greatly improved when plants are mycorrhizal (Ross and Gilliam, 1973; Boutros-Mikhail, 1976; Nyabyenda, 1977), although mycorrhizal rice was unable to utilize strengite (Sanni, 1976*b*). Figs. 13 and 14 are reproduced from a thesis in which Nyabyenda (1977) showed some very remarkable effects of temperature on the utilization of apatite, $FePO_4$, and $AlPO_4$ by mycorrhizal and nonmycorrhizal plants. Sorghum kept at 25°C and given hydroxy-apatite weighed twice as much when it was mycorrhizal than when it was not (Fig. 13), and the tropical weed *Eupatorium odoratum* given $FePO_4$ and kept at 30°C weighed six times as much when it was mycorrhizal than when it was not (Fig. 14). The nonmycorrhizal *Eupatorium* seedlings made no response to $FePO_4$ in the temperature range 20–35°C. These results have obvious importance, particularly for tropical soils, and the chemistry of the processes involved should be further studied. Cooper and Tinker (1978) found that phosphate translocation from an external source into the mycorrhizal root ceased at 8°C.

The better utilization of sparingly soluble phosphates led to the obvious conclusion that mycorrhizal fungi mobilized soil phosphate not otherwise available to plant roots. Work with isotopically labelled soils, however, has not confirmed this. To understand the implications of these findings, it is necessary to know something about the chemistry of soil P.

Table 5. Utilization of sparingly soluble phosphate by nonmycorrhizal (NM) and mycorrhizal (M) plants (examples of published results)

Host	Data expression	Yield (g) and % P (in parentheses)				Phosphate source and treatment
		Without phosphate		With phosphate		
		NM	M	NM	M	
Zea mays[1]	Dry wt/plant	7.5	12.4			control
				8.2	23.1	tricalcium phosphate (70 ppm P)
				8.7	20.8	rock phosphate (70 ppm P)
				40.4	42.0	monocalcium phosphate (70 ppm P)
Glycine max [2a]	Yield/pot	4.5	4.2			control
				1.7	9.1	$FePO_4$
				23.8	42.6	$AlPO_4$
				1.7	3.6	rock phosphate
				34.1	53.3	monocalcium phosphate
Stylosanthes guyanensis[3]	Dry wt/plant	0.021	0.172	0.099	0.484	Morrocan rock phosphate (400 mg/kg soil)
		(0.06)	(0.18)	(0.10)	(0.34)	
	Nodule wt/plant	0.09	0.7	0.3	4.5	
Pueraria phaseoloides[4]	Dry wt/pot	2.4	28.8	24.6	35.8	Jordanian rock phosphate (500 mg/kg soil)
		(0.18)[b]	(0.27)	(0.25)	(0.32)	
	Nodule dry wt/pot	0.004	1.28	0.21	1.93	
	μmoles C_2H_2/pot/hr	0.17	55.0	24.8	123.4	

References: 1. Murdock, Jackobs, and Gerdemann, 1967; 2. Ross and Gilliam, 1973; 3. Mosse, Powell, and Hayman, 1976; 4. Waidyanatha, Yogaratnam, and Ariyaratne, 1979.

[a] Soil contained 2 ppm dilute-acid extractable P.
[b] Transformed values.

Fig. 13. Response of nonmycorrhizal (A) and mycorrhizal (B) *Sorghum* spp. to hydroxyapatite at 20, 25, 30, and 35°C. (*Courtesy P. Nyabyenda*)

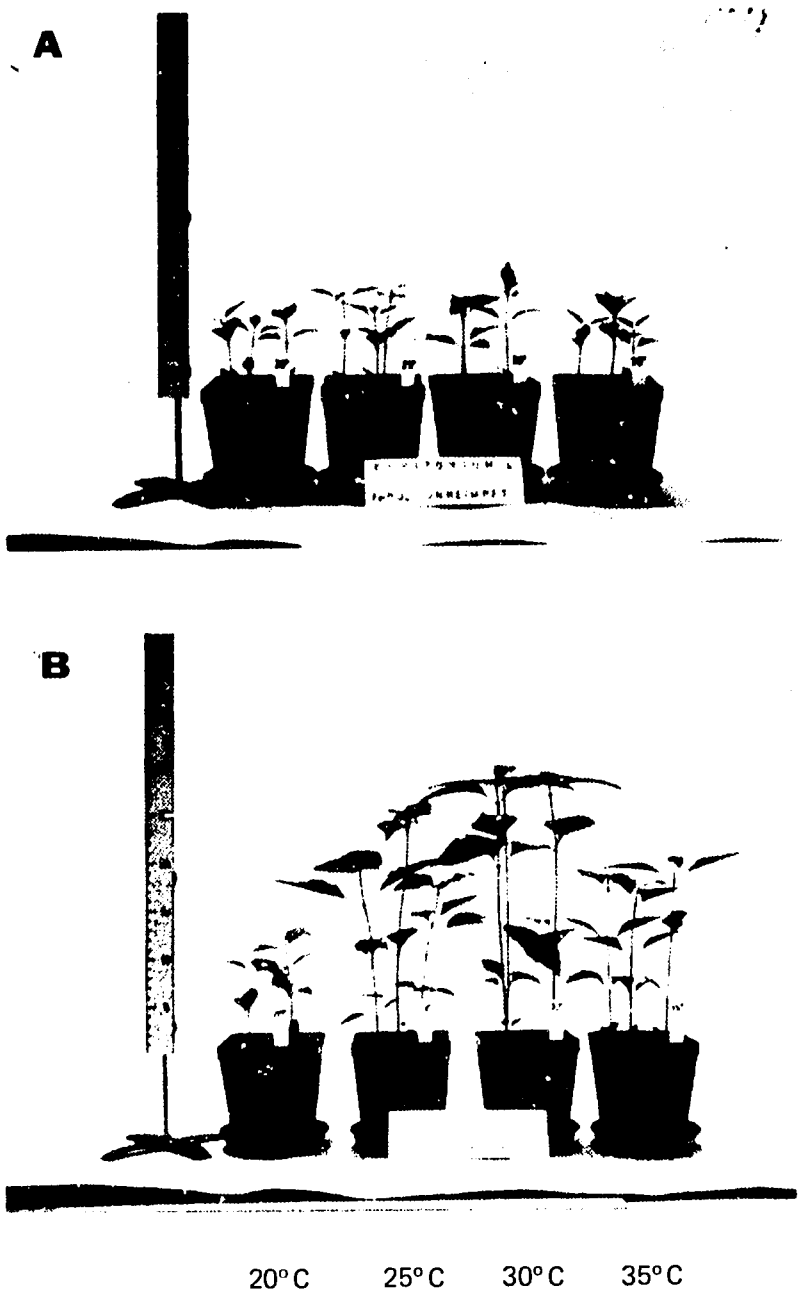

Fig. 14. Growth of *Eupatorium odoratum* at different temperatures without (A) and with (B) mycorrhiza. All plants given $FePO_4$. (*Courtesy P. Nyabyenda*)

Forms of Soil Phosphorus

The study of soil P is very specialized and will be covered by other reports. This is a simplified account concerned only with some aspects relevant to an understanding of mycorrhizal function.

Plant roots take up P from the soil solution. Concentrations here are often less than 0.01 to 0.02 ppm P, especially in tropical soils. The P in solution is in equilibrium with phosphate ions reversibly adsorbed on clay particles. These ions represent a reserve of potentially available P that can go into solution when the concentration in the soil solution drops owing to uptake by the plant. However, as much as 98% of total soil P (more in many tropical soils) is unavailable to plants because it is present as insoluble mineral phosphate or as organic phosphate, or it has been irreversibly adsorbed on iron and aluminum complexes. Maximum solubility of mineral phosphate occurs around pH 6.3 and decreases at a lower or a higher pH. If the P concentration in the soil solution falls below the solubility product of the insoluble phosphate, some will go into solution. The factor limiting plant P uptake in most soils is the slow diffusion rate of PO_4 ions, due in part to the tortuosity of the pathway to the root surface and in part to adsorption on clay particles. The more P deficient the soil, the greater will be the unsaturation of the adsorption sites and the slower the diffusion rate. The rate of P uptake at the root surface exceeds that of replenishment, and, thus, depletion zones develop around roots, further reducing the number of ions available for uptake.

The soil chemistry of P in relation to mycorrhizal effects was considered by Tinker (1975*b*). He classified P sources in the soil as (1) phosphate ions in solution or held on surfaces in such a way that they are in rapid equilibrium with phosphate in the soil solution; (2) mineral phosphates held in crystal lattices or otherwise such that they are not in rapid equilibrium with the soil solution, and (3) P in organic compounds. The first source is considered to be available to plants and is the "labile pool" isotopically exchangeable with ^{32}P. The second and third types are essentially insoluble; they are not isotopically exchangeable with ^{32}P over reasonably short periods and are unavailable to plants. The solubility of this fraction might be increased if mycorrhiza induced a pH change in the rhizosphere, bringing the pH closer to 6.3; or if they induced or increased exudation of anions, such as polygalacturonate, citrate, or oxalate, that could occupy adsorption sites; or if they increased phytase activity. Any changes in soil P that made more of the nonlabile P available to plants should lower the ration of ^{32}P to ^{31}P and and decrease the specific activity ($^{32}P/^{31}P$) of P in plants grown in ^{32}P-equilibrated soil.

Specific Activity of Phosphorus in Mycorrhizal and Nonmycorrhizal Plants

In two experiments (Hayman and Mosse, 1972*a*; Sanders and Tinker, 1971, 1973), the P in mycorrhizal and nonmycorrhizal onions, grown in seven labelled soils or monitored at four different times during their growth, had the same specific activity. Pichot and Binh (1976) reported the same for an *Agrostis* sp. The evidence seemed clearcut that mycorrhiza utilized the same sources of soil P as uninfected roots but were able to tap more of it. Further experiments with other plants in even more deficient soils from Brazil and England essentially confirmed these results. Differences in P uptake between mycorrhizal and nonmycorrhizal plants were

very large in these soils, with cpm/plant sometimes being 100 times greater in the mycorrhizal plants, although their root weight was only twice as great as that of the nonmycorrhizal plants (Mosse, 1973*c*). The results also showed that *Paspalum notatum* and *Centrosema pubescens* took up no phosphate at all from two Brazilian soils unless the plants were mycorrhizal (Mosse, Hayman, and Arnold, 1973). We concluded, in support of a previous hypothesis (Rorison, 1968), that there might be a threshold, solution-P concentration below which some plant species could not take up P, whereas fungi and some other plant species might have no such limitations, or at least might have lower limits. This might eventually lead to more solubilization of mineral phosphate, but the process would, at best, be slow and did not show up as a difference in specific activity. Autoradiography of ^{33}P-labelled soil also showed less radioactivity in the depletion zone around mycorrhizal onion roots than around nonmycorrhizal, suggesting a lower soil-solution concentration (Owusu-Bennoah and Wild, 1979). Supporting evidence for the greater depletion of soil-available P after a mycorrhizal crop also comes from chemical soil analysis after harvest (Gerdemann, 1965) and from biological assay. Radishes, which do not become mycorrhizal, grew much worse after mycorrhizal strawberries than after nonmycorrhizal.

Nevertheless, some doubt remains. Benian and Barber's (1972) finding, that P in mycorrhizal barley had a lower specific activity than in nonmycorrhizal, tends to be overlooked because the difference was just below the 5% level of statistical significance, and the soil was unusual in that different plant species had different L values. Results of Swaminathan and Verma (1977) indicated that mycorrhizal potatoes had taken up relatively more ^{31}P than nonmycorrhiza from two labelled soils in India. Gianinazzi-Pearson and Gianinazzi (1976) reported an alkaline phosphatase present in mycorrhizal but not in nonmycorrhizal onion roots and believe that this may have some function in P mobilization. If this occurred, even to a small extent, mycorrhiza may have an important long-term function in mobilizing phosphate in undisturbed ecosystems.

Because mycorrhiza, in the main, utilize the same sources of soil P as uninfected roots, the competitive ability of two plant species can be affected if they react differently to mycorrhizal infection. This occurred when one plant (pine) was a host and the other (*Sorghum*) was not (Stone, 1949), or when both species were hosts but one (*Holcus*) derived more benefit from the association than the other (*Lolium*) (Fitter, 1977). In other experiments, however, mycorrhizal infection in different grass species grown together was little affected, and growth interactions between the species were not attributable to mycorrhiza (Christie, Newman, and Campbell, 1978). Under some conditions a mycorrhizal system may help a poor phosphate feeder to compete with a better one (Powell, 1977*d*). This is particularly relevant to legumes in pastures.

For annual crops, the undoubted rapid depletion of the labile phosphate by a mycorrhizal crop means that better crop production through mycorrhiza can only be maintained with some fertilizer input. It is also evident from a rapidly growing number of results, however, that mycorrhiza, at least in pot experiments, greatly improve the utilization of sparingly soluble phosphates. In practice, rock phosphate is the most important of these.

Uptake through the External Mycelium

If the extra phosphate taken up by mycorrhizal plants comes chiefly from the labile pool, then no changes in root metabolism, surface properties, or root exudates brought about by the infection are likely to affect P uptake because this is limited by the presence of depletion zones. That leaves the extra-absorbing surface provided by the external mycelium beyond the depletion zone as the most likely explanation of the increased uptake. The surface provided by the soil mycelium is very large: some length and weight measurements have been given (*see* discussion on p. 13). The problem with all estimates of hyphal mass in soils is to distinguish between live and dead mycelium. Morphologically, the external mycelium is extremely well adapted for nutrient uptake. The hyphae are essentially aseptate: their frequent anastomoses make them into a very efficient interconnected network well able to repair or bypass damaged parts. Using a Petri-dish assembly Rhodes and Gerdemann (1975, 1978) demonstrated unequivocably that external hyphae took up ^{32}P applied 7 cm from the root surface and ^{35}S applied 8 cm from the root, and transferred them into the plant. Exploration of nutrient-rich microsites by ephemeral-feeding hyphae can occur at almost any point because the angular projections of the hyphae are potential growing points. Making an extra absorbing surface by hyphal growth requires a minimal expenditure of energy, because of the large surface/volume ratio of fungal hyphae. In effect, the hyphal system in the soil, because of its ability to move cytoplasm and regrow, can be regarded as essentially mobile, and this enables it to overcome the constraints of the depletion zone which the plant can only overcome by energy-demanding root extension. Once an ion has been taken up into a hypha, it is protected against further adsorption in the soil.

Uptake through a mycorrhizal system can be considered as a three-stage process: uptake by the soil hyphae, transfer into the root-based mycelium, and release into the plant. Any one of these stages can be rate limiting. The number of entry points into the root has generally been considered as the biggest obstacle to effective nutrient transfer. Many observations have been made (Mosse, 1978), ranging from 17/mm^2 root surface in strawberries to 0.6/mm root length in onions. Numbers are affected by soil, fertilizer treatment, season (Mosse, 1956), endophyte (Powell, 1977*b*), and plant species. Because infection of new rootlets has to come from the soil, every infected rootlet has at least one connecting link. But hyphae may grow along the root surface sending out infection branches at intervals, and therefore every observed entry point, particularly in microscope sections, does not necessarily represent a separate, direct link to the soil mycelium. Many workers in the 1930s were convinced of the impossibility of significantly increased nutrient uptake by VA mycorrhiza because of the paucity of connecting hyphae. Sanders and Tinker (1973) calculated that, given the number and size of connecting links and the amount of P obtained by the plant, transport within the hyphal system must be by mass flow rather than by diffusion. Even then, extremely high flow rates would be needed. The presence of polyphosphate granules in the vacuoles of the hyphae has now been demonstrated by electronmicroscopy (Cox, et al., 1975; Cox and Tinker, 1976) and confirmed by chemical analysis (Callow, et al., 1978). In this more concentrated form, required rates of phosphate inflow became

more feasible. Pearson and Tinker (1975) calculated flow rates of ^{32}P in the hyphae between $0.3-1.0 \times 10^{-9}$ moles $cm^{-2}s^{-1}$, and inflow rates into the root system were calculated at about 20×10^{-14} moles $cm^{-1}s^{-1}$ (Sanders, et al., 1977).

Effect of Endophyte Species

The existence of different endophytes greatly increases the complexity of mycorrhizal systems because endophytes can differ greatly in the extent to which they improve plant growth. Symbiotic efficiency will be affected by factors controlling fungal spread in the soil, translocation to and release of P in the root, and latent pathogenicity of the fungus toward its host. The search for criteria that would enable one to select good endophytes has so far mainly emphasized the general complexity of these interactions and the unpredictability of results. It is probable that, like plant P uptake, endophyte efficiency depends on several factors. Nevertheless, some general principles are becoming known.

1. The efficiency of an endophyte may, but does not always, depend on the extent of infection or the development of the soil mycelium (Mosse, 1972*b*; Powell, 1976*b*; Sanders, et al., 1977; Graw, et al., 1979). Sometimes only 10% infection can markedly improve plant growth. At the same time, similar amounts of infection by two endophytes will not necessarily have the same effects on growth (Owusu-Bennoah and Mosse, 1979). Efficiency was also independent of the number of connecting hyphae between soil and root (Powell, 1977*b*).
2. Some endophytes are better in neutral or alkaline soils and others are better at low pH (Table 6; Mosse, 1972*a*, 1972*b*). Inoculation with six endophytes in each of four soils (Fig. 15), however, shows differential responses to other soil factors (Powell, 1977*b*). Therefore, the best endophyte in one soil or situation is not necessarily the best in another (Mosse, 1972*b*). The spore type E_3, good in four New Zealand soils (Fig. 15), was efficient also in pot experiments in Nigeria but proved disappointing in field experiments there. On the other hand, *Glomus mosseae*, which was a poor endophyte in the New Zealand soils, possibly because of unsuitable pH, was a good field inoculant for cowpea and corn in Nigeria at similar pH (Islam, priv. comm.). Some endophytes appear to be generally poor. It has also been suggested that there may be particular host-endophyte preferences (Powell and Sithamparanathan, 1977; Schenck and Kinloch, 1974; Crush, 1978).
3. Different endophytes use the same sources of soil phosphate. Two plant species inoculated with seven different endophytes had similar specific activities in each of two different soils (Powell, 1975*a*).
4. Endophytes differ in their reactions to added fertilizer. Often indigenous endophytes adapted to low-phosphate soils are sensitive to changes in soil fertility (Mosse, 1977*a*; Powell and Daniel, 1978*b*; Clarke and Mosse, 1980).
5. The indigenous endophytes in a soil are not always the best (Mosse, 1973*c*, 1975; Powell, 1976*a*, 1977*b*; Powell and Daniel, 1978*a*). In 24 out of 37 pasture soils, an introduced endophyte improved clover growth more than the indigenous fungi did (Powell, 1976*b*, 1977*a*). Improvements varied from eightfold to 6% but were frequently 50 to 100%. The advantage of the introduced fungus was not always related to infection levels or available P in

Table 6. Effect of soil pH on growth stimulation by different endophytes

Host	Endophyte	Shoot dry wt (mg) and infection rating[a] (in parentheses)	
		pH 7.0	pH 5.7
Allium cepa[1]	E3 (*Glomus fasciculatus*)	441 (3)	703 (3)
	YV (*G. mosseae*)	410 (2)	246 (1)
		pH 5.8	pH 4.8
Paspalum notatum[2]	HON (*Acaulospora laevis*)	41 (2)	65 (2)
	E3 (*G. fasciculatus*)	115 (2)	58 (2)
	Indigenous fungi	79 (2)	14 (2)

References: 1. Mosse, 1972*b*; 2. Mosse 1972*a*.

