

## Chapter (non-refereed)

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# Harnessing symbiotic associations: vesicular–arbuscular mycorrhizas

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## ABSTRACT

Although the majority of tropical trees form mycorrhizas with vesicular–arbuscular mycorrhizal (VAM) fungi, most mycorrhizal research on tropical trees has been on ectomycorrhizal fungi associated with a few tree species which have been widely planted as exotics in plantations. Despite this, the presence of appropriate and adequate VAM populations is likely to have a significant impact on tree performance, as many tree species are highly dependent upon their mycorrhizal associations for nutrient uptake, particularly in infertile soils.

Although naturally occurring inoculum is widespread in soils, site disturbance (as occurs when land is cleared for planting) can reduce the number of infective propagules, and change the proportions of different fungal species. Hence, the potential for mycorrhizal formation may be lowered at the critical time of tree establishment. The extent to which mycorrhizal populations are depleted and changed is related to the method of site clearance used. Short-term studies indicate that mycorrhizal inoculation improves tree growth in nurseries. Only a few studies have followed the progress of inoculated trees after outplanting. In these studies, improvements in both tree survival and growth rate have been found, but more extensive studies are needed.

A number of options exist for the management of mycorrhizal associations: minimising the change in indigenous populations by use of appropriate site preparation techniques; manipulating damaged populations to increase their inoculum potential; and inoculating trees in nurseries either with single isolates or mixtures. Where the performance of particular tree/symbiont combinations is being assessed, the criteria for selection need to be carefully defined.

## INTRODUCTION

Mycorrhizal fungi are an integral part of practically all plant communities, natural or managed, and form the link by which mineral nutrients are transferred from the soil to the plant, while carbon compounds are transported in the opposite direction. Thus, they have a fundamental role in determining plant productivity and in the functioning of ecosystems. Despite their importance, they tend to be ignored by foresters and agriculturalists, although an understanding of their role is essential to the development of sustainable land use systems (Bethlenfalvai & Linderman 1992).

Vesicular–arbuscular mycorrhizal (VAM) fungi possess a worldwide distribution. Published records indicate that 71% of tropical plant species are VAM (Sieverding 1991), and about 95% of the tree species in natural tropical forest ecosystems are mycorrhizal exclusively with VAM fungi (Le Tacon, Garbaye & Carr 1987). Although VAM trees predominate in the tropics, they have until recently received comparatively little attention from mycorrhizal researchers, who have focused instead on a few ectomycorrhizal trees, such as members of the Pinaceae, *Casuarina* and various *Eucalyptus* species which are widely used in plantations (Le Tacon *et al.* 1987; see also Lapeyrie & Högberg, pp158–164). The VAM mycorrhizas of the great majority of tropical

forest trees, which include many valuable species, are virtually unstudied. The failures of ectomycorrhizal trees as a result of mycorrhizal deficiencies when planted as exotics are well documented (eg Mikola 1970). By comparison, failures or poor performance of VAM trees after planting have rarely been attributed to mycorrhizal problems. The more widespread distribution of VAM fungi might suggest that mycorrhizal deficiencies would be unlikely to occur; however, as this paper will indicate, there are many circumstances in which VAM propagules may be restricted in number or form ineffective associations, resulting in trees performing suboptimally.

Consideration of VAM fungal populations is important not only because of their role in ecosystem function, but also because they have direct and immediate effects upon tree performance. Evidence from short-term studies suggests that many tropical trees are highly dependent upon their VAM associations for survival and growth. Although VAM fungi are widely distributed, site disturbance, such as occurs during land clearance, can adversely affect mycorrhizal populations, reducing the amount of inoculum available to infect root systems during the period when trees are becoming established. Hence, the conservation of indigenous VAM populations, or the inoculation of

trees with VAM fungi, may be needed to ensure that adequate inoculum is present to support tree growth.