[a]Infection ratings: 1 = slight; 2 = moderate; 3 = abundant.

the soil. When placed in undisturbed (unsterilized) cores of eight hill-country soils, at least one out of three endophytes tested improved clover growth by 16 to 117% over the indigenous fungi (Powell and Daniel, 1978*a*).

In order to compare the efficiency of introduced and indigenous endophytes, it is necessary to isolate the indigenous endophytes by some baiting technique and to build up their infectivity to a level comparable with that of the introduced endophytes so that infection levels are similar when test seedlings infected with the indigenous or introduced endophytes are transferred to the experimental soil. If inoculated and uninoculated seedlings are placed directly into an unsterile soil of low infectivity, infection by indigenous endophytes and consequent growth stimulation may be slow to develop. Introduced endophytes may therefore appear to be better when plants are only showing the benefits of earlier infection. This may persist throughout the experiment. While, under such circumstances, the improved growth is a genuine result of inoculation, it does not necessarily indicate a qualitative superiority of the introduced endophyte.

In evolutionary terms, it is perhaps surprising that the indigenous endophytes in a given soil are not the best. Changes in endophyte populations can occur quite rapidly when virgin land is brought into cultivation (Schenck and Kinloch, 1976), and Crush (1978) believes that adaptations between host, endophyte, and environment quickly lead to the natural selection of the most efficient combinations. The evidence, however, is conflicting. Many soils have been in agricultural use for relatively short periods, so that evolutionary adjustments may still be occurring and may never keep up with changes in agricultural practice. Also, the underlying causes of the distribution pattern of different endophytes are by no means clear; the best endophytes may not occur within a limited area and therefore would be unlikely to arrive there by natural selection.

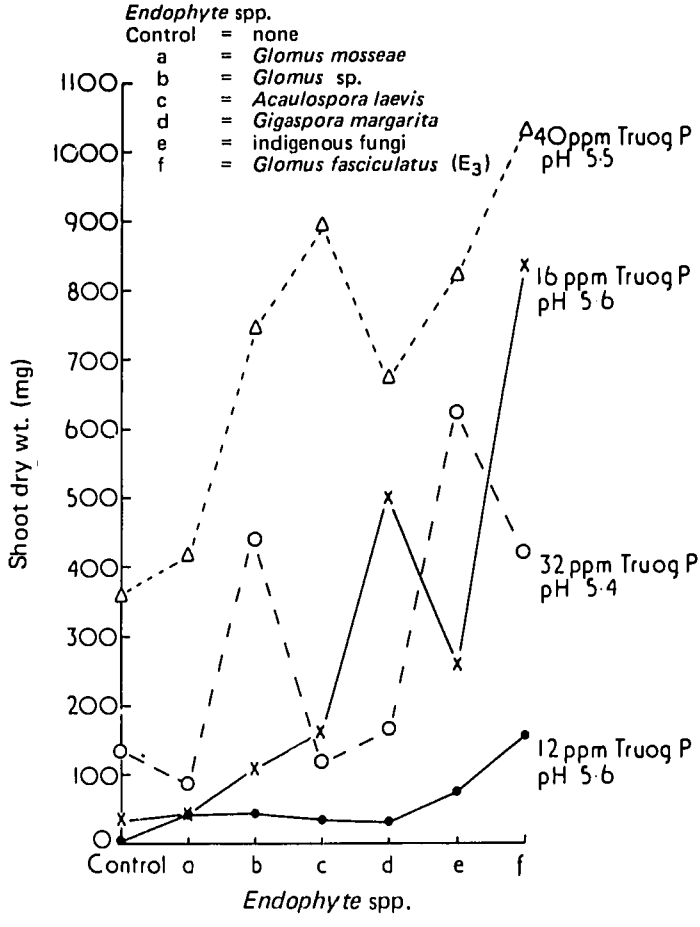

Fig. 15. Diagram showing the effect of six different VA endophytes on the growth of white clover in four sterilized soils. (*After Powell, 1977b*)

The variety of VA endophytes and the range of their effects have given a new dimension to VA mycorrhizal research, because it opens up the possibility of improving plant growth in natural soils by inoculation with better endophytes.

Inoculation of Unsterile Soils

Inoculation of an unsterile soil may benefit plant growth for two reasons: because indigenous endophytes are too few so that infection develops only slowly, or because they are relatively inefficient. In general, one may expect the benefits of inoculation to be smaller in unsterile than in sterile soils (Mosse, 1975; Islam, 1977) because the noninoculated plants in unsterilized soil will, sooner or later, also become mycorrhizal. Furthermore, growth potential is generally higher in sterilized soils (provided P is not limiting), because pathogens have been elim-

inated, available N is increased, and the introduced endophyte faces less competition from other soil microorganisms. Pot experiments in unsterile soil have been useful as a preliminary step to field inoculation; they have provided information on techniques of inoculation, the establishment of endophytes in unsterile soils, and the ability of these endophytes to utilize added phosphate fertilizer.

Inoculation procedures in natural (unsterilized) soils need not differ from those in sterilized soils, but for experimental purposes the infectivity of the natural soil should be changed as little as possible. Extensive sieving will break up the inoculum; passing a soil through a 2-mm sieve rendered it noninfective (Clark, 1964). Powell(1977*c*) has pioneered the use of undisturbed soil cores taken from pastures to test establishment of inoculated clovers. This technique has the added advantage of leaving the natural soil profile intact—important because the P-rich top layer will be near the emerging seedling roots. Noninoculated control plants should be allowed to become infected at the rate normal to the test soil. If, as a result, infection develops earlier in the inoculated plants, this is one of the purposes of inoculation in unsterile soils and does not invalidate the results.

In general, it is difficult to alter the microbial population of unsterile soils. Introduced organisms either die out within a few months, or, if indigenous, revert to their original level. VA endophytes, however, are partly root inhabiting and, given a suitable host, appear to establish quite readily. Two methods of inoculation have been widely used: transplantation of preinoculated seedlings, and sowing seeds above a pad of inoculum. While the former would appear to be a more certain method, the latter has quite often led to apparently greater improvements (Mosse and Hayman, 1971; Islam, 1977). Naturally, the transplants have an initial advantage over seed sown at the time of transplanting, but in field experiments in Nigeria the inoculated transplants generally lost this advantage after 48 days. Uninoculated seeds, however, remained smaller than uninoculated transplants, and therefore the relative advantage of inoculation was greater in the seeded plants.

Pot Experiments

Phosphorus uptake and plant growth in unsterile soils have been improved by inoculation with VA endophytes in pot experiments with corn (Gerdemann, 1964; Jackson, Franklin, and Miller, 1972; Islam, 1976), onion (Mosse and Hayman, 1971), citrus (Kleinschmidt and Gerdemann, 1972), yellow poplar (Starkey and Brown, 1977), cowpea (Islam, 1976), clover (Powell, 1977*c*; Powell and Daniel, 1978*a*), *Stylosanthes* (Mosse, 1977*a*), and subterranean clover (Abbott and Robson, 1978). Table 7 gives a summary of growth responses in *Stylosanthes guyanensis* to inoculation in some tropical soils with and without added rock phosphate. Improvements were greatest in soils of low infectivity, but even with indigenous infection at 70 and 90%, inoculation was beneficial. Some of the growth responses were clearly due to interactions between mycorrhiza and a better supply of N, which was due to better nodulation. The introduced endophytes established well and appeared to become dominant in eight of the soils, coexisted with indigenous endophytes in the same root in three soils, and died out in one. It is difficult to monitor the establishment of an introduced endophyte unless it has some distinctive anatomical feature by which root

Table 7. Growth increases in *Stylosanthes guyanensis* in unsterile soils with and without added rock phosphate (RP)

Soil no.	Infection of uninoculated plants (%)	Growth increase of inoculated plants	
		Without RP	With RP[a]
1	0	x 9.0	x 13.0
2	0	x 9.0	x 10.0
3	0	x 4.5	x 6.0
4	10	x 2.0	x 1.7
5	10	x 1.5	x 3.7
6	15	x 1.9	x 2.2
7	20	x 2.0	x 2.1
8	50	x 1.0	x 3.1
9	70	x 1.3[b]	x 1.0[b]
10	70	x 1.0	x 1.3
11	90	x 1.2	x 1.4

After Mosse, 1977*b*.

[a]Treatment = 33 mg rock phosphate/kg soil + sand.
[b]Introduced endophyte did not become established.

infections can be recognized. Often establishment is simply assumed when the percentage of infection is greater in the inoculated plants.

While the inoculation of unsterile soils in pots has provided some valuable information and given impetus to field experimentation, it now seems that the results bear little relation to those obtained from inoculation in the field. In a Welsh hillside pasture, inoculation benefited growth of white clover, but there was no response in the same soil in pot experiments (Hayman and Mosse, 1979).

In New Zealand, results of inoculation in the glasshouse were better or worse than those in the field according to the soil and fungal species (Table 8, Exp. 6). The growth of corn was markedly improved by inoculation in a pot experiment in Nigeria, but in the same soil in the field, all plants grew much better and there was no response to inoculation (Islam, 1977). In experiments with tussock grassland species (Crush, 1973*b*), and in much earlier experiments with potatoes (Magrou and Magrou, 1940), plants were more responsive at high-altitude sites than in a glasshouse. Crush attributed this to higher rates of P mineralization in the glasshouse. Similar discrepancies between pot and field experiments have occurred in some fertilizer trials. This is not altogether surprising, because pots are kept permanently moist, soil temperatures are often higher, and root spread is generally much restricted. The first two increase P availability, and the latter affects spatial relationships, which, as shown, are a very important factor in the functioning of mycorrhizal systems.

Field Experiments

There have now been some dozen field experiments involving grain crops (Khan, 1972*a*,

Table 8. Growth responses to inoculation in the field: unsterilized soil without inoculation (C), inoculated with mycorrhiza (I), and with added phosphate (P)

Exp. no.	Test plant	Data expression	Results				Notes on treatments
			C	C + P	I	I + P	
1	Corn	Dry wt (g)/plant	119	175	263	244	I = preinoculated seedling
2	Wheat	Yield (g)/m²	86	215	276	235	P = 280 kg/ha triplesuperphosphate (21% P)
3	Barley	Yield (g)/m²	71	191	277	245	
4	Soybean						
	Soil 1	Yield (g)/10-ft row	757		821		
	Soil 2		755		744		
5	Potato	Yield (kg)/plot	6.1	9.5	7.4	9.8	C = low-infectivity soil, 1 spore/ml I = high-infectivity soil, 13 spores/ml P = 100 kg P/ha triplesuperphosphate
			C	I_1	I_2	I_3	
6	White clover	Total dry wt (g)					
	Soil 1	2 harvests	1.34	1.04	0.96	1.04	I = preinoculated seedlings
	Glasshouse	4 harvests	1.77	2.16	3.29	1.96	I_1 = *Glomus fasciculatus*
	Field						I_2 = *G. tenuis*
							I_3 = *Gigaspora margarita*
	Soil 2						Soil 1: +35 kg/P ha
	Glasshouse	3 harvests	2.39	2.39	2.33	3.00	Soil 2: +40 kg/P ha
	Field	3 harvests	0.55	0.93	0.67	1.20	
7	White clover	Dry wt (mg)/plant	19	26	34		I_1 = *G. tenuis*
		Root infection	68%	78%	77%		I_2 = *G. tenuis* + *Gigaspora margarita*

			C	C + P_1	C + P_2	I	I + P_1	I + P_2
8	White clover	Dry wt (mg)/plant	90	99	238	121	204	599
		Nodule wt (mg)/plant	0.1	0.1	1.6	1.1	2.3	9.3

I = preinoculated seedlings
P_1 = 24 kg P/ha (basic slag)
P_2 = 95 kg P/ha (basic slag)

			C	I_1	I_2
9	Onion	Dry wt (g)/m^{-1} row	0.32	1.68	4.36
	Lucerne		2.09	4.46	15.34
	Barley		10.18	13.95	14.31

I = approx. 1 cm^3 of infected soil placed below seed
I_1 = mixed inoculum
I_2 = laminate inoculum (*G. caledonius*)

			Dry wt	Nodule wt	Grain yield
10	Cowpea	Increase after inoculation	28%	140%	25%
	Corr		–	–	61%

References: Exp. no. 1, Khan, 1972*b;* 2, Khan, 1975; 3, Saif & Khan, 1977; 4, Ross & Harper, 1970; 5, Black & Tinker, 1977; 6, Powell & Daniel, 1978*a;* 7, Powell, 1979; 8, Hayman & Mosse, 1979; 9, Owusu-Bennoah & Mosse, 1979; 10, Islam, 1977.

1975; Saif and Khan, 1977; Islam, 1977; Clarke and Mosse, 1980), pasture legumes (Powell, 1977*c*; Powell and Daniel, 1978*a*; Powell, 1979*a*; Hayman and Mosse, 1979; Owusu-Bennoah and Mosse, 1979), grain legumes (Islam, et al., 1980; Ross and Harper, 1970; Bagyarj, et al., 19[illegible]; La Torraca, priv. comm.)., potatoes (Black and Tinker, 1977), and onions (Owusu-Bennoah and Mosse, 1979). There have also been some experiments in fumigated nurseries with citrus (Kleinschmidt and Gerdemann, 1972; Hattingh and Gerdemann, 1975) and peaches (La Rue, et al., 1975), and in a fumigated field soil with different levels of available P (Yost and Fox, 1979). Table 8 gives results of some of these experiments. A more up-to-date table is given by Mosse and Hayman, 1980*a*.

Experiments 1 to 3 (Table 8) were done in Pakistan in a fallow field containing 15 ppm $NaHCO_3$-soluble P and approximately 50 *Endogone* spores/kg soil. Seedlings were inoculated and transplanted after they had become infected. Inoculation promoted growth of corn, wheat, and barley as much as or more than did the application of 280 kg/ha triplesuperphosphate. Wheat was the most responsive to fertilizer only. In all three crop species, P fertilizer added to inoculated plants reduced infection and did not increase yield. In an experiment in Nigeria, inoculation of a soil containing 6 ppm Bray-extractable P increased corn yield by 61% to 1800 kg/ha. Seeds were planted over a 10-g inoculum of heavily infested soil (Islam, 1977).

Cowpea appears to be very responsive to mycorrhiza, and inoculation produced consistently good responses in a series of experiments over 2 years (Islam, et al., 1980). Results in Experiment 10 (Table 8) are an example. This experiment was on a freshly cleared bush soil, which had carried one crop of corn. At the end of the experiment, uninoculated plants had approximately 50% infection, and inoculated plants had 10% more. Soybeans, on the whole, seem less responsive than cowpeas and did not respond to inoculation in a similar field experiment. A yield increase of 8% (statistically non-significant) occurred in one of two soils (Table 8, Exp. 4). In a much larger factorial experiment in Brazil, inoculated plants, with or without added phosphate, were consistently larger. In an experiment in India (Bagyaraj, et al., 1979) inoculation increased grain yield, although not significantly, N and P content of plants, and size and dry weight of nodules.

The effects of inoculation on clover establishment in hillside pastures have been tested in experiments in New Zealand and Britain (Table 8, Exps. 6 to 8). Powell and Daniel (1978*a*) transplanted mycorrhizal seedlings into undisturbed soil cores kept in a glasshouse or replanted into the pasture from which they had been taken. Seedlings inoculated with indigenous fungi were used as controls, thus overcoming the effects of possible low infectivity in the natural soil and favoring the control plants which might have taken longer to become mycorrhizal under natural conditions. The figures in Table 8, (Exp. 6) give the total dry-matter yield over several harvests. Both soils were from paddocks given annual dressings of phosphate. In another trial (Powell, 1979*a*), the seed was rolled into a 1-cm pellet with infested soil and this was broadcast on the surface of a pasture. This much more practicable method of inoculation again resulted in a marked stimulation of growth by the introduced endophytes, particularly from a mixed inoculum (Table 8, Exp. 7). With this method

of inoculation, infection began after 17 days. It reached 60% 2 weeks later than in preinoculated seedlings. At harvest, infection levels were very similar for all three inoculants, showing again that there are qualitative differences between endophytes for which no really satisfactory explanation has yet been found.

Clover establishment in a Welsh hillside pasture was improved at three sites when seedlings, preinoculated with two endophytes, were placed into slits cut into the pasture or into a narrow band from which the sward had been removed. Growth of controls and inoculated plants was better in the cleared strips, and inoculation was most beneficial when P fertilizer was also given (Table 8, Exp. 8). Nodulation increased severalfold, and dry-matter production doubled in the best treatments (Hayman and Mosse, 1979).

When a soil inoculum of high infectivity (3 kg/m² furrow) was added to a low-infectivity field soil, potato yield increased by 20%, accompanied by an eightfold increase in infection (Black and Tinker, 1977) (Table 8, Exp. 5). Addition of 481 kg/ha triple-superphosphate (21% P) increased yield, wiped out the mycorrhizal effect, and reduced infection.

Inoculation of a fallow field soil at Rothamsted produced significant ($P < 0.01$) growth increases in lucerne, onion, and barley sown in the field above a 10-g inoculum of heavily infested soil (Table 8, Exp. 9). Inoculation responses of onion and lucerne, but not of barley, were greatest at the most fertile end of the plot containing 13 ppm ($NaHCO_3$) soluble P. At harvest the noninoculated plants had about 50% mycorrhizal roots compared to 75% in the inoculated. The different growth responses to the two inocula were not related to infection level.

Reinoculation with VA endophytes was beneficial in three experiments in a fumigated nursery, though in two of the experiments the noninoculated sour-orange seedlings were also mycorrhizal at harvest (Table 9). The seed was pelleted with the inoculum using methyl cellulose as an adhesive (Hattingh and Gerdemann, 1975). La Rue, et al. (1975) cured zinc deficiency in peach seedlings in a fumigated nursery by mycorrhizal inoculation. Fertilization with P and zinc was much less effective, and inoculation plus fertilization was slightly less beneficial than inoculation alone.

The question of spread of the introduced endophytes and of persistence of their bene-

Table 9. Growth responses to inoculation in the field: fumigated soil (host: sour orange)

Exp. No.	Fresh weight (g) and mycorrhizal status[a] at harvest (in parentheses)			
	Without inoculation		With inoculation[b]	
1	37	(M)	60	(M)
2	12	(NM)	40	(M)
3	42	(M)	59	(M)

Reference: Hattingh and Gerdemann, 1975.

[a]M = mycorrhizal, NM = nonmycorrhizal.
[b]Seed pelleted with inoculum.

ficial effects is very relevant to the economics of field inoculation. Powell and Daniel (1978*a*, 1978*b*) have collected some data on repeatedly cut clover and ryegrass. In seven soils, the benefit of the introduced endophytes was decreased after the initial harvest and was then maintained at a lower level over subsequent harvests; in one soil, benefits increased steadily over six harvests. The benefits of inoculation shown in Exp. 8, Table 8 were even greater in the second year than in the first. Sparling and Tinker (1978*b*) recorded a spread of 1 cm/week in a dense grass sward, but in fumigated citrus nurseries spread is faster. Warner (1980) found different rates of spread with different host plants and measured a maximum spread of 22 cm over 13 weeks in the field. In the same experiment, Mosse, Warner, and Clarke (1980) recorded a spread over 2¼ m in 15 months, and Powell (1979*b*) calculated a similar rate of spread in an unsterile soil on the basis of a short-term pot experiment. More data is needed on this aspect of field inoculation, especially in larger field plots.

OTHER FUNCTIONS OF VA MYCORRHIZA

Uptake of Other Mineral Nutrients

The improved nutrient uptake of VA mycorrhiza is not confined to phosphate. Infection can also help plants to overcome limitations imposed by the low mobility of other nutrient ions in the soil. Zinc is an example. Zinc deficiency in peach seedlings was alleviated or cured by mycorrhizal inoculation (Gilmore, 1971; La Rue, et al., 1975) and again endophytes differed in their ability to do this. Apple seedlings showing zinc deficiency in a fumigated soil grew better with mycorrhiza. Combined zinc fertilization (5 ppm) and inoculation more than doubled seedling weight and increased the zinc concentration of leaves from 11 to 22 ppm (Benson and Covey, 1976). One endophyte was somewhat more effective than another. Improved zinc uptake has also been shown for maple (Daft and Hacskaylo, 1977), potato (Swaminathan and Verma, 1979), pinto bean (McIlveen, et al., 1975), and detached roots of hoop pine (Bowen, et al., 1974). Metcalf (1978) found a strong correlation between mycorrhizal infection and ability of cotton plants to take up zinc adsorbed on vermiculite. He thought his results could be explained by postulating some exudation of a chelating agent from mycorrhizal roots. Cooper and Tinker (1978) reported transfer of ^{32}P, ^{35}S, and ^{65}Zn into clover seedlings with mean flux ratios of 50:8:1.

Uptake of radioactive sulfur into onions and sweet gum was increased by mycorrhiza (Gray and Gerdemann, 1973), but this was attributed to the normal uptake by a larger root system rather than to a specific involvement of the mycorrhizal roots (Rhodes and Gerdemann, 1976). A later paper (Rhodes and Gerdemann, 1978) reported the transfer of radioactive sulfur, applied 8 cm from the root surface, into mycorrhizal onions but not into nonmycorrhizal. Mycorrhizal soybeans took up more radioactive strontium from solution (Jackson, Miller, and Franklin, 1973), but molybdenum deficiency of beans growing in soil was not relieved (Hayman and Day, 1978) by mycorrhizal infection.

The literature contains many records of tissue analysis of mycorrhizal and nonmycorrhizal plants, and figures for total uptake of major and minor nutrients are given. As P-

deficient soils were usually chosen, mycorrhizal plants were generally larger, and, therefore, their total nutrient uptake was greater. Only an increase in percentage of dry matter indicates a possible involvement of mycorrhiza in uptake. Here results are inconsistent. The copper content of mycorrhizal plants seems consistently greater in many reports, and this was very striking in some experiments with coffee seedlings (de Souza, priv. comm.). Copper-deficiency symptoms developed in citrus receiving so much phosphate that mycorrhizal infection was reduced (Timmer and Leyden, 1978).

Except for the important involvement of mycorrhiza in the symbiotic N fixation of rhizobia, there is no evidence that mycorrhiza play any part in the N uptake of plants. An early theory was that they might utilize combined N in the soil. It has also occasionally been suggested that exudates from mycorrhizal roots may stimulate the fixation of atmospheric N by free-living rhizosphere microorganisms. Membrane permeability is increased in many symbiotic systems, and it is likely that there will be qualitative and quantitative differences in exudates from mycorrhizal and nonmycorrhizal roots, which should affect rhizosphere populations of microorganisms, although there is no experimental evidence concerning such effects.

In many tropical soils, mineral toxicities, particularly of aluminum and manganese, and salinity problems may be as important in restricting plant growth as nutrient deficiencies. Hirrel and Gerdemann (1979) reported that mycorrhizal pepper and onions withstood salinity better than nonmycorrhizal because of their better P nutrition. The impact of deicing salts on mycorrhiza in sugar maple was studied. Damaged trees had diminished root systems, particularly in the surface layers where mycorrhiza were prevalent (Guttay, 1976).

The possibility that mycorrhizal and nonmycorrhizal plants may react differently to water stress is repeatedly discussed, and the work of Safir, et al. (1971) is quoted in evidence. They found that the root system of mycorrhizal plants had a lower resistance to water flow than that of nonmycorrhizal plants, but later showed (Safir, et al., 1972) that this was a result of P deficiency in the nonmycorrhizal plants rather than a direct effect of mycorrhiza on water transport. Menge, Davis, et al. (1978) reported that mycorrhizal avocado seedlings suffered less from drought following transplanting than did nonmycorrhizal. Increased susceptibility of P-deficient plants to water stress is well documented (Atkinson and Davison, 1972).

Mycorrhiza and Plant Diseases

The study of interactions between mycorrhiza and plant pathogens (viruses, fungi, and nematodes) has centered mainly in the United States and with Professor F. Schönbeck at the University of Hannover, in Germany. As with most other systems of biological control, results have been either inconsistent or highly specific, or both.

The chief mechanisms involved are:

1. The better or changed nutrient status of the host allowing:
   a. Increased development of the pathogen,
   b. Strengthening of the plant so that damage caused by the pathogen was offset by improved plant growth due to mycorrhiza.
2. Competition for infection sites.
3. Special interaction between endophytes and pathogens.

Changed Nutrient Status

More tobacco mosaic virus lesions formed in mycorrhizal tobacco than in nonmycorrhizal (Schönbeck and Schinzer, 1972), and there was more extractable tomato, potato, and *Arabis* mosaic virus in strawberry, petunia, and tomato plants when they were mycorrhizal (Daft and Okusanya, 1973). Roncadori and Hussey (1977) noted that joint inoculation of cotton with an endophyte and a root-knot eelworm (*Meloidogyne incognita*) largely nullified the stunting caused by the nematode alone. Growth and yield reductions were small in the mycorrhizal plants and very large in the nonmycorrhizal. Mycorrhiza decreased development of the migratory endoparasitic nematode *Pratylenchus brachyurus* and increased square production in cotton sevenfold (Hussey and Roncadori, 1977). Dehne and Schönbeck (1975) reported reduced damage by *Fusarium* and various other wilt diseases when the plants were mycorrhizal, although the incidence of wilt disease was not lessened (Dehne, 1977). Enzyme changes and changes in the composition of the amino acid pool, particularly an increase in arginine, were thought to affect plant susceptibility, often leading to increased development of leaf pathogens (Schönbeck, 1979).

Competition for Sites

Becker (1976) found that the pink-rot fungus *(Pyrenochaeta terrestris)* did not colonize parts of onion roots that were mycorrhizal, although immunity did not extend to nonmycorrhizal roots on the same plants or even parts of the same root. Mycorrhiza increased the weight of *Poinsettia* cuttings threefold. Simultaneous inoculation with an endophyte and a *Pythium ultimum/Rhizoctonia solani* mixture reduced their weight to that of nonmycorrhizal cuttings, but if the pathogens were added 20 days after the endophyte, there was no weight reduction (Stewart and Pfleger, 1977). No data are given on the incidence of the pathogen. The reverse, i.e., increased susceptibility to a pathogen, was reported by Ross (1972) for *Phytophthora* root rot of soybean, but experiments elsewhere with other isolates had the opposite effect (Woodhead, et al., 1977). Mycorrhizal alfalfa, citrus, and avocado roots attracted *Phytophthora* zoospores, and the plants were more susceptible to root rot than nonmycorrhizal (Davis, et al., 1978).

Special Interaction

Baltruschat and Schönbeck (1975) found that mycorrhizal tobacco plants were less damaged by *Thielaviopsis basicola* than nonmycorrhizal, and that the endophyte inhibited chlamydospore formation of the pathogen both in vivo and in vitro.

A new aspect of interaction between endophytes and pathogenic fungi is introduced into VA mycorrhiza studies by the report that a species of *Phlyctochytrium* and a fungus resembling *Pythium* parasitized endophyte spores in the soil, leading to a reduction in their numbers (Ross and Ruttencutter, 1977). A *Rhizidiomycopsis* sp. parasiting *Gigaspora margarita* has also been described (Schenck and Nicolson, 1977).

Interactions between endophytes and nematodes have been summarized by Schenck, Kinloch and Dickson (1975); they are highly specific, reciprocal, and further complicated by the degree of host susceptibility to the nematodes. Endophytes may affect nematode reproduction, leading to more or fewer cysts, and the nematodes may affect sporulation of the endophyte. Rich and Bird (1974), Fox

and Spasoff (1972), and Bird, et al. (1974) report a negative correlation between mycorrhizal infection in cotton roots and plant parasitic nematodes. Bagyaraj (priv. comm.) found that, in mycorrhizal soybean, gall formation was much reduced, and most galls were primary rather than multiple. Schenck and Kellam (1978) give a comprehensive review of the influence of VA mycorrhiza on disease development.

Various herbicides, systematic fungicides, pesticides, and fumigants affect VA endophytes (Pfleger and Stewart, 1976; Bailey and Safir, 1977; Bertoldi, et al., 1977; Boatman, et al., 1978; Hayman, Macdonald, and Spokes, 1978; Menge, Johnson, and Minassian, 1979; Menge, Munnecke, et al., 1978). Fumigation with rmaldehyde or with methyl bromide with or without chloropicrin is used quite extensively to eliminate endophytes from soil. Benomyl and PCNB (pentachloronitrobenzene) are among the most effective fungicides when applied as soil drenches, but as a systemic, benomyl has little effect. Ethazole and DBCP (1,2-dibromo-3-chloropropane), applied 60 days after inoculation, actually increased spore production by 76 and 63%, respectively, and some nematicides have similar effects. Very large and varied spore populations can build up in pineapple soils regularly fumigated against nematodes.

Soil Aggregation

VA endophytes are very effective in the colonization of dune sands (Koske, et al., 1975; Sutton and Sheppard, 1976); they increased aggregate weight from 0.9 to 25 g/kg dune sand and to 127 g/kg after a second crop. Although other soil fungi were present, the mycelium of VA endophytes predominated in the aggregates. This binding action of the external mycelium is very clear in many pot experiments. It is attributed by Clough and Sutton (1978) to the production by the fungus of binding substances, possibly polysaccharides. Nicolson (1960) considered heavy mycorrhizal infection as a developmental stage in the colonization and stabilization of dune sands. It could be an important factor in erosion control.

IMPORTANCE OF MYCORRHIZA IN THE NATURAL ECOSYSTEM

In the foregoing discussion, most emphasis has been placed on mycorrhiza in relation to agricultural crops, Actually, mycorrhiza achieve their greatest spread in undisturbed ecosystems. Their precise significance in this environment is hard to assess, both technically and because of the importance of nutrient cycling within the permanent vegetation. For instance, it was calculated that in a 20-year-old Loblolly pine stand, 60% of the annual P requirement was recycled within the standing crop, 20% came from the litter, and less than 1% from the soil (Switzer and Nelson, 1972). It is also well known that the soil below the luxurious tropical forests of Amazonia is so poor in available P that it is virtually impossible to raise a crop in it after the forest has been removed. In such an environment, long-term processes have significance, and the lowering of the P concentration in the soil solution by hyphae of mycorrhizal fungi may mobilize small amounts of P by chemical solution. Undoubtedly, other fungi and bacteria will do the same, but the mycorrhizal system is a functional unit, and having once entered the system, the ions

are protected against readsorption and remain accessible to the plant, whereas nutrients taken up or mobilized by free-living soil microorganisms will return to the soil when the organisms die. Nutrients then released from them remain subject to readsorption in the soil unless the organisms live on the root surface. Roots themselves, by virtue of ion absorption, can affect soil pH in their immediate vicinity and thus affect P availability.

Many mycorrhizal roots permeate the litter layer, and many nutrients are taken up directly from this layer without ever entering the soil. There is much conjecture about the role of mycorrhiza in recycling from the litter layer (Went, 1971; Went and Stark, 1968; Stark, 1977) but no supporting evidence. In the case of ectotrophic mycorrhiza, it seems probable that the fungal mantle surrounding the roots could store significant amounts of P released during periods of rapid mineralization and that this P would remain available to the plant; if, instead, it leached out of the litter layer, it would very quickly become fixed. A similar storage function is less likely for VA mycorrhiza because of their small bulk, but they may assist in the degradation of the litter. In pot experiments, they clearly affect the breakdown of peat particles and increase the colloidal content of the drainage water (Mosse, 1959).

In an intensive study of nutrient cycling in a mixed deciduous forest in England, an attempt was made to quantify the effect of VA mycorrhiza in P uptake (Paget and Mosse, 1975; Mosse and Hayman, 1980*b*). The study ran into some technical difficulties and demonstrated the inadequacy of pot experiments for such an investigation. There were two chief obstacles. First, disturbance of the natural soil profile completely changed the phosphate distribution in the soil. Without the nutrient-rich litter and A horizon, or even when these were mixed with B-horizon soil, seedlings of tree and ground cover species were very strongly mycorrhiza-dependent: about 60 to 90% of their uptake was calculated to go through the endophyte. When an attempt was made to reconstitute a normal soil profile, dependence on mycorrhiza was inversely proportional to the depth of the humus layer, which, in the site chosen, was very uneven. The technique of using soil cores that has been developed in New Zealand to simulate pasture conditions would certainly have been more realistic, but the large mass of decaying tree-root material in the core would have introduced another set of artifacts and might even have been toxic. The second interesting finding was that the initial size of the plant used in the experiment affected its ability to become established in the absence of mycorrhiza. Blackberry seedlings were strongly mycorrhiza-dependent, but cuttings grown in the same soil were much less so. This probably reflects the effect of nutrient cycling within the plant and illustrates an important difference between annuals and perennials. Contrary to its behavior in the soil, the phosphate ion is extremely mobile in the plant.

In some plants, not only mycorrhiza dependence but even the type of mycorrhizal association formed may change with age. Seedlings of *Helianthemum chamaecistus* growing in a grassland sward had many VA mycorrhiza at first but later formed sheathing mycorrhiza with *Cenococcum graniforme* (Read, Kianmehr, and Malibari, 1977).

POSSIBLE APPLICATION OF MYCORRHIZA RESEARCH TO CROP PRODUCTION WITH SPECIAL REFERENCE TO TROPICAL CONDITIONS

Appendixes A and B show how greatly scientific interest in VA mycorrhiza has recently increased and spread to many tropical countries. For both agronomic and economic reasons—phosphate-deficient soils, inaccessibility and cost of manufactured fertilizers, and greater fungal activity at high temperatures—mycorrhiza research may have particular relevance in the tropics. It has the added advantage that techniques are simple, requiring little specialized equipment beyond a good dissecting microscope and a standard compound microscope. Also technical help that is necessary for the survey and field inoculation work now needed might be available without too much difficulty.

A definition of some of the problems of tropical agriculture might be useful to show where mycorrhizal research programs may have some impact. The problems can be summarized as follow.

Economic

Agriculture in many tropical areas is at subsistence level, and shifting cultivation is the usual practice. A limited amount of phosphate becomes available after burning, and when this is used up, the land is left to revert to bush. There is no fertilizer input. Even if a build-up of mycorrhiza improved crop production, it would simply shorten the rotation and thereby increase pressure on land. In slightly more developed regions where some kind of larger-scale farming is practiced, possible fertilizer inputs are often very restricted due to high costs. In many such regions, local phosphates, usually of relatively low availability, could be used. Such deposits exist in parts of tropical Africa (e.g., Senegal), Turkey, India, Sri Lanka, Brazil, and Colombia, and probably in many other countries. Very large deposits exist in northern Australia and would be available for direct export to southeast Asia with minimum processing. In such situations, optimization of mycorrhizal effects could be useful.

Climatic

Permanent or temporary lack of water and very high soil temperatures are often limiting factors to plant growth. Unless a permanent soil cover is maintained, erosion problems may well arise. Increased mycorrhizal development may account for some of the unexplained, beneficial results of mulching. The effects of permanent ground cover and mulches on mycorrhizal development have not been adequately studied.

Agronomic

In many tropical soils, lack of phosphate is the most important constraint to plant growth. As the soils are brought into production and some phosphate fertilizer is applied, responses to N may occur after some years. Other problems in tropical soils are sulfur deficiency and aluminum and manganese toxicity. The usual method of overcoming these toxicities, and allowing better root penetration of the soil, is by liming. The indigenous endophytes may be poorly adapted to the changed conditions, and better ones might profitably be introduced.

Mycorrhiza may therefore have particular relevance to the following aspects of tropical agriculture.

1. The improved utilization of applied fertilizer, particularly some rock phosphates.
2. The improved nodulation and N_2 fixation of grain legumes and the better establishment of forage legumes in pastures where their competitive ability for scarce phosphate is poor.
3. Reestablishment of infection after soil sterilization, particularly in tree nurseries.
4. Erosion control and rehabilitation of degraded sites.

Better Utilization of Applied Fertilizers

As has been shown, mycorrhiza do not, at least in the short term, increase the amount of available soil phosphate. They are therefore not a substitute for phosphate fertilizer, but they do greatly increase the utilization of the P that is present in the soil or added to it. To obtain the same growth response, a plant with an efficient mycorrhiza system would need less fertilizer than one without or with inefficient endophytes. In pot experiments, some nonmycorrhizal plants have required three times or more the amount of phosphate to make as much growth as mycorrhizal plants, but such responses cannot be quantified without reference to particular plant species and soils. In practice, few plants in the field will be totally without mycorrhiza, but for annuals an adequate supply of phosphate during early growth is important. With low soil infectivity, mycorrhizal development at the critical time might be too low.