Unfortunately, while understanding of the ecological role of these fungi has increased in recent years, it has not been matched by developments in their practical application or management. A number of short-term studies have demonstrated that inoculation can improve the growth of trees in nurseries, but (with the exception of the *Citrus* industry) VAM inoculation of trees has not become part of nursery practice. A serious limitation to progress is the lack of evaluations of the performance of inoculated plants over periods longer than a few months, which hampers any appraisal of long-term effects in the field.

## **IMPORTANCE OF VAM FUNGI FOR PLANT GROWTH IN THE TROPICS**

### **Function and distribution of VA mycorrhizas**

The functions of VAM associations have been reviewed extensively elsewhere (eg Harley & Smith 1983; Powell & Bagyaraj 1984; Barea 1991), and will only be summarised briefly here. However, it should be pointed out that the majority of experiments have been conducted in pots, with isolated plants. Observations of the activities of mycorrhizas under field conditions are far more limited, and much work remains to be done to understand their functioning in ecosystems (Fitter 1985).

The mycorrhizal fungus takes up mineral nutrients from the soil, via the extramatrical fungal mycelium which can reach for a considerable distance away from roots. The presence of a widely ramifying extramatrical mycelium is particularly important for the uptake of minerals (P and others) that have a slow rate of diffusion (Cooper 1984). It has been demonstrated that this mycelium can extend phosphate depletion zones up to at least 7 cm from roots, compared with the 1–2 mm depletion zones associated with non-mycorrhizal roots, and therefore it can absorb nutrients from a much greater soil volume than a non-mycorrhizal root (Rhodes & Gerdemann 1975). The ability of mycorrhizal fungi to access P is likely to be particularly important to plants in dry conditions, as the diffusion coefficient for phosphate in soil decreases linearly with increasing soil dryness (Fitter 1985). In addition to the enhancement of nutrient uptake through exploitation of increased soil volume, there is some evidence that VAM hyphae have the capacity to alter the weathering rates of soil P and increase the pool of available P (Bolan 1991). Mycorrhizal infection has also been found to improve plant water relations, as a result of either indirect effects upon plant nutrient status or more direct effects on water uptake

(Cooper 1984); improved resistance to pathogens has also been noted (Sharma, Johri & Gianinazzi 1992).

The distribution of VAM and ectomycorrhizal fungi in the tropics is reviewed briefly by Lapeyrie and Högborg (pp158–164). In broader terms, when the major plant communities of the world are surveyed, it becomes apparent that each has its distinctive population of mycorrhizal types: VA, ecto-, ericoid or arbutoid mycorrhizas (Read 1991a). The changes in dominance of different mycorrhizal types in contrasting ecosystems have been attributed to variations in their ability to access or mobilise the plant nutrients that are limiting growth in that particular ecosystem (Read 1991b). Evidence suggests that domination by VAM plant species increases with decreasing soil organic matter and increasing base status of soil, where phosphorus replaces nitrogen as the major limiting nutrient (Read 1991b), although there are exceptions to this rule (Allen 1991). Lowland tropical soils are characteristically lacking in organic matter. In the oxisols and ultisols which account for two-thirds of the world's tropical soils by area, organic matter decomposition is fairly rapid, and there is often little accumulation of litter. These soils are acid clays which possess high potential aluminium toxicity, low cation exchange capacity and, as a consequence, low availability of many minerals (Janos 1987). In this situation, phosphorus is present in soil solution at very low concentrations mainly because of its incorporation into less soluble forms (Alexander 1989). In such circumstances, the formation of effective mycorrhizal associations confers a strong competitive advantage, and mycorrhizal associations with VAM fungi, which (with their extensive extramatrical mycelium) are effective scavengers for phosphate, predominate (Read 1991a, b).

Under these conditions, the uptake of phosphorus by plants, especially tropical trees possessing the coarse root morphology characteristic of obligate mycorrhizal plants (see below), will be limited by the slow diffusion of phosphate ions in the soil and by the development of depletion zones around roots. The presence of effective VAM associations will reduce the constraints of soil nutrition. As it has been estimated (Sieverding 1991) that plant production is limited by low mineral nutrient availability on 30% and by drought on 33% of tropical soils, the development of effective mycorrhizal associations is likely to be beneficial to tree growth over a wide range of tropical sites.