If rock phosphate is used, it must be remembered that, unlike superphosphate, it contains no sulfur. It may be necessary to add sulfur separately to meet plant requirements, particularly those of legumes. Swaby (1974) has pioneered the complexing of rock phosphate, sulfur, and *Thiobacilli* into a product he has called "biosuper," which has been designed to increase the availability of the phosphate. If it is practically feasible, addition of VA mycorrhiza inoculum to such a product might increase the effectiveness of both the mycorrhiza and the biosuper. It must be remembered that the mycorrhiza must quickly find a host root, and that placement of the rock phosphate near the root also has obvious advantages. Brazilian experiments have demonstrated the advantage of placing rock phosphate in seed rows rather than broadcasting it. Jackson, Franklin, and Miller (1972) have reported one placement experiment with mycorrhizal inoculum that showed some differential effects. An additional advantage of rock phosphate is that, in certain circumstances, it may depress mycorrhizal infection less than superphosphate (Islam, 1977).

When soil pH is changed by liming and fertilizers are applied, the new soil conditions may be unsuitable for some of the indigenous endophytes and thus lead to reduced mycorrhiza formation. Such changes have occurred in pot experiments, and field observations support the findings. Just how the endophyte population adjusts to such changes, and how endophyte strains that are adapted to the new situation arrive and spread, is unknown, but the process is bound to be slow. Spreads of 2 m/year from known infection sites have been recorded. If, as seems possible, generally good, less-sensitive strains of endophytes exist, it would be worthwhile to search for them and to examine the feasibility of introducing them into soils that have recently been brought into cultivation. Even the pos-

sibility of arranging crop rotations to build up high soil infectivity for the more mycorrhiza-dependent crops is worth considering.

Improved Nitrogen Fixation and Establishment of Legumes in Pastures

Legumes, because of their restricted root systems, are generally poor competitors against grasses for scarce soil phosphate. They may fail to get established because they are grazed out, or because they are shaded and overgrown by the more vigorous grasses. They may die unless they develop a mycorrhizal system that will supply the phosphate needed for nodulation and N fixation. Once N fixation begins, it gives a competitive advantage to the legume. Mycorrhiza can thus be very important for legume establishment. They also help to assure that the legume obtains a reasonable share of any subsequently applied phosphate.

Many tropical legumes, including *Stylosanthes* species, *Pueraria phaseoloides, Macroptilium atropurpureum,* and *Centrosema pubescens,* are strongly dependent on mycorrhizal uptake. *Stylosanthes* is the preferred pasture legume in many tropical situations. Although it has become so vigorous in certain pastures in Queensland, Australia, that it is outgrowing the grasses, there are difficulties in its establishment in parts of South America. A very large number of species and cultivars exist; it is likely, though as yet not demonstrated, that they vary in their responsiveness to mycorrhiza and their dependence on mycorrhizal uptake.

Reestablishment of Mycorrhizal Association after Soil Sterilization

Many perennial plantation crops, such as citrus and coffee; timber trees, such as yellow poplar and sweet gum; and ornamentals are now raised in fumigated nurseries or as containerized plants in sterilized media. Many of these tree species have thick, fleshy roots with few root hairs and are highly dependent on mycorrhizal uptake. Even heavy fertilization quite often fails to produce healthy seedlings (Bryan and Kormanik, 1977; Timmer and Leyden, 1978), and many seedlings transplant badly or even die after being transplanted to their permanent sites (Menge, Davis, et al., 1978; Pavan, priv. comm.). Coffee in Brazilian plantations often has to be replanted twice before it becomes established, and this is costly. Inoculation of nursery stock is feasible because many plants are concentrated in a relatively small area, and infections are likely to develop strongly in the sterilized soil. Costs of raising the seedling are small in relation to total production costs, and growth advantages during the first 2 to 3 years are generally maintained throughout the subsequent performance of the tree.

Reestablishment of Ground Cover in Eroded and Degraded Sites

The structure of VA mycorrhiza and their sensitivity to high fertility levels suggest that they may have evolved as a particular mechanism to enable plants to survive in low fertility or difficult environments. Schramm (1966) first pointed out the widespread occurrence of mycorrhiza in coal wastes, and this has been confirmed by surveys in Scotland, Pennsylvania, New South Wales (Australia), and elsewhere (Daft and Nicolson, 1974; Daft, et al., 1975; Daft and Hacskaylo, 1976, 1977; Khan, 1978). These surveys show that ground cover plants, shrubs, and trees on all recolonized sites were, with few

exceptions, strongly VA mycorrhizal with infection levels commonly between 40 and 60%. Not unexpectedly, many of the colonizers were legumes or nodulated nonlegumes with the dual advantage of additional N, through symbiotic N_2 fixation, and additional P through mycorrhiza. Several experiments, usually with crop plants such as corn or onions rather than with colonizer plants, showed that plants with mycorrhiza survived longest or grew better in such soils, provided obvious obstacles to plant growth (such as a pH of 2.7) were first rectified. It seems very probable that natural recolonization of such sites will be accompanied by mycorrhizal infection and that any planned revegetation should be with preinoculated plants. The case for mycorrhizal inoculation (ectotrophic) of tree species to be planted in such sites has been ably argued by Marx (1977), who has also demonstrated some very striking field responses. The argument applies equally to colonizer plants with VA mycorrhiza.

Leucaena leucocephala is a perennial shrub, which in its tree form is believed to have great potential for reafforestation of denuded sites in the tropics (Vietmeyer and Cottom, 1977). It is a legume totally devoid of root hairs and highly dependent on mycorrhiza for nodulation. A practical evaluation of mycorrhiza as a factor in erosion control would be interesting.

CONSTRAINTS OF LARGE-SCALE INOCULATION

If inoculation with VA endophytes is shown to have potential value for improved crop production, how feasible is it in practice?

Two types of crops need separate consideration—annuals, such as wheat, corn, or soybean that are seeded over large areas; and perennials, such as coffee, citrus, and cassava, or annuals, such as tobacco, which are raised in nurseries and subsequently transplanted. Transplanted crops obviously present fewer problems since they can be inoculated in the nursery where they usually occupy a relatively restricted area. For seeded crops, inoculum can be attached to the seed or it can be drilled with the seed, either mixed dry or in a slurry. There is no particular advantage in attaching the inoculum directly to the seed (i.e., pelleting) as the inoculum is relatively immobile and will be little use if it remains attached to the seed coat. Even when moistened, it will move little in drainage water.

Inoculum must be grown under conditions where quality control and freedom from contaminating pathogens can be assured, and it must remain viable during storage and transport. A scheme for medium-scale inoculum production has been outlined by Menge, Lembright, and Johnson (1977).

Three types of inocula are possible: pure fungal cultures, infected roots, and infested soil. Inability to culture VA endophytes axenically is frequently regarded as the biggest obstacle to large-scale inoculation. Recently in South America, an endophyte was found that formed aboveground sporocarps containing hundreds of easily detachable spores (Daniels, 1979). A search for other such species is obviously one solution to the problem of inoculum production. Production of large quantities of infected roots or infested soil would probably require more space than fungal cultures, but it is questionable whether they might not make better inocula that would be less liable to lose infectivity during storage. Hall (1976) found that an inoculum

of root segments caused more rapid growth stimulation than spores, and Powell (1976*a*) found that spores needed a preinfection stage during which the hyphae ramified over the root surface before infection took place. It is arguable that, either in roots or in soil containing root fragments, the fungus would have a stronger base than as pure-culture mycelium.

Infected Roots

Problems in the use of infected roots are the production of large quantities of clean material, free from fungal contaminants and nematodes, and storage. Heavy infections can develop in sand culture (Daft and Nicolson, 1969) and in sand and vermiculite (Hepper, priv. comm.), particularly if bone meal is used as a phosphate source. Well-infected roots of beans and corn have been grown in nutrient flow culture (Mosse and Thompson, 1981). The composition of the nutrient solutions is important and affects the type of infection produced and possibly the infectivity of the inoculum. Some research into this aspect of inoculum production is likely to be rewarding. Jackson, Franklin, and Miller (1972) reported successful inoculation from lyophilized infected roots, but in more extensive trials (Crush and Pattison, 1975), lyophilization led to marked reduction of infectivity. Suspending media used for lyophilization of bacteria were unsuitable and simple air-drying may be the best way of preserving the roots (Mosse, unpubl.). If this succeeded, the material might be incorporated into multiseeded pellets, with an inert carrier such as charcoal and a fertilizer base. L-drying of spores in the soil in which they developed was also a very effective method of preservation (Tommerup and Kidby, 1979).

Infested Soil

For many years, inoculation of forest trees was by simple transfer of surface soil from an infested site to the planting hole of the new seedlings. Inoculum and disease control were insufficient, but the method could be improved and adapted for VA inoculum production by preparing the infested soil under controlled conditions in large containers or even on a semifield scale. Soil could be sterilized in situ with formalin or by fumigation, planted with a suitable host plant, and reinoculated with material raised in properly controlled pot cultures. Eventually, soil and roots would be harvested, stored, and used as inoculum. As little as 10 g of infected soil/plant proved sufficient inoculum for field-grown cowpeas and corn (Islam, 1977; Owusu-Bennoah and Mosse, 1979), and Powell (1979*a*) succeeded with a 1-cm-diameter soil pellet. Storage of infested soil is not unduly difficult, and it retains its infectivity well for 3 to 6 months. The soil could be drilled directly with the seed.

No doubt more sophisticated methods would evolve if the value of field inoculation were demonstrated and the need arose. Methods presently available are sufficient for small field trials, and some commercial firms are researching techniques of inoculum production. Practical aspects of field inoculation, including techniques of inoculation, and inoculum production and quantities required have been reviewed by Mosse and Hayman (1980*a*).

DIRECTION OF FUTURE RESEARCH

What then is the outlook for research on VA mycorrhiza, and what should its priorities be?

Field Inoculation: Logical Continuation of Present Research

This research has reached an exciting stage. Enough pot experiments have now been done to show clearly how much both plant P uptake from soil and the utilization of soluble and relatively insoluble phosphate fertilizers depend on mycorrhiza and on particular endophyte species. Adding further examples will not prove anything new. The logical application of this research is to test the value of inoculation in field experiments. Due to limited inoculum, the size of experiments is bound to be restricted, but this does not matter if the experimental designs are sound. There is no limitation on the size or number of control plots. Nor is it relevant, at the moment, how enough inoculum can be produced for field-scale inoculation and what the economics of such a process would be. What is now at issue is whether field inoculation of annual crops, including grain legumes, will produce significant growth responses and a better utilization of added fertilizer. What is needed is a range of results covering different crops grown in different areas of the world under different climatic and cultural conditions. These should not be standardized, but should be those normal to the region. However, certain requirements of inoculation should be observed: e.g., inoculum must have good contact with the roots, must be uncontaminated with eelworms and other pathogens, and must be viable.

Present indications are that inoculation responses in the field may be better or worse than those obtained in pot experiments. This inconsistency makes pot experiments useless as a method for selecting sites where field inoculation may be worth testing. At present, a better method may be to select sites and crops representative of fairly large areas where phosphate deficiencies are acute. From a range of such experiments some picture will emerge of the overall scope of field inoculation. Because of the complexity of mycorrhizal systems, however, such information can only be empirical. If, on balance, good responses are obtained, questions of feasibility will have to be studied. Two crucial questions are whether inoculation would have to be repeated periodically or would be a one-time process, and what natural rate of spread can be expected.

Whether or not field inoculation for annuals becomes a practical proposition, inoculation of transplanted perennials raised in sterilized soils has already been shown to be of value. Such plants may be plantation crops, timber trees, ornamentals, or plants intended for difficult sites. Here, also, the question of how best to prepare, store, and apply inoculum will need further study.

Fundamental Research

Workers in other disciplines are beginning to realize that mycorrhizal studies may have relevance to their investigations. Soil chemists are interested in improving forecasts of nutrient (particularly phosphate) requirements based on chemical soil analysis. They also suspect that some of the unexpected responses to fertilizer applications may be explained by taking into account the mycorrhizal status of the plants. Ecologists with interests in nutrient cycling are beginning to consider mycorrhiza as a possible important link in the chain. Also the competition between plant species in their natural habitat may be affected by dependence on mycorrhizal infection. For all such studies, a standardized, workable method of estimating numbers and efficiency of

endophytes at particular sites would be very useful. It would also be valuable for selecting sites worth inoculating. A standardized soil-dilution technique, using sterilized soil, might be developed to measure soil infectivity. Efficiency of the indigenous endophytes would be more difficult to assess. The ideal solution to the problem would be a systemic fungicide that could be applied as a foliar spray and would move downward and inactivate the endophytes in the root.

Many commercial firms are searching for a systemic fungicide active against phycomycete root pathogens. If they succeed, and if the substance also inhibits mycorrhiza, it might have unexpected secondary effects on plant nutrition. For this and other reasons, the development of a standard test for evaluating the effect of biocides on mycorrhiza may need to be evolved. This is currently being discussed by various international committees.

Of particular interest in tropical soils are the problems of salinity, and of aluminum and manganese toxicity. Little is known about the possible effects of mycorrhiza on the uptake of sodium, chlorine, aluminum, and manganese. Equally very little is known about effects of these ions on VA endophytes, either directly or through host metabolism. Samuel (1926) reported heavier mycorrhizal infection in manganese-deficient soils than in nondeficient, and, in water agar, as little as 0.14 ppm manganese inhibited spore germination (Hepper and Smith, 1976). In a trial of three temperate soils, the benefits of mycorrhiza decreased with increasing aluminum content of the soil (Boutros-Mikhail, 1976). High levels of sodium chloride in an agar medium decreased mycorrhizal infection in clover seedlings (Mosse and Phillips, 1971). Recently, an endophyte strain or species was found adapted to soils in which zinc toxicity was a problem, although most endophyte species were sensitive to high levels of zinc (Gilding, priv. comm.). Similarly, a search may reveal endophyte strains tolerant to high concentrations of manganese, aluminum, and sodium.

It is probable that the endophyte species of tropical soils have not yet been adequately surveyed and that economically interesting species adapted to tropical conditions could be found. Other species with aboveground sporocarps would certainly be interesting.

So far, nearly all research has centered on nutritional effects of mycorrhiza on plant growth. There are indications [i.e., the improved rooting of cuttings (Linderman and Call, 1977), and effects of mycorrhiza in mist culture (Graham, et al., 1976)] that hormonal effects may also occur. Kormanik, et al. (1977*b*), have drawn attention to the need for studying this. A group of Spanish workers (Azcon, et al., 1978) have found effects of hormones, applied at concentrations comparable to those found in bacterial cultures, on the development of mycorrhizal infection and on plant growth stimulation by mycorrhiza. By analogy with ectotrophic mycorrhiza, hormonal effects are quite likely. They could involve hormone production by the endophyte or changes in plant hormone balances as a result of infection. Such effects would appear more clearly when nutritional effects were less marked—i.e., when the nonmycorrhizal plants were not acutely P deficient.

The soil/root interface, which is presently receiving much attention, is a region in which the interests of many scientific disciplines converge. Quantitative and qualitative studies of root exudates are very relevant to such investigations because the exudates are thought to be important determinants of the

microbial population of the rhizosphere. Many symbiotic associations increase membrane permeability of the partners, and studies of mycorrhizal effects on root exudations have begun (Ratnayakee, et al., 1978) and will undoubtedly increase.

Axenic Culture of VA Endophytes

No report on VA mycorrhiza would be complete without some mention of the axenic culture of VA endophytes that has been the ambition of every research worker in this field. Apart from its intrinsic value, successful culture would very likely have important implications in the study of host/parasite interactions, particularly in relation to other obligate haustorial parasites in the Erisyphaceae and Perenosporaceae.

Before the discovery of *Endogone* resting spores, surface-sterilized, infected roots were used as starting material in attempts to culture VA endophytes. Many common soil fungi were isolated, but they did not produce VA infections on reinoculation. In cases in which the endophytes did grow from root pieces, contamination by bacteria was often considered a major obstacle to their culture.

Recently, surface-sterilized spores or axenically-raised infected roots have most commonly been used as starting material. Growth from infected root pieces can be quite vigorous for 1 to 2 weeks, but, when the root dies, fungal growth also ceases, indicating that the fungus depends on the metabolically active root rather than on some storage product, such as starch or sugar. Germ tubes growing from sterilized spores can make considerable growth that can be further extended by various additions to the medium, particularly biotin and thiamine and seed pieces (Hepper, 1979*b*). Normally, germ tube growth is limited. If no suitable host root is near, the cytoplasm is withdrawn from the germ tube, septa are laid down, and the spore resumes dormancy. If stimulated, it may germinate a second and third time. Growth of the germ tube stops when it is cut from the parent spore but resumes if the germ tube can reestablish contact with the cut end or with another hypha connected to a spore. Crushed-spore contents placed near the tip of a germ tube do not stimulate growth to any appreciable extent.

Normal mycorrhizal infections can be established in root organ cultures (Hepper and Mosse, 1975; Mosse and Hepper, 1975), in which organized roots were grown in a medium containing sugar but no stem or leaf material. Stems and leaves therefore produce no product essential for the fungus. Histochemical studies indicated that the enzymes required for an Embden-Meyerhof-Parnass system, a tricarboxylic acid cycle and a hexose-monophosphate shunt were present in the hyphae (MacDonald and Lewis, 1978). Work with various metabolic inhibitors applied to germinating spores has not pinpointed the absence of any particular enzyme system normally present in fungi (Hepper, 1979*a*).

Barret (1961) isolated some phycomycete fungi from nonsterile roots by using a hemp-seed baiting technique. After an initial adaptation period on the hemp seed, the fungi grew in normal mycological media. The procedure was successfully repeated by Gerdemann (priv. comm.). These cultures no longer exist, and there is no certain evidence that they produced VA infections. A species of *Endogone* that produced ectotrophic mycorrhiza on eucalyptus was recently grown on lima bean agar (Warcup, 1975).

The culture of VA endophytes is the Mount Everest of mycorrhizal research.

While progress of VA mycorrhiza research does not depend on it, it has been considered of sufficient practical interest to be taken up by some commercial firms. If axenic culture succeeds, it might be possible to proceed to the even more ambitious objective of incorporating, by genetic manipulation, N_2 fixation into VA endophytes. The practical benefits of this would be very great indeed.

BIBLIOGRAPHY

Abbott, L. K., and A. D. Robson. 1977. Growth stimulation of subterranean clover with vesicular-arbuscular mycorrhizas. Australian J. Agric. Res. 28:639–649.

, and . 1978. Growth of subterranean clover in relation to the formation of endomycorrhizas by introduced and indigenous fungi in a field soil. New Phytol. 81:575–585.

Ambler, J. R., and J. L. Young. 1977. Techniques for determining root length infected by vesicular-arbuscular mycorrhizae. Soil Sci. Soc. Amer. J. 41:551–556.

Asai, T. 1944. Über die Mykorrhizenbildung der Leguminosen-Pflanzen. Japanese J. Bot. 13:463–485.

Atkinson, D., and A. W. Davison. 1972. The effects of phosphorus deficiency on water content and response to drought. New Phytol. 72:307–313.

Azcon, R., D. Azcon de Anguilar, and J. M. Barea. 1978. Effects of plant hormones in bacterial cultures on the formation and responses to VA endomycorrhiza. New Phytol. 80:395–364.

, J. M. Barea, and D. S. Hayman. 1976. Utilization of rock phosphate in alkaline soils by plants inoculated with mycorrhizal fungi and phosphate-solubilizing bacteria. Soil Biol. Biochem. 8:135–138.

Bagyaraj, D. J., Manjunath, A., and R. B. Patil. 1979. Interaction between a vesicular-arbuscular mycorrhiza and *Rhizobium* and their effects on soybean in the field. New Phytol. 82:141–145.

Bailey, J. E., and G. R. Safir. 1977. Effect of benomyl on soybean endomycorrhizae and the uptake of benomyl by mycorrhizal and nonmycorrhizal plants. Abstr. Third North Amer. Conf. on Mycorrhizae (Athens, Georgia, Aug. 23–25, 1977) Inst. of Mycorrhizal Res. Devel., U.S. Dept. Agric.–Forest Serv. p. 11.

Bakerspigel, A. 1956. *Endogone* in Saskatchewan and Manitoba. Amer. J. Bot. 45:471–475.

Bakshi, B. K. 1974. Mycorrhiza and its role in forestry. P. L. 480 Project Report. Forest Res. Inst. and Colleges, Dehra Dun, India. 89 pp.

Baltruschat, H., and F. Schönbeck. 1975. Untersuchungen über den Einfluss der endotrophen Mycorrhiza auf den Befall von Tabak mit *Thielaviopsis basicola*. Phytopathol. Z. 84:172–188.

Barea, J. M., R. Azcon, and D. S. Hayman. 1975. Possible synergistic interactions between *Endogone* and phosphate-solubilizing bacteria in low-phosphate soils. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 409–417.

Barley, K. P. 1970. The configuration of the root system in relation to nutrient uptake. Adv. Agron. 22:159–201.

Barrett, J. T. 1961. Isolation, culture and root relation of the phycomycetoid vesicular-arbuscular mycorrhizal endophyte *Rhizophagus*, Rec. Adv. in Botany (Univ. of Toronto Press) 2:1725.

Barrow, N. J., N. Malajczuk, and T. C. Shaw. 1977. A direct test of the ability of vesicular-arbuscular mycorrhiza to help plants take up fixed soil phosphate. New Phytol. 78:269–276.

Baylis, G. T. S. 1959. Effect of vesicular-arbuscular mycorrhizas on growth of *Griselinia littoralis* (Cornaceae). New Phytol. 58:274–280.

. 1967. Experiments on the ecological significance of phycomycetous mycorrhizas. New Phytol. 66:231–243.

. 1969. Synthesis of mycorrhiza of *Podocarpus* and *Agathis* with *Endogone* spores. Nature (London) 22:1267–1268.

_____. 1971. Endogonaceous mycorrhizas synthesized in *Leptospermum* (Myrtaceae). New Zealand J. Bot. 9:293–296.
_____. 1975. The magnolioid mycorrhiza and mycotrophy in root systems derived from it. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 373–389.
_____, R. F. R. McNabb, and T. M. Morrison. 1963. The mycorrhizal nodules of Podocarps. Trans. British Mycol. Soc. 46:378–384.
Becker, W. N. 1976. Quantification of onion vesicule-arbuscular mycorrhizae and their resistance to *Pyrenochaeta terrestris*. Ph.D. thesis, Univ. of Illinois, Champaign, Illinois.
_____, and J. W. Gerdemann. 1977. Colorimetric quantification of vesicular-arbuscular mycorrhizal infection in onion. New Phytol. 78:289–295.
Benians, G. J., and D. A. Barber. 1972. Influence of infection with *Endogone* mycorrhiza on the absorption of phosphate by barley plants. Letcombe Lab. Annu. Rep. Lettcombe, England. pp. 6–9.
Benson, N. R., and R. P. Covey. 1976. Response of apple seedlings to zinc fertilization and mycorrhizal inoculation. J. Amer. Soc. Hort. Sci. 11:252–253.
Bertoldi, M., M. Giovannetti, M. Griselli, and A. Rambelli, 1977. Effects of soil application of benomyl and captan on growth of onions and the occurrence of endophytic mycorrhizas and rhizosphere microbes. Ann. Appl. Biol. 86:111–115.
Bevege, D. I. 1971. Vesicular-arbuscular mycorrhizas of *Araucaria*. Aspects of their ecology and physiology and role in nitrogen fixation. Ph.D. thesis, Univ. of New England, Armidale, New South Wales, Australia.
_____, G. D. Bowen, and M. F. Skinner. 1975. Comparative carbohydrate physiology of ecto- and endomycorrhizas. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 149–174.
Bird, G. W., J. R. Rich, and S. U. Glover. 1974. Increase in endomycorrhizae of cotton roots in soil treated with nematicides. Phytopathology 64:48–51.
Black, R. L. B., and P. B. Tinker. 1977. Interaction between effects of vesicular-arbuscular mycorrhiza and fertilizer phosphorus on yields of potatoes in the field. Nature (London) 267:510–511.
Boatman, N., D. Paget, D. S. Hayman, and B. Mosse. 1978. Effects of systemic fungicides on vesicular-arbuscular mycorrhizal infection and plant phosphate uptake. Trans. British Mycol. Soc. 70:443–450.
Boutros-Mikhail, N. 1976. Einfluss symbiotischer Mikroorganismen auf Wachstum und Nährstoffaufnahme von *Eupatorium odoratum* L. bei Angebot verschiedener Phosphatformen. Ph.D. dissertation, Univ. Göttingen, Göttingen, West Germany.
Bowen. G. D., M. F. Skinner, and D. I. Bevege. 1974. Zinc uptake by mycorrhizal and uninfected roots of *Pinus radiata* and *Araucaria cunninghamii*. Soil Biol. Biochem. 6:141–144.
Bryan, W. C., and P. P. Kormanik. 1977. Mycorrhizae benefit survival and growth of sweetgum seedings in the nursery. Southern J. Appl. Forestry 1:21–23.
_____, and J. L. Ruehle. 1976. Growth stimulation of sweetgum seedings induced by the endomycorrhizal fungus *Glomus mosseae*. Tree Planters' Notes 27:9, 24.
Butler, E. J. 1939. The occurrences and systematic position of the vesicular-arbuscular type of mycorrhizal fungi. Trans. British Mycol. Soc. 22:274–301.
Callow, J. A., L. C. M. Capaccio, G. Parish, and P. B. Tinker. 1978. Detection and estimation of polyphosphate in vesicular-arbuscular mycorrhizas. New Phytol. 80:125–134.
Christie, P., E. I. Newman, and R. Campbell. 1978. The influence of neighbouring grassland plants on each others endomycorrhizas and root surface microorganisms. Soil Biol. Biochem. 10:521–527.
Ciferri, R. 1928. Preliminary observations on sugar cane mycorrhizae and their relationships to root diseases. Phytopathology 18:249–261.
Clark, F. B. 1964. Microorganisms and soil structure affect yellow poplar growth. U.S. Forest Serv. Res. Paper CS-9. 12 pp.
_____. 1969. Endotrophic mycorrhizal infection of tree seedlings with *Endogone* spores. Forest Sci. 15:134–137.
Clarke, A. C., and B. Mosse. 1981. Plant growth responses to vesicular-arbuscular mycorrhiza. XII. Field inoculation responses of barley at two soil P levels. New Phytol. 87 (in press)
Clough, K. S., and Sutton, J. C. 1978. Direct observation of fungal aggregates in sand dune soil. Canadian J. Microbiol. 24:333–335.
Cooper, K. M. 1973. Mycorrhizal associations of New Zealand ferns. Ph.D. thesis, Univ. of Otago, Otago, New Zealand.

_____. 1975. Growth responses to the formation of endotrophic mycorrhizas in *Solanum*, *Leptospermum*, and New Zealand ferns. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 391–407.

_____, and P. B. Tinker. 1978. Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. II. Uptake and translocation of phosphorus, zinc and sulphur. New Phytol. 81:43–52.

Cox, G., and F. E. Sanders. 1974. Ultrastructure of the host-fungus interface in a vesicular-arbuscular mycorrhiza. New Phytol. 73:901–912.

_____, _____, P. B. Tinker, and J. A. Wild. 1975. Ultrastructural evidence relating to host-endophyte transfer in a vesicular-arbuscular mycorrhiza. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 297–312.

_____, and P. B. Tinker. 1976. Translocation and transfer of nutrients in vesicular-arbuscular mycorrhizas. I. The arbuscule and phosphorus transfer: a quantitative ultrastructural study. New Phytol. 77:371–378.

Crush, J. R. 1973*a*. The effect of *Rhizophagus tenuis* mycorrhiza on ryegrass, cocksfoot and sweet vernal. New Phytol. 72:965-973.

_____. 1973*b*. Significance of mycorrhizas in tussock grassland in Otago, New Zealand. New Zealand J. Bot. 11:645–660.

_____. 1974. Plant growth responses to vesicular-arbuscular mycorrhiza. VII. Growth and nodulation of some herbage legumes. New Phytol. 73:743–749.

_____. 1976. Endomycorrhizas and legume growth in some soils of the Mackenzie Basin, Canterbury, New Zealand. New Zealand J. Agric. Res. 19:473–476.

_____. 1978. Changes in effectiveness of soil endomycorrhizal fungal populations during pasture development. New Zealand J. Agric. Res. 21:683–685.

_____, and A. C. Pattison. 1975. Preliminary results on the production of vesicular-arbuscular mycorrhizal inoculum by freeze drying. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 485–493.

Daft, M. J., and A. A. El-Giahmi. 1974. Effect of *Endogone* mycorrhiza on plant growth. VII. Influence of infection on the growth and nodulation in French beans (*Phaseolus vulgaris*). New Phytol. 73:1139–1147.

_____, and _____. 1975. Effects of *Glomus* infections on three legumes. *In* F. E. Sanders, B. Mosse, and P.B. Tinker, (ed.), Endomycorrhizas. Academic Press, London. pp. 581–592.

_____, and _____. 1976. Studies on nodulated and mycorrhizal peanuts. Ann. Appl. Biol. 83:273–276.

_____, and E. Hacskaylo. 1976. Arbuscular mycorrhizas in the anthracite and bituminous coal wastes of Pennsylvania. J. Appl. Ecology 13:523–531.

_____, and _____. 1977. Growth of endomycorrhizal and non-mycorrhizal red maple seedlings in sand and anthracite spoil. Forest Sci. 23:297–216.

_____, _____, and T. H. Nicolson. 1975. Arbuscular mycorrhizas in plants colonizing coal spoils in Scotland and Pennsylvania. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas Academic Press, London. pp. 561–580.

_____, and T. H. Nicolson. 1966. Effect of *Endogone* mycorrhiza on plant growth. New Phytol. 65:343–350.

_____, and _____. 1969. Effect of *Endogone* mycorrhiza on plant growth. II. Influence of inoculum concentration on growth and influence in tomato. New Phytol. 68:953–963.

_____, and _____. 1972. Effect of *Endogone* mycorrhiza on plant growth. IV. Quantitative relationships between the growth of the host and the development of the endophyte in tomato and maize. New Phytol. 71:287–295.

_____, and _____. 1974. Arbuscular mycorrhizas in plants colonizing coal wastes in Scotland. New Phytol. 73:1129–1138.

_____, and B. O. Okusanya. 1973. Effect of *Endogone* mycorrhiza on plant growth. V. Influence of infection on the multiplication of viruses in tomato, petunia and strawberry. New Phytol. 72:975–983.

Daniels, B. A. 1979. *Glomus epigaeus* sp. nov. a useful fungus for vesicular-arbuscular mycorrhizal research. Canadian J. Bot. 59:539.

Davis, R. M., J. A. Menge, and G. A. Zentmyer. 1978. The influence of vesicular-arbuscular mycorrhizae on *Phytophthora* root rot of three crop plants. Phytopathology 68:1614–1617.

Dehne, H. W. 1977. Untersuchungen über den Einfluss der endotrophen Mykorrhiza auf die *Fusarium*-Welke der Tomate und Gurke. Ph.D. thesis, Friedrich-Wilhelm Univ., Bonn, West Germany.

, and F. Schönbeck. 1975. Untersuchungen über den Einfluss der endotrophen Mykorrhiza auf die *Fusarium*-Welke der Tomate. Z. für Pflanzenkrankheiten und Pflanzenschutz 82:630–632.

Dowding, E. S. 1955. *Endogone* in Canadian rodents. Mycologia 47:51–57.

El-Giahmi, A. A., T. H. Nicolson, and M. J. Daft. 1976. Endomycorrizal fungi from Libyan soils and a list of their symbiotic hosts including field crops. Trans. British Mycol. Soc. 67:164–169.

Filer, T. H., and E. R. Toole. 1968. Effect of methyl bromide on mycorrhizae and growth of sweetgum seedlings. Plant Dis. Reptr. 52:483–485.

Fitter. A. H. 1977. Influence of mycorrhizal infection on competition for phosphorus and potassium by two grasses. New Phytol. 79:119–125.

Fox, J. A., and L. Spasoff. 1972. Interaction of *Heterodera solanacearum* and *Endogone gigantea* on tobacco. J. Nematol. 4:224–225.

Furlan, V., and J. A. Fortin. 1973. Formation of endomycorrhizae by *Endogone calospora* on *Allium cepa* under three temperature regimes. Naturaliste Canadien 100:467–477.

, and . 1975. A flotation-bubbling system for collecting Endogonaceae spores from sieved soil. Naturaliste Canadien 102:663–667.

Gerdemann, J. W. 1955*a*. Relation of a large soil-borne spore to phycomycetous mycorrhizal infections. Mycologia 47:619–632.

——. 1955*b*. Wound healing of hyphae in a phycomycetous mycorrhizal fungus. Mycologia 47:916–918.

. 1964. The effect of mycorrhiza on the growth of maize. Mycologia 56:342–349.

. 1965. Vesicular-arbuscular mycorrhizae formed on maize and tulip-tree by *Endogone fasciculata*. Mycologia 57:562–575.

. 1968. Vesicular-arbuscular mycorrhiza and plant growth. Annu. Rev. Phytopath. 6:397–418.

. 1975. Vesicular-arbuscular mycorrhiza. *In* J. G. Torrey and D. T. Clarkson (ed.), The development and function of roots. Academic Press, London. pp. 575–591.

, and T. H. Nicolson. 1963. Spores of mycorrhizal *Endogone* species extracted from soil by wet sieving and decanting. Trans.British Mycol. Soc. 46:235–246.

, and J. M. Trappe. 1974. The Endogonaceae of the Pacific Northwest. Mycologia Memoir No. 5. 75 pp.

Gianinazzi-Pearson, V., and S. Gianinazzi. 1976. Enzymatic studies on the metabolism of vesicular-arbuscular mycorrhiza. I. Effect of mycorrhiza formation and phosphorus nutrition on soluble phosphatase activities in onion roots. Physiol. Vegetale 14:833–841.

Gilmore, A. E. 1971. The influence of endotrophic mycorrhizae on the growth of peach seedlings. J. Amer. Soc. Hort. Sci. 96:35–38.

Giovannetti, M., and B. Mosse. 1980. An evaluation of techniques to measure vesicular-arbuscular infection in roots. New Phytol. 84:489–500.

Graham, S., N. E. Green, and J. W. Hendrix. 1976. The influence of vesicular-arbuscular mycorrhizal fungi on growth and tuberization of potatoes. Mycologia 68:925–929.

Gray L. E., and J. W. Gerdemann. 1967. Influence of vesicular-arbuscular mycorrhiza on the uptake of phosphorus-32 by *Liriodendron tulipifera* and *Liquidambar styraciflua*. Nature (London) 213:106–107.

, and . 1969. Uptake of phosphorus-32 by vesicular-arbuscular mycorrhizae. Plant and Soil 30:415–422.

, and . 1973. Uptake of sulphur-35 by vesicular-arbuscular mycorrhizae. Plant and Soil 39:687–689.

Graw, D. 1979. The influence of soil pH on the efficiency of vesicular-arbuscular mycorrhiza. New Phytol. 82:687–695.

, M. Moawad, and S. Rehm. 1979. Untersuchungen zur Wirts- und Wirkungsspezifität der VA-Mykorrhiza. 2. Acker- und Pflanzenbau 148:85–98.

Green, N. E., S. O. Graham, and N. C. Schenck. 1976. The influence of pH on the germination of vesicular-arbuscular mycorrhizal spores. Mycologia 68:929–934.

Greenall, J. M. 1963. The mycorrhizal endophytes of *Griselinia littoralis* (Cornaceae). New Zealand J. Bot. 1:389–400.

Greny, A. 1973. Anatomical and morphological study of the endomycorrhizae of maize, oats, wheat, barley, and various Gramineae occurring in grassland and as weeds. Comptes Rendus des Séances de L'Academie d'Agriculture de France 59:1077–1083.

Guttay, A. J. R. 1976. Impact of de-icing salts upon the endomycorrhizae of roadside sugar maple. Soil Sci. Soc. Amer. J. 40:952–954.

Haines, B. L., and G. R. Best. 1976. *Glomus mosseae* endomycorrhizal with *Liquidambar styraciflua* L. seedlings retards NO_3, NO_2, and NH_4 nitrogen loss from a temperate forest soil. Plant and Soil 45:257–261.

Hall, I. R.. 1975. Endomycorrhizas of *Metrosideros umbellata* and *Weinmannia racemosa*. New Zealand J. Bot. 13:463–472.

. 1976. Response of *Coprosma robusta* to different forms of endomycorrhizal inoculum. Trans. British Mycol. Soc. 67:409–411.

. 1978. Effect of vesicular-arbuscular mycorrhizas on two varieties of maize and one of sweet-corn. New Zealand J. Agric. Res. 21:517–519.

Harley, J. L. 1969. The biology of mycorrhiza. 2nd ed. Leonard Hill, London. 334 pp.

Hattingh, M. J., and J. W. Gerdemann. 1975. Inoculation of Brazilian sour orange seed with an endomycorrhizal fungus. Phytopathology 65:1013–1016.

Hayman, D. S. 1970. *Endogone* spore numbers in soil and vesicular-arbuscular mycorrhiza in wheat as influenced by season and soil treatment. Trans. British Mycol. Soc. 54:53–63.