### **Mycorrhizal dependency**

Most plants in natural ecosystems have mycorrhizas (Brundrett 1991). However, the benefit which individuals are likely to receive

from the presence of VA mycorrhizas varies according to the plant species under consideration, because plant species differ in the extent to which they depend on VAM fungi for survival and growth at a given soil fertility (Janos 1980a, 1987). They have been characterised as either non-mycorrhizal, obligately mycotrophic or facultatively mycotrophic: obligately mycotrophic plant species cannot grow without mycorrhizas even in the most fertile soil where they normally grow, whereas facultative mycotrophs can survive and grow without mycorrhizas, but perform better when they are mycorrhizal, particularly in less fertile soils (Janos 1987). For tropical plants, dependence upon VA mycorrhizas is related to their root morphological characteristics and phosphate requirements. Superficial, small root systems that have low orders and frequencies of branching, and coarse ultimate rootlets with few or no root hairs, are characteristic of trees having a high mycorrhizal dependency (Baylis 1975; St John 1980; Janos 1987; Manjunath & Habte 1991). Recent studies by Manjunath and Habte (1992) indicate that mycorrhizal dependency is also related to phosphate usage: when non-mycorrhizal plants of species possessing a range of degrees of mycorrhizal dependency were grown in soils containing different concentrations of P, the mycorrhizal-dependent species required higher concentrations of P in the soil solution for maximum dry matter production, while the concentrations of P in their shoots at maximum dry matter production were lower than for non-dependent species.

### **Occurrence of mycorrhizal-dependent species**

In determining the importance of conserving and managing VA mycorrhizal populations in association with tropical trees, an appreciation of the frequency of occurrence of non-, facultatively or obligately mycotrophic tree species is needed. Certain families of plants, including tropical trees, appear to be characteristically non-mycorrhizal, or to have some non-mycorrhizal genera (Brundrett 1991). They include members of the Lecythidaceae, Sapotaceae and Proteaceae. While extensive studies of mycorrhizal dependency have not been conducted, and more work needs to be done, the results of a study by Janos (1980b) and other studies reported in this review indicate that a high proportion of other trees are likely to be dependent upon their mycorrhizas. In a study of Central American lowland tropical moist forest plant species (Janos 1980b), VAM inoculation improved growth and/or survival of 24 out of the 28 species tested, when they were grown in a sterilised soil in containers. Sixteen of these species ceased growth in the absence of mycorrhizas and were found to be completely dependent on VAM for sustained growth.

The mycorrhizal dependency of plant species

appears to be related to their position in the successional development of plant communities (eg Allen 1991; Brundrett 1991). On the basis of his data from the tropical moist forest, Janos (1980a, b) has suggested that early successional species are likely to be facultatively mycotrophic or non-mycorrhizal, with a well-branched root system and small easily dispersed seeds. Seral species tend to be facultative mycotrophs, while mature forest canopy and subcanopy species are obligate mycotrophs, and large-seeded to provide nutrient reserves until the root system has developed mycorrhizal infection to enhance nutrient uptake. Consequently, plants that are less dependent on their VA mycorrhizas or are non-mycorrhizal are likely to become progressively more dominant in disturbed ecosystems where mycorrhizal inoculum is limited (Janos 1987; Miller 1987), although it will depend upon nutrient availability (Allen & Allen 1990). This evidence suggests that there is a direct mycorrhizal role in the determination of the structure and composition of plant communities. These patterns of change in mycorrhizal dependency with ecological succession have important practical implications for the growth of VAM trees in plantations and for the regeneration of degraded land.