. 1974. Plant growth responses to vesicular-arbuscular mycorrhiza. IV. Effect of light and temperature. New Phytol., 73:71–80.

. 1975. The occurrence of mycorrhiza in crops as affected by soil fertility. *In* F.E. Sanders, B. Mosse, and P. B. Tinker (ed.). Endomycorrhizas. Academic Press, London. pp. 495–509.

. 1977. Mycorrhizal effects on white clover in relation to hill land improvement. Agric. Res. Council Res. Rev. 3:82–85.

. 1978*a*. Endomycorrhizae. *In* Y. R. Dommergues and S. W. Krupa (ed.), Interactions between non-pathogenic soil microorganisms and plants. Elsevier Sci. Publ. Co., Amsterdam, Netherlands. pp. 401–442.

. 1978*b*. Mycorrhizal populations of sown pastures and native vegetation in Otago, New Zealand. New Zealand J. Agric.Res. 21:271–276.

, J. M. Barea, and R. Azcon. 1976. Vesicular-arbuscular mycorrhiza in southern Spain: its distribution in crops growing in soils of different fertility. Phytopathologia Mediterranea 15:1–6.

, and J. M. Day. 1978. Influence of VA mycorrhiza on plant growth. Uptake of molybdenum. Rothamsted Annu. Rep. for 1977. Rothamsted Exp. Sta , Harpenden, England. p. 240.

, A. M. Johnson, and I. Ruddlesdin. 1975. The influence of phosphate and crop species on *Endogone* spores and vesicular-arbuscular mycorrhiza under field conditions. Plant and Soil 43:489–495.

, R. M. Macdonald, and J. R. Spokes. 1978. The effects of pesticides on VA mycorrhiza. Rothamsted Annu. Rep. for 1977. Rothamsted Exp. Sta., Rothamsted, England. p. 238.

, and B. Mosse. 1971. Plant growth responses to vesicular-arbuscular mycorrhiza. I. Growth of *Endogone*-inoculated plants in phosphate-deficient soils. New Phytol. 70:19–27.

, and . 1972*a*. Plant growth responses to vesicular-arbuscular mycorrhiza. III. Increased uptake of labile P from soil. New Phytol. 71:41–47.

, and . 1972*b*. The role of vesicular-arbuscular mycorrhiza in the removal of phosphate from soil by plant roots. Rev. ecol. biol. sol 9:463–470.

, and . 1979. Improved growth of white clover in hill grasslands by mycorrhizal inoculation. Ann. Appl. Biol. 93:141–148.

, and G. E. Stovold. 1979. Spore populations and infectivity of vesicular-arbuscular mycorrhizal fungi in New South Wales. Australian J. Bot. 27:227–233.

Hepper, C. M. 1977. A colorimetric method for estimating vesicular-arbuscular mycorrhizal infection in roots. Soil Biol. Biochem. 9:15–18.

. 1979*a*. Germination and growth of *Glomus caledonius* spores: the effects of inhibitors and nutrients. Soil Biol. Biochem. 11:269–277.

. 1979*b*. Nutritional and biochemical studies of fungi involved in vesicular-arbuscular mycorrhiza. Ph.D. thesis. Univ. of London, London, England.

..... , and B. Mosse. 1975. Techniques used to study the interaction between *Endogone* and plant roots. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 65–75.

..... , and G. Smith. 1976. Observations on the germination of *Endogone* spores. Trans. British Mycol. Soc. 66:189–194.

Hirrel, M. C., and J. W. Gerdemann. 1979. Effects of salinity on the growth and P nutrition of vesicular-arbuscular mycorrhizal bell pepper and on the germination of *Gigaspora margarita*. Abstr. Fourth North Amer. Conf. on Mycorrhizae (Fort Collins, Colorado, 1979).

Ho, I., and J. M. Trappe. 1973. Translocation of ^{14}C from *Festuca* plants to their endomycorrhizal fungi. Nature (London), 244:30–31.

Holevas, C. D. 1966. The effect of a vesicular-arbuscular mycorrhiza on the uptake of soil phosphorus by strawberry (*Fragaria* sp., var. Cambridge Favourite). J. Hort. Sci. 41:57–64.

Holley, J. D., and R. L. Peterson. 1979. Development of vesicular-arbuscular mycorrhiza in bean roots. Canadian J. Bot. 57:1960–1978.

Hussey, R. S., and R. W. Roncadori. 1977. Interaction of *Pratylenchus brachyurus* and an endomycorrhizal fungus on cotton. Abstr. Third North Amer. Conf. on Mycorrhizae (Athens, Georgia, Aug. 23–25, 1977) Inst. of Mycorrhizal Res., U. S. Dept. Agric.–Forest Serv. p. 2.

Iqbal, S. H., and K. S. Qureshi. 1977. The effect of vesicular-arbuscular mycorrhizal associations on growth of sunflower (*Helianthus annus* L.) under field conditions. Biologia (Pakistan) 23:189–196.

..... , K. Sultana, and B. Parveen. 1975. *Endogone* spore numbers in the rhizosphere and the occurrence of VA mycorrhizas in plants of economic importance. Biologia (Pakistan) 21:227–237.

Islam, R. 1976. Progress report on mycorrhiza research at IITA. Internal Report, Internat. Inst. Trop. Agric., Ibadan, Nigeria. 25 pp.

..... 1977. Effect of several *Endogone* spore types on the yield of *Vigna unguiculata*. Internal Report, Internat. Inst. Trop. Agric., Ibadan, Nigeria. 19 pp.

..... , A. Ayanaba, and F. E. Sanders. 1980. Response of cowpea (*Vigna unguiculata*) to inoculation with VA mycorrhizal fungi and to rock phosphate fertilization in some sterilized Nigerian soils. Plant and Soil 54:107–117.

Jackson, N. E., R. E. Franklin, and R. H. Miller. 1972. Effects of VA mycorrhiza on growth and phosphorus content of three agronomic crops. Proc. Soil Sci. Soc. Amer. 36:64–67.

..... , R. H. Miller, and R. E. Franklin. 1973. The influence of vesicular-arbuscular mycorrhiza on uptake of 90 Sr from soil by soybeans. Soil Biol. Biochem. 5:205–212.

Janos, D. P. 1975. Effects of vesicular-arbuscular mycorrhiza on lowland tropical rain forest trees. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 437–446.

..... 1977. Vesicular-arbuscular mycorrhiza affect the growth of *Bactris gasipaes*. Principes 21:12–18.

Johnson, C. R., and S. Michelini. 1974. Effect of mycorrhizae on container grown *Acacia*. Proc. Florida State Hort. Soc. (Miami Beach, Nov.5–7, 1974) 87:520–522.

Johnson, P. N. 1976. Effects of soil phosphate level and shade on plant growth and mycorrhizas. New Zealand J. Bot. 14:333–340.

..... 1977. Mycorrhizal *Endogone* in a New Zealand forest. New Phytol. 78:161–170.

Joseph, N. 1977. Untersuchungen über den Einfluss des endotrophen Mykorrhizapilzes *Glomus mosseae* Gerd. and Trappe. (*Endogone mosseae* Nicol. and Gerd.) auf *Zea mays* L. Thesis, Friedrich-Wilhelm Univ., Bonn, West Germany.

Kaspari, H. 1973. Elektronenmikroskopische Untersuchung zur Feinstruktur der endotrophen Tabakmykorrhiza. Arch. Mikrobiol. 92:201–207.

..... 1975. Fine structure of the host-parasite interface in endotrophic mycorrhiza of tobacco. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp.325–334.

Khan, A. G. 1971. Occurrence of *Endogone* species in West Pakistan soils. Trans. British Mycol. Soc. 56:217–224.

..... 1972*a*. The effect of vesicular-arbuscular mycorrhizal association on growth of cereals. I. Effects of maize growth. New Phytol. 71:613–619.

..... 1972*b*. Mycorrhizae and their significance in plant nutrition. Biologia (Pakistan) Special supplement. pp. 42–78.

_____. 1972*c*. Podocarp-like mycorrhizal nodules in *Aesculus indica*. Ann. Bot. 36:229–238.
_____. 1974. The occurrence of mycorrhizae in halophytes, hydrophytes and xerophytes and of Endogone spores in adjacent soils. J.Gen. Microbiol. 81:7–14.
_____. 1975. The effect of vesicular-arbuscular mycorrhizal association on growth of cereals. II. Effect on wheat growth. Ann. Appl. Biol. 80:27–36.
_____. 1978. Vesicular-arbuscular mycorrhizas in plants colonizing black wastes from bituminous coal mining in the Illawarra region of New South Wales. New Phytol. 81:53–63.
_____, and S. R. Saif. 1973. Some observations on mycorrhizae of *Olea cuspidata*. Pakistan J. Bot. 5:65–70.
Khanaqua, A. 1979. Einfluss der vesikulär-arbuskulären Mykorrhiza auf Wachstum und Phosphataufnahme von *Nicotiana tabacum* L. unter besonderer Berücksichtigung verschiedener Phosphatdüngerformen und pH Werte. Ph.D. dissertation, Univ. Göttingen, Göttingen, West Germany.
Kinden, D. A., and M. F. Brown. 1975*a*. Electron microscopy of vesicular-arbuscular mycorrhizae of yellow poplar. I. Characterization of endophytic structures by scanning electron stereoscopy. Canadian J. Microbiol. 21:989–993.
_____, and _____. 1975*b*. Electron microscopy of vesicular-arbuscular mycorrhizae of yellow poplar. II. Intracellular hyphae and vesicles. Canadian J. Microbiol. 21:1768–1780.
_____, and _____. 1975*c*. Electron microscopy of vesicular-arbuscular mycorrhizae of yellow poplar. III. Host endophyte interactions during arbuscular development. Canadian J. Microbiol. 21:1930–1939.
_____, and _____. 1976. Electron microscopy of vesicular-arbuscular mycorrhizae of yellow poplar. IV. Host-endophyte interactions during arbuscular deterioration. Canadian J. Microbiol. 22:64–75.
Kleinschmidt, G. D., and J. M. Gerdemann. 1972. Stunting of citrus seedlings in fumigated nursery soils related to the absence of endomycorrhizae. Phytopathology 62:1447–1453.
Kormanik, P. P., W. S. Bryan, and T. Schultz. 1977*a*. Influence of endomycorrhizae on growth of sweetgum seedlings from eight mother trees. Forest Sci. 23:500–506.
_____, _____, and _____. 1977*b*. The role of mycorrhizae in plant growth and development. *In* H. M. Vines (ed.), Physiology of root-microorganism associations. Proc. Symp. Southern Section Amer. Soc. Plant Physiologists, Atlanta, Georgia, Feb. 1977. pp. 1–10.
Koske, R. E. 1975. *Endogone* spores in Australian sand dunes. Canadian J. Bot. 53:668–672.
_____, J. C. Sutton, and B. R. Sheppard. 1975. Ecology of *Endogone* in Lake Huron sand dunes. Canadian J.Bot. 53:87–93.
Koucheki, H. K., and D. J. Read. 1976. Vesicular-arbuscular mycorrhiza in natural vegetation systems.II. The relationship between infection and growth in *Festuca ovina* L. New Phytol. 77:665–666.
Kruckelmann, H. W. 1973. Die vesikulär-arbuskuläre Mykorrhiza and ihre Beeinflussung in landwirtschaftlichen Kulturen. Ph.D. dissertation, Tech. Univ. Braunschweig, Braunschweig, West Germany.
_____. 1975. Effects of fertilizers, soils, soil tillage and plant species on frequency of *Endogone* chlamydospores and mycorrhizal infection in arable soils. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 511–525.
Lambert, D. 1978. Mycorrhizae establishment for strip mine revegetation. M.Sc. thesis. Pennsylvania State Univ., State College.
La Rue, J. H., W. D. McClellan, and W. L. Peacock. 1975. Mycorrhizal fungi and peach nursery nutrition. California Agric. 29:7.
Laycock, D. H. 1945. Preliminary investigations into the function of the endotrophic mycorrhiza of *Theobroma cacao* L. Trop.Agric. 22:77–80.
Lily, V. G. 1975. Note on the development of VA mycorrhiza *Endogone fasciculata* in coconut root. Curr.Sci. 44:201–202.
Lindermann, G., and C. A. Call. 1977. Enhanced rooting of woody plant cuttings by mycorrhizal fungi. Abstr. Third North Amer. Conf. on Mycorrhizae (Athens, Georgia, Aug. 23–25, 1977) Inst. of Mycorrhizal Res. Devel., U.S. Dep. Agric.-Forest Serv. p. 106.
Macdonald, R. M., and M. Lewis. 1978. The occurrence of some acid-phosphatases and dehydrogenases in the vesicular-arbuscular mycorrhizal fungus *Glomus mosseae*. New Phytol. 80:135–141.

Magrou, M. J., and M. Magrou. 1940. Essai de culture de champignon symbiotique de la pomme de terre. Acad. des Sci., Paris 211:234.
Marsh, B. a'B. 1971. Measurement of length in random arrangement of lines. J. Appl. Ecol. 8:265–267.
Marx, D. H. 1977. The role of mycorrhizae in forest production. Tappi conference papers. Annual meeting, Tech. Assoc. of the Pulp and Paper Industry, Inc. Atlanta, Georgia. pp. 151–161.
, W. C. Bryan, and W. A. Campbell. 1971. Effect of endomycorrhizae formed by *Endogone mosseae* on growth of citrus. Mycologia 63:1222–1226.
Mason, D. T. 1964. A survey of numbers of *Endogone* spores in soil cropped with barley, raspberry and strawberry. Hort. Res 4:98–103.
Mbaga, M. T. 1977. Mycorrhizal infections in rice. M.Sc. thesis, Univ. Dar-Es-Salaam, Tanzania.
McIlveen, W. D., and H. Cole. 1976. Spore dispersal of Endogonaceae by worms, ants, wasps, and birds. Canadian J. Bot. 54:1486–1489.
, R. A. Spotts, and D. D. Davis. 1975. The influence of soil zinc on nodulation, mycorrhizae and ozone-sensitivity of pinto beans. Phytopathology 65:647–648.
Mehraveran, H. 1977. Mycorrhizal dependency of six citrus cultivars. Ph.D. thesis, Univ. of Illinois, Urbana-Champaign, Illinois.
Meloh, K. A. 1963. Untersuchungen zur Biologie der endotrophen Mykorrhiza bei *Zea mays* L. und *Avena sativa* L. Arch. Mikrobiol. 46:369–381.
Menge, J. A., R. M. Davis, E. L. V. Johnson, and G. A. Zentmyer. 1978. Mycorrhizal fungi increase growth and reduce transplant injury in avocado. California Agric. 32:6–7.
, E. L. V. Johnson, and V. Minassian. 1979. Effect of heat treatment and three pesticides upon the growth and reproduction of the mycorrhizal fungus *Glomus fasciculatus*. New Phytol. 82:473–480.
, and R. G. Platt. 1978. Mycorrhizal dependency of several citrus cultivars under three nutrient regimes. New Phytol. 81:553–559.
, H. Lembright, and E. L. V. Johnson. 1977. Utilization of mycorrhizal fungi in citrus nurseries. Proc. Int. Soc. Citriculture 1:129–132.
, D. E. Munneke, E. L. V. Johnson, and D. W. Carnes. 1978. Dosage responses of vesicular-arbuscular mycorrhizal fungi to methyl bromide fumigation. Phytopathology 68:1368–1372.
, D. Steirle, D. J. Bagyaraj, E. L. V. Johnson, and R. T. Leonard. 1978. Phosphorus concentrations in plants responsible for inhibition of mycorrhizal infection. New Phytol. 80:575–578.
Metcalf, S. M. 1978. The influence of vesicular-arbuscular mycorrhiza on uptake of zinc and phosphorus by cotton. Ph.D. thesis, Univ. of California, Berkeley, California.
Meyer, F. H. 1973. Distribution of ectomycorrhiza in native and man-made forests. *In* G. C. Marks and T. T. Koslowski (ed.), Ectomycorrhizae. Academic Press, London. pp. 79–106.
Mikola, P. (ed.) 1981. Tropical Mycorrhizal Research. Oxford Univ. Press, Oxford, England.
Morley, C., and B. Mosse. 1976. Lupin induced abnormal vesicular-arbuscular mycorrhizal infection in white clover. Trans. British Mycol. Soc. 67:510–513.
Mosse, B. 1953. Fructifications associated with mycorrhizal strawberry roots. Nature (London) 171:974.
. 1956. Studies on the endotrophic mycorrhiza of some fruit plants. Ph.D. thesis, Univ. of London, London, England.
. 1957. Growth and chemical composition of mycorrhizal and non-mycorrhizal apples. Nature (London) 179:922–924.
. 1959. Observations on the extramatrical mycelium of a vesicular-arbuscular endophyte. Trans. British Mycol. Soc. 42:439–448.
. 1962. The establishment of vesicular-arbuscular mycorrhiza under aseptic conditions. J. Gen. Microbiol. 27:509–520.
. 1972*a*. Effects of different *Endogone* strains on the growth of *Paspalum notatum*. Nature (London) 239:221–223.
. 1972*b*. The influence of soil type and *Endogone* strain on the growth of mycorrhizal plants in phosphate deficient soils. Rev. ecol. biol. sol 9:529–537.
. 1973*a*. Advances in the study of vesicular-arbuscular mycorrhiza. Annu. Rev. Phytopath. 11:171–196.
. 1973*b*. Plant growth responses to vesicular-arbuscular mycorrhiza. IV. In soil given additional phosphate. New Phytol. 72:127–136.

_____. 1973*c*. The role of mycorrhiza in phosphorus solubilization. *In* J. S. Furtado (ed.), Global impacts of applied microbiology (GIAM). Proc. Fourth Internat. Conf., São Paulo, Brazil, 1971. pp. 543–561.

_____. 1975. Specificity in VA mycorrhizas. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 470–484.

_____. 1977*a*. Plant growth responses to vesicular-arbuscular mycorrhiza. X. Responses of *Stylosanthes* and maize to inoculation in unsterile soils. New Phytol. 78:277–288.

_____. 1977*b*. The role of mycorrhiza in legume nutrition on marginal soils. *In* J. M. Vincent, A. S. Whitney, and J. Bose (ed.), Exploiting the Legume-*Rhizobium* Symbiosis in Tropical Agriculture. Misc. Pub. 145. Coop. Ext. Serv., College of Trop. Agric., Univ. of Hawaii. pp. 275–292.

_____. 1978. Mycorrhiza and plant growth. *In* A. H. J. Freysen and J. W. Woldendorp (ed.), Structure and functioning of plant populations. North Holland Publ. Co. Elsevier, pp. 269–291.

_____, and G. D. Bowen. 1968. A key to the recognition of some *Endogone* spore types. Trans. British Mycol. Soc. 51:485–492.

_____, and D. S. Hayman. 1971. Plant growth responses to vesicular-arbuscular mycorrhiza. II. In unsterilized field soils. New Phytol. 70:29–34.

_____, and _____. 1980. Mycorrhiza in agricultural plants. *In* P. Mikola (ed.), Tropical Mycorrhizal Research. Oxford Univ. Press, Oxford, England. pp. 213–230.

_____, and _____. 1981. Mycorrhiza. *In* J. E. Satchell (ed.), Production Ecology of an English Oak Wood. Springer-Verlag, Berlin.

_____, and _____, and D. Arnold. 1973. Plant growth responses to vesicular-arbuscular mycorrhiza. V. Phosphate uptake from ^{32}P labelled soil solution by three plant species. New Phytol 72:809–815.

_____, _____, and G. J. Ide. 1969. Growth responses of plants in unsterilized soils to inoculation with vesicular-arbuscular mycorrhiza. Nature (London) 224:1031–1032.

_____, and C. M. Hepper. 1975. Vesicular-arbuscular mycorrhizal infections in root organ cultures. Physiol. Plant Pathol. 5:215–223.

_____, and G. W. Jones. 1968. Separation of *Endogone* spores from organic soil debris by differential sedimentation on gelatine columns. Trans. British Mycol. Soc. 51:604–608.

_____, and J. M. Phillips. 1971. The influence of phosphate and other nutrients on the development of vesicular-arbuscular mycorrhiza in culture. J. Gen. Microbiol. 69:157–166.

_____, C. Ll. Powell, and D. S. Hayman. 1976. Plant growth responses to vesicular-arbuscular mycorrhiza. IX. Interactions between VA mycorrhiza, rock phosphate and symbiotic nitrogen fixation. New Phytol. 76:331–342.

_____, and J. P. Thompson. 1981. Nutrient-film culture of vesicular-arbuscular mycorrhiza for mass production of inoculum: Exploratory experiments with beans *(Phaseolus vulgaris)* J. exp. Bot. (submitted).

_____, and P.B. Tinker. 1981. Effects of mycorrhizas on nutrition of higher plants. CRC Handbook of Nutrition and Food, Critical Reviews Rubber Co., Rockville, Md. (in press).

_____, A. Warner, and C. A. Clarke. 1981. Plant growth responses in vesicular-arbuscular mycorrhiza. XIII. Spread of an introduced VA endophyte in the field and residual growth effects of inoculation in the second year. New Phytol. (in press).

Murdoch, C. L., J. A. Jackobs, and J. W. Gerdemann. 1967. Utilization of phosphorus sources of different availability by mycorrhizal and non-mycorrhizal maize. Plant and Soil 27:329–334.

Munns, D. N., and B. Mosse. 1980. Mineral nutrition of legume crops. *In* R. J. Summerfield and A. H. Bunting (eds.), Advances in legume science, Proc. Internat. Legume Conf., Kew, 1978. pp. 115–125.

Nadarajah, P. 1980. Species of Endogonaceae and mycorrhizal association of *Elaeis guineensis* and *Theobroma cacao*. *In* P. Mikola (ed.), Tropical mycorrhizal research. Oxford Univ. Press, Oxford, England. pp. 232–237.

Nemec, S. 1974. Populations of *Endogone* in strawberry fields in relation to root rot infection. Trans. British Mycol. Soc. 62:45–49.

Newman, E. I. 1966. A method of estimating the total length of root in a sample. J. Appl. Ecology 3:139.

Nicolson, T. H. 1959. Mycorrhizae in the *Gramineae*. I. Vesicular-arbuscular endophytes, with special reference to the external phase. Trans. British Mycol. Soc. 42:421–438.

_____. 1960. Mycorrhiza in the *Gramineae*. II. Development in different habitats, particularly sand dunes. Trans. British Mycol. Soc. 43:132–145.

. 1967. Vesicular-arbuscular mycorrhiza—a universal plant symbiosis. Sci. Prog. (England) 55:561–581.

, and N. C. Schenck. 1979. Endogonaceous mycorrhizal endophytes in Florida. Mycologia 71:178–198.

Nyabyenda, P. 1977. Einfluss der Bodentemperatur und organischer Stoffe auf die Wirkung der vesikulär-arbuskulären Mykorrhiza. Ph.D. dissertation, Univ. Göttingen, Göttingen, West Germany.

Nye, P. H., and P. B. Tinker. 1977. Solute movement in the soil-root system. Blackwell Scientific Publications, London. 342 pp.

Ocampo, J. A., and D. S. Hayman. 1981. Influence of plant interactions on vesicular-arbuscular mycorrhizal infections. II. Crop rotations and residual effects on non-host plants. New Phytol. 87:334–343.

Ohms. R. E. 1957. A flotation method for collecting spores of a phycomycetous mycorrhizal parasite from soil. Phytopathology 47:751–752.

Owusu-Bennoah, E., and B. Mosse. 1979. Plant growth responses to vesicular-arbuscular mycorrhiza. XI. Responses of onion, lucerne, and barley to field inoculation with two endophytes. New Phytol. 83:1–9.

, and A. Wild. 1979. Autoradiography of the depletion zone of phosphate around onion roots in the presence of vesicular-arbuscular mycorrhiza. New Phytol. 82:133–140.

Paget, D. and B. Mosse. 1975. Effects of mycorrhiza on phosphate cycling at Meathop Wood, Lancs. Rothamsted Annu. Rep. for 1974. Rothamsted Exp. Sta., Harpenden, England. pp. 251–252.

Pandey, S., and A. P. Misra. 1971. *Rhizophagus* in mycorrhizal association with *Litchi chinensis* Sonn. Mycopath. et Mycol. Appl. 45:337–354.

Pearson, V., and P. B. Tinker. 1975. Measurement of phosphorus fluxes in the external hyphae of endomycorrhizas. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.). Endomycorrhizas. Academic Press, London. pp. 277–287.

Peuss, H. 1958. Untersuchungen zur Ökologie und Bedeutung der Tabakmycorrhiza. Arch. Mikrobiol. 29:112–142.

Pfleger, F. L., and E. L. Stewart. 1976. The influence of fungicides on endemic populations of *Glomus* species in association with field grown peas. Proc. Amer. Phytopath. Soc. 3:274.

Phillips, J. M., and D. S. Hayman. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. British Mycol. Soc. 55:158–161.

Pichot, J., and T. Binh. 1976. Action des endomycorrhizes sur la croissance el la nutrition phosphate de l'Agrostis en vases de vegetation et sur le phosphate isotopiquement diluable du sol. Agronomie Tropical 31:375–378.

Porter, W. M. 1979. The "most probable number" method of enumerating infective propagules for vesicular-arbuscular mycorrhizal fungi in soil. Australian J. Soil Res. 17:515–519.

Porter, D. M., and M. K. Beute. 1972. *Endogone* species in roots of Virginia type peanuts. Phytopathology 62:783, abstr.

Possingham, J. V., and J. G. Obbink. 1971. Endotrophic mycorrhiza and the nutrition of grape vines. Vitis 10:120–130.

Powell, C. Ll. 1975*a*. Plant growth responses to vesicular-arbuscular mycorrhiza. VIII. Uptake of P by onion and clover infected with different *Endogone* spore types in ^{32}P labelled soils. New Phytol. 75:563–566.

. 1975*b*. Potassium uptake by endotrophic mycorrhizas. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.). Endomycorrhizas. Academic Press, London. pp. 461–468.

. 1976*a*. Development of mycorrhizal infections from *Endogone* spores and infected root segments. Trans. British Mycol. Soc. 66:439–445.

. 1976*b*. Mycorrhizal fungi stimulate clover growth in New Zealand hill country soils. Nature (London) 264:436–438.

. 1977*a*. Mycorrhizas in hill country soils. I. Spore-bearing mycorrhizal fungi in thirty-seven soils. New Zealand J. Agric. Res. 20:53–57.

. 1977*b*. Mycorrhizas in hill country soils. II. Effect of several mycorrhizal fungi on clover growth in sterilized soils. New Zealand J. Agric. Res. 20:59–62.

. 1977*c*. Mycorrhizas in hill country soils. III. Effect of inoculation on clover growth in unsterile soils. New Zealand J. Agric. Res. 20:343–348.

. 1977*d*. Mycorrhizas in hill country soils. V. Growth responses in ryegrass. New Zealand J. Agric. Res. 20:495–502.

1979*a*. Introduction of mycorrhizal fungi into pasture soils on pelleted seed. New Phytol. 83:81–85.

. 1979*b*. Spread of mycorrhizal fungi through soil. New Zealand J. Agric. Res. 22:335–339.

, and J. Daniel. 1978*a*. Growth of white clover in undisturbed soils after inoculation with efficient mycorrhizal fungi. New Zealand J. Agric. Res. 21:675–681.

, and . 1978*b*. Mycorrhizal fungi stimulate uptake of soluble and insoluble phosphate fertilizer from a phosphate-deficient soil. New Phytol. 80:351–359.

, and J. Sithamparanathan. 1977. Mycorrhizas in hill country soils. IV. Infection rate in grass and legume species by indigenous mycorrhizal fungi under field conditons. New Zealand J. Agric. Res. 20:489–502.

Ramirez, B. N., D. J. Mitchell, and N. C. Schenck. 1975. Establishment and growth effects of three vesicular-arbuscular mycorrhizal fungi on papaya. Mycologia 67:1039–1043.

Ratnayake, M., R. T. Leonard, and J. A. Menge. 1978. Root exudation in relation to supply of phosphorus and its possible relevance to mycorrhizal formation. New Phytol. 81:543–552.

Read, D. J., H. Kianmehr, and A. Malibari. 1977. The biology of mycorrhiza in *Helianthemum* Mill. New Phytol. 78:305–312.

, H. K. Koucheki, and J. Hodgson. 1976. Vesicular-arbuscular mycorrhiza in natural vegetation systems. I. The occurrence of infection. New Phytol. 77:641–654.

Redhead, J. F. 1968. Mycorrhizal associations in some Nigerian forest trees. Trans. British Mycol. Soc. 51:377–387.

. 1973. Aspects of the biology of mycorrhizal associations occurring in tree species in Nigeria. Ph.D. thesis, Univ. of Ibadan, Ibadan, Nigeria.

. 1975. Endotrophic mycorrhizas in Nigeria. Some aspects of the ecology of the endotrophic mycorrhizal association of *Khaya grandifoliola* C. Dc. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp.447–459.

. 1977. Endotrophic mycorrhizas in Nigeria: species of the Endogonaceae and their distribution. Trans. British Mycol. Soc. 69:275–280.

Rhodes, L. H., and J. W. Gerdemann. 1975. Phosphate uptake zones of mycorrhizal and non-mycorrhizal onions. New Phytol. 75:555–561.

, and . 1976. Effect of vesicular-arbuscular mycorrhiza on sulfate uptake by onion plants. Proc. Am. Phytopath. Soc. 3:274–275.

, and . 1978. Hyphal translocation and uptake of sulphur by vesicular-arbuscular mycorrhizae of onion. Soil Biol. Biochem. 10:355–360.

Rich, J. R., and G. W. Bird. 1974. Association of early-season vesicular-arbuscular mycorrhizae in increased growth and development of cotton. Phytopathology 64:1421–1425.

Roncadori, R. W., and R. S. Hussey. 1977. Interaction of the endomycorrhizal fungus *Gigaspora margarita* and root-knot nematode on cotton. Phytopathology 67:1507–1511.

Rorison, I. H. 1968. The response to phosphorus of some ecologically distinct plant species. I. Growth rates and phosphorus absorption. New Phytol. 67:913–923.

Ross, J. P. 1971. Effect of phosphate fertilization on yield of mycorrhizal and non-mycorrhizal soybeans. Phytopathology 61:1400–1403.

. 1972. Influence of *Endogone* mycorrhiza on *Phytophthora* rot of soybean. Phytopathology 62:895–897.

, and J. W. Gilliam. 1973. Effect of *Endogone* mycorrhiza on phosphorus uptake by soybeans from inorganic phosphates. Soil Sci. Soc. Amer. Proc. 37:237–239.

, and J. A. Harper. 1970. Effect of *Endogone* mycorrhiza on soybean yields. Phytopathology 60:1552–1556.

, and R. Ruttencutter. 1977. Population dynamics of two vesicular-arbuscular endomycorrhizal fungi and the role of hyperparasitic fungi. Phytopathology 67:490–496.

Sabet, Y. 1940. Mycorrhizal habit in the date palm (*Phoenix dactylifera*). Nature 145:782–783.

Safir, G. R., J. S. Boyer, and J. W. Gerdemann. 1971. Mycorrhizal enhancement of water transport in soybean. Science 172:581–583.

, J. S. Boyer, and J. W. Gerdemann. 1972. Nutrient status and mycorrhizal enhancement of water transport in soybean. Plant Physiol. 49:700–703.

Saif, S. R. 1975. The occurrence of mycorrhizas and *Endogone* spores in the rhizospheres of plants growing around University campus, Islamabad, Pakistan. Pakistan J. Bot. 7:175–182.

, I.Ali, and A. A. Zaidi. 1977. Vesicular-arbuscular mycorrhizae in plants and endogonaceous spores in soil of northern areas of Pakistan. III. Dir and Chitral. Pakistan J. Bot. 9:129–148.

, and N. Iffat. 1976. Vesicular-arbuscular mycorrhizae in plants and endogonaceous spores in the soils of northern Pakistan. I. Hunza, Nagar and Gilgit. Pakistan J. Bot. 8:163–179.

, and A. G. Khan. 1975. The influence of season and stage of development of plant on *Endogone* mycorrhiza of field grown wheat. Canadian J. Microbiol. 21:1020–1024.

, and . 1977. The effect of vesicular-arbuscular mycorrhizal associations on growth of cereals. III. Effects on barley growth. Plant and Soil 47:17–26.

, and D. Parveen. 1976. Vesciular-arbuscular mycorrhizae in plants and endogonaceous spores in soils of northern areas of Pakistan. II. Kaghan Valley and Baburar (Gilgit), Islamabad. Pakistan J. Sci. (in press).

, N. A. Sheikh, and A. G. Khan. 1975. Ecology of *Endogone*. I. Relationship of *Endogone* spore population with physical soil factors. Pakistan J. Sci. 2:1–5.

Samuel, G. 1926. Note on the distribution of mycorrhiza. Trans. Royal Soc. South Australia 50:245–246.

Sanders, F. E. 1975. The effect of foliar-applied phosphate on the mycorrhizal infections of onion roots. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 261–276.

. 1976. What direction should be taken in future research at IITA on the role of mycorrhizas in crop nutrition? Internal report, Internat. Inst. Trop. Agric., Ibadan, Nigeria. 68 pp.

, and P. B. Tinker. 1971. Mechanism of absorption of phosphate from soil by *Endogone* mycorrhizas. Nature (London) 233:278–279.

, and P. B. H. Tinker. 1973. Phosphate flow into mycorrhizal roots. Pest. Sci. 4:385–395.

, , R. L. B. Black, and S. M. Palmerley. 1977. The development of endomycorrhizal root systems: I. Spread of infection and growth promoting effects with four species of vesicular-arbuscular endophyte. New Phytol. 78:257–268.

Sanni, S. O. 1976*a*. Vesicular-arbuscular mycorrhiza in some Nigerian soils and their effect on the growth of cowpea (*Vigna unguiculata*), tomato (*Lycopersicum esculentum*) and maize (*Zea mays*). New Phytol. 77:667–671.

.1976*b*. Vesicular-arbuscular mycorrhiza in some Nigerian soils. The effect of *Gigaspora gigantea* on the growth of rice. New Phytol. 77:673–674.

Scannerini, S. P., F. Bonfante, and A. Fontana. 1975. An ultrastructural model for the host symbiont interaction in the endotrophic mycorrhizae of *Ornithogalum umbellatum* L. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Encomycorrhizas. Academic Press, London. pp. 313–324.

Schenck, N. C., S. O. Graham, and N. E. Green. 1975. Temperature and light effect on contamination and spore germintion of vesicular-arbuscular mycorrhizal fungi. Mycologia 57:1189–1192.

, and K. Hinson. 1973. Response of nodulating and nonnodulating soybeans to a species of *Endogone* mycorrhiza. Agron. J. 65:849–850.

, and M. .K. Kellam. 1978. The influence of vesicular-arbuscular mycorrhizae on disease development. Tech. Bull. 798. Florida Agric. Exp. Sta., Gainesville. 16 pp.

, and R. A. Kinloch. 1974. Pathogenic fungi, parasitic nematodes and endomycorrhizal fungi associated with soybean roots in Florida. Plant Dis. Reptr. 58:169–172.

, and . 1976. Mycorrhizal fungi colonizing field crops on a newly cleared woodland site. Proc. Amer. Phytopath. Soc. 3:274.

, and , and D. H. Dickson. 1975. Interaction of endomycorrhizal fungi and root-knot nematode on soybeans. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 607–617.

, and T. H. Nicolson. 1977. A zoosporic fungus occurring on species of *Gigaspora margarita* and other vesicular-arbuscular mycorrhizal fungi. Mycologia 69:1050–1053.

, and V. N. Schröder. 1974. Temperature response of *Endogone* mycorrhiza on soybean roots. Mycologia 66:600–605.

, and D. P. H. Tucker. 1974. Endomycorrhizal fungi and the development of citus seedlings in Florida fumigated soils. J. Amer. Soc. Hort. Sci. 99:284–287.

Schönbeck, F. 1979. Endomycorrhiza in relation to plant diseases. *In* B. Schippers and W. Gams (ed.), Soil-borne pathogens. Academic Press, London. pp. 271–280.

, and U. Schinzer. 1972. Untersuchungen über den Einfluss der endotrophen Mycorrhiza auf die TMV-Läsionenbildung in *Nicotiana tabacum* L. var. Xanthi-nc. Phytopath. Z. 73:78–80.

Schramm, J. R. 1966. Plant colonization studies on black wastes from anthracite mining in Pennsylvania. Trans. Amer. Phil. Soc. 56: 194 pp.

Smith, S. E. and M. J. Daft. 1977. Interactions between growth, phosphate content and N_2 fixation in mycorrhizal and non-mycorrhizal *Medicago sativa* (alfalfa). Australian J. Plant Physiol. 4:403–413.

Sparling, G. P., and P. B. Tinker. 1975. Mycorrhizae in Pennine grassland. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 545–560.

, and . 1978*a*. Mycorrhizal infection in Pennine grassland. I. Levels of infection in the field. J. Appl. Ecol. 15:943–950.

, and . 1978*b*. Mycorrhizal infection in Pennine grassland. II. Effects of mycorrhizal infection on the growth of some upland grasses on irradiated soils. J. Appl. Ecol. 15:951–958.

, and . 1978*c*. Mycorrhizal infection in Pennine grassland. III. Effects of mycorrhizal infection on the growth of white clover. J. Appl. Ecol. 15:959–964.