Recently, the level of VAM dependency of some fast-growing leguminous trees for sustainable land use systems in the subhumid and semi-arid tropics has been examined (Habte & Turk 1991). Among the plant species that have been suggested as important for reforestation and agroforestry systems are *Leucaena leucocephala*, *Cassia spectabilis* and *Gliricidia sepium* (see Brewbaker & Sorensson, pp195–204; Simons, MacQueen & Stewart, pp91–102). Short-term studies with potted seedlings have shown that *L. leucocephala* is very highly dependent upon VAM fungi (Habte & Manjunath 1987), while *C. spectabilis* and *G. sepium* also exhibit VAM dependency, although to a lesser extent (Habte & Turk 1991).

Throughout the tropics, a clear assessment of the mycorrhizal dependency of tree species would enable much more precise recommendations to be made about the conditions under which different tree species are likely to succeed, and indicate a particular need for inoculation or care in conservation of indigenous mycorrhizal populations when planning for plantations of mycorrhizal-dependent tree species. This information would aid the successful development of domestication strategies and promote predictable harnessing of VAM symbioses in practical forestry across the tropics.

### **EFFECTS OF DISTURBANCE ON VAM FUNGI**

Access to adequate VAM inoculum is, as already indicated, a prerequisite for the growth of many

tropical trees because of their dependence upon mycorrhizas. Sources of potential infection are resting spores, fungal hyphae in the soil, and colonised root fragments. These sources of inoculum can be adversely affected by many factors, including fires, soil erosion, loss of vegetation, cultivation, long fallow periods, soil compaction, changes in soil temperature, moisture and chemistry, colonisation by non-mycorrhizal plants, and biocide application (Abbott & Robson 1991; Sieverding 1991). Hence, many of the processes involved in deforestation of tropical forest areas have serious implications for mycorrhizal inoculum and, consequently, the performance of trees other than species which are unresponsive to inoculation. However, there is little quantitative information to indicate the degree of inoculum availability which is required for the growth of obligately or facultatively mycorrhizal tree species. Based on his extensive studies of *Manihot esculenta* (cassava), which is obligately mycorrhizal, Sieverding (1991) has suggested that field responses to inoculation of this crop may be obtained when there are less than 900 indigenous infective propagules per 100 g of dry soil. If tree crops respond in a similar manner, very extensive areas of the tropics are likely to be deficient in mycorrhizal inoculum for acceptable levels of productivity in managed systems.

The different forms of VAM propagules vary in their longevity. While spores can survive for up to several years in the soil, fungal mycelium only retains its ability to infect after separation from the host plant for two to four weeks in field conditions. Colonised root fragments can retain their viability for several months under dry conditions, but rapidly lose viability under moist conditions (Hetrick 1984; Sieverding 1991). Consequently, the abundance of different types of propagule in the soil before disturbance may determine the impact of disturbance on mycorrhizal infection. If vegetation cover is lost, spores will become increasingly important as mycelium rapidly loses its infectivity, resulting in a shift in mycorrhizal populations after disturbance, in favour of those fungi which sporulated prior to the disturbance.

Effects of disturbance will vary with ecosystem. When Jasper, Abbott and Robson (1991) examined the impact of disturbance on soils removed from an annual pasture, forest and heathland growing in a mediterranean climate in south-west Australia, they noted that the extent of mycorrhizal infection on the roots of *Trifolium subterraneum* (subterranean clover) plants growing in the pasture soil was little affected by disturbance. In contrast, the extent of infection in both disturbed jarrah forest and heathland soils was reduced by almost half. Parallel soil dilution experiments indicated that VAM propagule

numbers were much lower in the undisturbed forest and heathland soils than in the pasture. Jasper *et al.* (1991) inferred that, where propagule numbers were naturally low, as in the forest and heathland soils, disturbance would inevitably lead to a further reduction in the number of infective propagules and, as a consequence, a reduction in the soils' potential infectivity. However, in soils which harboured a large number of propagules, like the native grassland soils, disturbance even of a highly damaging nature might not reduce the overall number of VAM propagules below a level which would limit mycorrhizal development (see also Jasper, Abbott & Robson 1992).

The studies described above indicate that those ecosystems that support a high number of VAM propagules will be more resilient, and more likely to maintain infectivity and hence plant productivity after disturbance. However, it should be noted that, in these studies, the test plants were pre-germinated and were planted into the soils soon after disturbance, and grown in favourable conditions. The impact of disturbance on mycorrhizal infection in the field is likely to be greater, as plants will colonise disturbed ground more slowly and environmental conditions may be more severe. Both these factors will lead to a decline in inoculum infectivity and are likely to have an adverse effect on mycorrhizal infection of colonising plants. Continued monitoring of the recovery of the jarrah forest site indicated that mycorrhizal infectivity gradually recovered, but patches of high and low infectivity remained for several years. A uniform distribution of infectivity, equivalent to that of the undisturbed forest, was not achieved for seven years after vegetation was re-established (Jasper *et al.* 1992).

In ecosystems lacking robust VAM propagules (spores), disturbance can rapidly destroy mycorrhizal infectivity. Jasper *et al.* (1989) observed changes in VAM infectivity in jarrah forest soil on land disturbed by bauxite mining. Spores were not found in this soil before the disturbance. The proportion of root length on bait plants of *Trifolium* which became infected by mycorrhizal fungi declined from 21% before clearance to 5% one month afterwards (although soil disturbance was slight during this operation), and no mycorrhizal infection was found six weeks after the soil was stripped and respread on another site. It is likely that the cause of this extreme loss of infectivity was related to the absence of mycorrhizal spores in the original soil; consequently, infection was dependent upon mycelial and root fragments which were damaged during the processes of soil transfer.

Even slight surface erosion can have severe effects upon all types of mycorrhizal propagules, as they tend to be concentrated close to the soil

surface (Abbott & Robson 1991). Erosion leads to a loss not only of surface soil particles and nutrients, but also much of the mycorrhizal population, thereby reducing the number of fungal propagules available for colonising plants. Maintaining vegetation cover is important for mycorrhizal populations. Recent assessments of VA mycorrhizal propagule densities in semi-arid bushland of Somalia (Michelsen & Rosendahl 1989) have shown that, where there was good cover (of *Terminalia brevipes* forest), the concentration of propagules was 200 per 100 ml soil. In neighbouring bushland degraded by heavy grazing, logging and clearing for shifting agriculture, and where only 8% of the surface remained covered by vegetation, infective VAM propagule numbers were only 30 per 100 ml soil. The extent to which such damage can deplete semi-arid ecosystems of their active VAM inoculum, and the impact of such a reduction, was clearly displayed following disturbance of a western Colorado *Teucrium* (sage) community (Moorman & Reeves 1979). The root systems of test maize seedlings were 77% infected when grown in undisturbed soil but only 2% infected when harvested from adjacent disturbed soil.

In lowland tropical rainforests, spore numbers can be considerably lower than those found in tropical agronomic and grassland ecosystems (Redhead 1977; Louis & Lim 1987; Sieverding 1989; Musoko 1991), although there may be a greater diversity of species (Sieverding 1989). In normal circumstances, the high degree of vegetation cover found in such forests should ensure all-year-round access to external mycelium and mycorrhizal roots, and therefore little dependence upon the presence of spores. However, this heavy reliance on easily damaged infected roots and extramatrical hyphae means that the stable equilibrium between plant and soil microbes in undisturbed tropical moist forest can become greatly disrupted when the forest is opened for cultivating agricultural crops or forest trees.

In semi-deciduous moist forest at Mbalmayo, Cameroon, the extent of damage resulting from different methods of forest clearance was examined by following short-term changes in the VAM spore populations in plots subjected to manual canopy opening, partial or complete clearance by bulldozer, and an undisturbed control treatment. When the spore populations were initially examined, the study site was found to possess a homogeneous spore distribution. However, when spore numbers were subsequently re-assessed in samples taken six months later (three months after the different methods of site preparation had been applied), the picture changed considerably. Although seasonal effects appear to have led to a fall in spore numbers in all four treatments, the

reduction in numbers was greatest in the completely cleared plot, which had received the most disturbance. It retained only 34% of its original spore numbers, while the undisturbed forest retained 73% (Musoko 1991; Mason, Musoko & Last 1992). Additional assessments of spore numbers, 18 months after the initial assessments, indicated that the decrease in spore numbers had been a short-term effect of logging, and that there had been a subsequent increase in numbers on the disturbed sites, so that they were higher than they had been originally. Results from a study of *Terminalia* plantations in Côte d'Ivoire (Wilson *et al.* 1992), which examined both undisturbed forest and forest which had been manually or mechanically cleared and replanted up to 23 years previously, indicated that forest clearance and replanting can result in long-term increases in spore numbers, lasting at least 16 years.