Stark, N. 1977. Direct nutrient cycling by endomycorrhizae. Abstr. Third North Amer. Conf. on Mycorrhizae. (Athens, Georgia, Aug. 23–25, 1977) Inst. of Mycorrhizal Res., U.S. Dep. Agric.–Forest Serv. p. 69.

Starkey, D. A. and M. F. Brown. 1977. Vesicular-arbuscular mycorrhizae of yellow poplar: Effects on seedling growth in forest nursery soil and in an artifical medium. Abstr. Third North Amer. Conf. on Mycorrhizae (Athens, Georgia, Aug. 23–25, 1977) Inst. of Mycorrhizal Res., U.S. Dep. Agric. –Forest Serv. p. 42.

Stelz, T. 1968. The nature of fungi responsible for vesicular-arbuscular mycorrhizal infections. Bull. Soc. Linn. Normandie 9:129–143.

Stewart, E. L., and F. L. Pfleger. 1977. Development of Poinsettia as influenced by endomycorrhizae, fertilizer and root rot pathogens *Phythium ultimum* and *Rhizoctonia solani*. Florists Rev. 159:37, 79–81.

St. John, T. 1977. A survey of mycorrhizal infection in a tropical environment. Abstr. Third North Amer. Conf. on Mycorrhizae (Athens, Georgia, Aug. 23–27, 1977) Inst. of Mycorrhizal Res. Devel., U. S. Dep. Agric.–Forest Serv. p. 68.

Stone, E. L. 1949. Some effects of mycorrhiza on the phosphorus nutrition of Monterey pine seedlings. Proc. Soil Sci. Soc. Amer. 14:340–345.

Stribley, D. P., P. B. Tinker, and J. H. Rayner. 1980. Internal phosphorus concentration and carbon loss in plants infected by vesicular-arbuscular mycorrhiza. J. Soil Sci. 31:655–672.

Sutton, J. C. 1973. Development of vesicular-arbuscular mycorrhizae in crop plants. Canadian J. Bot. 51:2487–2493.

, and G. L. Barron, 1972. Population dynamics of *Endogone* spores in soil. Canadian J. Bot. 50:1909–1914.

, and B. R. Sheppard. 1976. Aggregation of sand-dune soil by endomycorrhizal fungi. Canadian J. Bot. 54:326:333.

Swaby, R. J. 1974. Biosuper-biological superphosphate. *In* K. D. McLachlan (ed.), Sulphur in Australian agriculture. Sydney Univ. Press, Sydney, Australia.

Swaminathan, K., and B. C. Verma. 1977. Symbiotic effect of vesicular-arbuscular mycorrhizal fungi on the phospate nutrition of potatoes. Proc. Indian Acad. Sci. Sect. B. 85:310–318.

, and . 1979. Responses of three crop species to vesicular-arbuscular mycorrhizal infection on zinc-deficient Indian soils. New Phytol. 82:481–487.

Switzer, G. L., and L. E. Nelson. 1972. Nutrient accumulation and cycling in Loblolly pine (*Pinus taeda* L.) plantation ecosystems: The first twenty years. Soil Sci. Soc. Amer. Proc. 36:143–147.

Thapar, H. S., and S. N. Khan. 1973. Studies on endomycorrhiza in some forest species. Proc. Indian Nat. Sci. Acad. 39:687–694.

Timmer, L. W., and R. F. Leyden. 1978. Stunting of citrus seedlings in fumigated soils in Texas and its correction by phosphorus fertilization and inoculation with mycorrhizal fungi. J. Amer. Soc. Hort. Sci. 103:533–537.

Tinker, P. B. 1975*a*. Effects of vesicular-arbuscular mycorrhizas on higher plants. *In* D. H. Jennings and D. L. Lee (ed.), Symbiosis. Proc. 29th Symp. Soc. Exp. Biol. Cambridge Univ. Press, Cambridge, England. pp. 325–350.

. 1975*b*. Soil chemistry of phosphorus and mycorrhizal effects on plant growth. *In* F. E. Sanders, B. Mosse, and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 353–371.

Tommerup, I. Z., and D. K. Kidby. 1979. Preservation of spores of vesicular-arbuscular endophytes by L-drying. Appl. Envir. Microbiol. 37:831–835.

Trinick, M. J. 1977. Vesicular-arbuscular infection and soil phosphorus utilization in *Lupinus* spp. New Phytol. 78:297–304.

Trudgill, D. L., R. Evans, and G. Faulkner. 1972. A fluidising column for extracting nematodes from soil. Nematologica 18:469–475.

Tupas, G. L., and P. E. Sajise. 1976. Mycorrhizal associations in some savanna and reforestation trees. Kalikasan 5:235–240.

Vanderploeg, J. F., R. W. Lighty, and M. Sasser. 1974. Mycorrhizal association between *Lilium* taxa and *Endogone*. Hort Sci. 9:383–384.

Vander Zaag, P., R. L. Fox, R. S. de la Peña, and R. S. Yost. 1978. P nutrition of cassava including mycorrhizal effects on P, K, S, Zn and Ca uptake. J. Ser. 2327, Hawaii Agric. Exp. Sta.

Vietmeyer, N., and B. Cottom. 1977. *In* F. R. Ruskin (ed.), Leucaena-promising forage and tree crops for the tropics. National Acad. Sci., Washington, D.C. 110 pp.

Waidyanatha, U. P. de S. 1980. Mycorrhizae of *Hevea* and leguminous ground cover in rubber plantations, *In* P. Mikola (ed.), Tropical Mycorrhiza Research. Oxford Univ. Press, Oxford, England. pp. 238–241.

, N. Yogoratnam, and W. A. Ariyaratne. 1979. Effects of mycorrhizal infection on growth and nitrogen fixation of *Pueraria* and *Stylosanthes* and uptake of phosphorus from two rock phosphates. New Phytol. 82:147–152.

Warcup, J. H. 1975. A culturable *Endogone* associated with eucalypts. *In* F. E. Sanders, B. Mosse and P. B. Tinker (ed.), Endomycorrhizas. Academic Press, London. pp. 53–63.

Warner, A. 1980. Factors affecting the spread of vesicular-arbuscular mycorrhizal fungi. Ph.D. thesis, Univ., of London, England. 174 pp.

, and B. Mosse. 1980. Independent spread of vesicular-arbuscular mycorrhizal fungi in soil. Trans. British Mycol. Soc. 74:407–410.

Wastie, R. L. 1965. The occurrence of an *Endogone* type of endotrophic mycorrhiza in *Hevea brasiliensis*. Trans. British Mycol. Soc. 48:167–178.

Webster, B. N. 1953. Mycorrhiza. Tea Quarterly (Ceylon) 24:26–30.

Went, F. W. 1971. Mycorrhizae in a Montana pine forest. *In* E. Hacskaylo (ed.), Mycorrhizae. Proc. First North Amer. Conf. on Mycorrhizae. USDA Pub. 1189:230–232.

, and N. Stark. 1968. Mycorrhiza. Bioscience 18:1035–1039.

Williams, S. E., A. G. Wollum II, and E. F. Aldon. 1974. Growth of *Atriplex canescens* (Punsh.) Nutt. improved by formation of vesicular-arbuscular mycorrhizae. Soil Sci. Soc. Amer. Proc. 38:962–965.

Woodhead, S. H., J. W. Gerdemann, and J. D. Paxton. 1977. Mycorrhizal infection of soybean roots reduced *Phytophthora* root rot. Abstr. Third North Amer. Conf. on Mycorrhizae (Athens, Georgia, Aug. 23–25, 1977) Inst. of Mycorrhizal Res. and Devel., U.S. Dep. Agric.–Forest Serv. p. 10.

Yost, R. S., and R. L. Fox. 1979. Contribution of mycorrhizae to the P nutrition of crops growing on an Oxisol. Agron. J. 71:903–908.

APPENDIXES

Apppendix A. Publications and Meetings, 1930–1978

Papers

Number of papers at 5-yearly intervals:

1930–34	14
1935–39	22
1948–52	17
1953–57	43
1958–62	56
1963–67	40
1968–72	100
1973–78	200

Meetings

1971 1st North American Conference on Mycorrhiza held at Urbana, Illinois. USDA Misc. Publ. 1189. 2 out of 27 papers were on VA mycorrhiza. Both were from the University of Illinois, Urbana-Champaign.

1974 1st International Symposium on Endomycorrhiza. Proceedings published in "Endomycorrhizas," ed. F. E. Sanders, B. Mosse, and P. B. Tinker. Academic Press, London. 626 pp.

1974 2nd North American Conference on Mycorrhiza held at Corvallis, Oregon. No publication.

1976 UNESCO training course in microbiological techniques. Jogjakarta, Indonesia. Mycorrhizal section. G. D. Bowen.

1977 3rd North American Conference on Mycorrhiza held at Athens, Georgia. Abstracts published. 33 out of 113 papers presented were on VA mycorrhiza.

1978 a) VA Mycorrhiza workshop, Adelaide, Australia.

b) Mycorrhiza meeting, Paris, France.

c) Training course at Campinas, Brazil. Organized jointly by the C.N. Pq., Brazil and the British Council, England; taught by B. Mosse and D. S. Hayman.

d) International workshop on Tropical Mycorrhiza Research. Kummasi, Ghana. Organized by the International Foundation of Science, Sweden. Proceedings published in "Tropical Mycorrhizal Research," ed. P. Mikola. Oxford Univ. Press, Oxford, England.

e) Joint IUFRO (Internat. Union of Forestry Res. Orgs.)/French Working Party on Root Studies: "Root Physiology and Symbiosis," held at Nancy, France.

1979 4th North American Conference on Mycorrhiza held at Fort Collins, Colorado. 63 out of 145 papers dealt with VA mycorrhiza. No publication.

Appendix B. Important Growth Experiments, by Crop

This list includes references to the most important growth responses to inoculation in plants of particular economic or ecological interest. It is not a complete list of all published results.

Crop	*Reference*
Acacia farnesiana	Johnson and Michelini, 1974
Acer rubrum (red maple)	Daft and Hacskaylo, 1977
Agrostis spp.	Pichot and Binh, 1976
Allium cepa (onion)	Furlan and Fortin, 1973; Gray and Gerdemann, 1969; Hayman, 1974; Hayman and Mosse, 1971, 1972*b*; Mosse, 1972*b*, 1973*b*; Mosse and Hayman, 1971; Mosse, Hayman, and Arnold, 1973; Mosse, Hayman, and Ide, 1969; Owusu-Bennoah and Mosse, 1979; Powell, 1975*a*, 1975*b*; Rhodes and Gerdemann, 1975, 1976, 1978; Sanders and Tinker, 1971; Sanders, Tinker, Black, and Palmerley, 1977
Arachis hypogaea (peanut)	Daft and El-Giahmi, 1976
Araucaria cunninghammi (Hoop pine)	Bevege, 1971; Bevege and Richards, 1971
Atriplex canescens (saltbush)	Williams, Wollum, and Aldon, 1974
Bactris gasipaes	Janos, 1977
Brachiaria spp.	Mosse, 1975
Carica spp. (papaya)	Ramirez, Mitchell, and Schenck, 1975
Centrosema pubescens	Crush, 1974; Mosse, 1975; Mosse, Hayman, and Arnold, 1973
Citrus spp.	Hattingh and Gerdemann, 1975; Kleinschmidt and Gerdemann, 1972; Marx, Bryan, and Campbell, 1971; Mehravaran, 1977; Menge, Johnson, and Platt, 1978; Menge, Steirle, Bagyaraj, Johnson, and Leonard, 1978; Schenck and Tucker, 1974; Timmer and Leyden, 1978

Coprosma robusta	Baylis, 1967; Hall, 1976; Hayman and Mosse, 1971; Johnson, 1976
Digitaria spp.	Mosse, 1975
Eupatorium odoratum	Boutros-Mikhail, 1976; Graw, Moawad, and Rehm, 1979; Nyabyenda, 1977
Euphorbia spp. (poinsettia)	Stewart and Pfleger, 1977
Ferns	Cooper, 1973, 1975
Festuca spp.	Ho and Trappe, 1973; Koucheki and Read, 1976; Sparling and Tinker, 1978*b*
Fragaria spp. (strawberry)	Holevas, 1966; Mosse and Hayman, 1980*b*
Glycine max (soybean)	Bagyaraj, Manjunath, and Patil, 1979; Jackson, Franklin, and Miller, 1972; Ross, 1971; Ross and Gilliam, 1973; Ross and Harper, 1970; Safir, Boyer, and Gerdemann, 1971, 1972; Schenck and Hinson, 1973; Schenck, Kinloch, and Dickson, 1975
Gossypium spp. (cotton)	Metcalf, 1978; Rich and Bird, 1974; Roncadori and Hussey, 1977
Grasses, temperate	Crush, 1973*a*; 1973*b*; Sparling and Tinker, 1978*b*
Griselinia littoralis	Baylis, 1959, 1967; Johnson, 1976; Powell, 1975*b*
Guizotia abyssinica (niger-seed)	Graw, 1979; Nyabyenda, 1977
Helianthus annus (sunflower)	Iqbal and Qureshi, 1977
Hordeum vulgare (barley)	Benians and Barber, 1972; Clarke and Mosse, 1981; Owusu-Bennoah and Mosse, 1979; Saif and Khan, 1977
Khaya grandifoliola (mahogany)	Redhead, 1975
Lavendula spica (lavender)	Azcon, Barea, and Hayman, 1976; Barea, Azcon, and Hayman, 1975

Legumes, temperate	Asai, 1944; Crush, 1976; Gray and Gerdemann, 1973
Leptospermum scoparium	Baylis, 1971; Cooper, 1975
Leucaena leucocephala (koa haole)	Munns and Mosse, 1979
Lilium spp.	Vanderploeg, Lighty, and Sasser, 1974
Liquidambar styraciflua (sweet gum)	Bryan and Ruehle, 1976; Filer and Toole, 1968; Gray and Gerdemann, 1967; Haines and Best, 1976
Liriodendron tulipifera (yellow poplar)	Clark, 1964, 1969; Gerdemann, 1965; Gray and Gerdemann, 1967
Lolium spp. (ryegrass)	Crush, 1973*a*; Powell, 1977*d*; Powell and Daniel, 1978*a*, 1978*b*
Lotus pedunculatus	Crush, 1974
Lycopersicum esculentum (tomato)	Daft and Nicolson, 1969, 1972; Sanni, 1976*a*
Manihot spp. (cassava)	Sanders, 1976; Yost and Fox, 1979
Medicago sativa (alfalfa, lucerne)	Daft and El-Giahmi, 1975; Mosse, Warner, and Clarke, 1981; Owusu-Bennoah and Mosse, 1979; Smith and Daft, 1977
Melinis minutifolia	Mosse, Hayman, and Arnold, 1973
Metrosideros umbellata	Hall, 1975
Nicotiana tabacum (tobacco)	Khanaqua, 1979; Peuss, 1958
Oryza sativa (rice)	Sanni, 1976*b*
Paspalum notatum	Mosse, 1972*a*, 1972*b*; Mosse, Hayman, and Arnold, 1973
Persea americana (avocado)	Menge, Davis, Johnson, and Zentmyer, 1978
Phaseolus vulgaris (French bean)	Daft and El-Giahmi, 1974; McIlveen, Spotts, and Davis, 1975
Podocarpus spp.	Baylis, McNabb, and Morrison, 1963

Prunus persica (peach)	Gilmore, 1971; La Rue, McClellan, and Peacock, 1975
Pyrus malus (apple)	Benson and Covey, 1976; Mosse, 1957
Solanum tuberosum (potato)	Black and Tinker, 1977; Graham, Green, and Hendrix, 1976; Swaminathan and Verma, 1977, 1979
Sorghum bicolor (Sudangrass)	Jackson, Franklin, and Miller, 1972; Nyabyenda, 1977; Stone, 1949
Stylosanthes guyanensis	Mosse, 1977*a*; Mosse, Powell, and Hayman, 1976
Trifolium subterraneum (subterranean clover)	Abbott and Robson, 1977, 1978; Barrow, Malajczuk, and Shaw, 1977
Trifolium repens (white clover)	Crush, 1974, 1976, 1978; Hayman and Mosse, 1979; Lambert, 1978; Powell, 1975*a*, 1976*b*, 1977*a*, 1977*c*; Powell and Daniel, 1978*a*, 1978*b*; Sparling and Tinker, 1978*c*
Triticum aestivum (wheat)	Khan, 1975
Vigna unguiculata (cowpea)	Islam, 1976, 1977; Sanni, 1976*a*
Vitis vignifera (grapevine)	Possingham and Obbink, 1971
Zea mays (corn)	Barea, Azcon, and Hayman, 1975; Daft, Hacskaylo, and Nicolson, 1975; Daft and Nicolson, 1966, 1972; Gerdemann, 1964; Hall, 1978; Joseph, 1977; Khan, 1972*a*; Meloh, 1963; Mosse, 1977*a*; Murdock, Jackobs, and Gerdemann, 1967; Sanni, 1976*a*

Appendix C. Some Other Important Subtropical and Tropical Plants in Which VA Mycorrhiza Have Been Reported

Crop	*Reference*
Aesculus indica	Khan, 1972*c*
Ananas comosus (pineapple)	Mosse, unpubl.
Caffea arabica (coffee)	de Souza (priv. comm.)
Cocos nucifera (coconut)	Lily, 1975
Crocus sativus (saffron)	Kianmehr (priv. comm.)
Elaeis guineensis (oil palm)	Nadarajah, 1980
Hevea brasiliensis (rubber)	Waidyanatha, 1980; Wastie, 1965
Litchi chinensis	Pandey and Misra, 1971
Olea europaspidata (olive)	Hayman, Barea, and Azcon, 1976; Khan and Saif, 1973
Papaver somniferum (opium poppy)	Iqbal, Sultana, and Parveen, 1975
Phoenix dactylifera (date palm)	Sabet, 1940
Saccharum officinarum (sugarcane)	Ciferri, 1928
Thea sinensis (tea)	Webster, 1953
Theobroma cacao (cocoa)	Janos, 1975; Laycock, 1945; Nadarajah, 1980

N. B. For list of Javanese plants with VA mycorrhiza, *see also* J. M. Janse, 1897. Ann. Jard. Botan., Buitenz., 14:53–212.

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NOTE: As part of a structural reorganization, the Hawaii Agricultural Experiment Station and the Hawaii Cooperative Extension Service have been merged administratively under the name HAWAII INSTITUTE OF TROPICAL AGRICULTURE AND HUMAN RESOURCES, College of Tropical Agriculture and Human Resources, University of Hawaii.

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College of Tropical Agriculture and Human Resources
University of Hawaii
Noel P. Kefford, Director of the Institute and Interim Dean of the College
Res. Bull 194–August 1981 (2M)