Decreases in spore numbers after logging have been reported from studies in Malaysian forest (Alexander, Ahmad & Su-See 1992), where there was a 75% reduction as a result of severe logging. Not only were spore numbers reduced, but most probable number (MPN) tests, and observations of root infection of plants along transects at the test sites both indicated that the overall inoculum potential of the sites was reduced where sites had been heavily logged, and adverse effects persisted for at least two years. Root systems of plants persisting on or colonising heavily logged forest were only 20–35% mycorrhizal, while those in the undisturbed forest were 70% mycorrhizal. Although there were large differences in species composition of the colonising plant species on the plots, which could affect the degree of mycorrhizal formation, comparisons of the extent of mycorrhizal infection on the few species which did occur in common between sites confirmed that mycorrhizal infection was lower on the plots which had been logged. Care must be taken with the interpretation of MPN tests because they themselves cause a lot of disturbance to inoculum; however, the root infection observations lend support to the view that logging reduced inoculum potential. It is likely that similar effects of logging on inoculum potential also occurred at Mbalmayo. Quantitative assessments (using field bioassays) of the impacts of logging on all sources of inoculum are needed to evaluate fully the effects in Cameroon, and complement the accumulated data on spore numbers. However, examination of the root systems of outplanted *Terminalia ivorensis* seedlings 18 months after plantation establishment did demonstrate that there were lower rates of mycorrhizal infection on the completely cleared plot, compared with the partially cleared plot (Musoko 1991). Survival of outplanted seedlings

was also lowest on the completely cleared plot (Mason *et al.* 1989).

An additional facet of the studies in Mbalmayo, Cameroon (Musoko 1991; Mason *et al.* 1992), is that, when spores proliferated after logging, the balance of species was changed. On the completely cleared plot, numbers of *Glomus occultum/Acaulospora scrobiculata* increased six-fold after disturbance. By contrast, the least damaging method of site preparation (manual canopy opening) maintained a species distribution similar to that in the undisturbed control plot, where *Glomus etunicatum* was the dominant spore type. Because spores are likely to be important sources of infection in disturbed soil after root systems and fungal mycelium are disrupted, such changes in species composition may have an impact upon the subsequent development of vegetation. Soil samples removed from the root zones of a range of plant species from Mbalmayo Forest indicated that the change in species distribution of spores within the severely disturbed plots was related to the rapid invasion of the herbaceous weed *Chromolaena odoratum* (Siam weed), with which spores of *G. occultum* and *A. scrobiculata* were strongly associated (Musoko 1991). In Côte d'Ivoire (Lawson *et al.* 1991; Wilson *et al.* 1992), spore species diversity was increased by site disturbance, for at least 16 years, and long-term changes in species dominance occurred, which were most marked on the mechanically cleared plots.

The combination of information from infectivity bioassays in Malaysia (Alexander *et al.* 1992) and the above observations on changes in spore species composition and number indicates that forest clearance has major effects upon mycorrhizal populations which are likely to be significant for the sustainability of forest plantations. Further studies are needed to assess the impact of logging on all sources of inoculum in different tropical forest ecosystems. Although most bioassays are effected under controlled conditions in pots, more precise information on how logging affects the onset and spread of infection will be obtained from testing bait plants of target tree species in the field, thereby avoiding the further disturbance to inoculum caused by sample collection. These studies now need to be developed in order to assess the importance of the extent and nature of the VAM inoculum remaining after logging for the survival and growth of tropical tree seedlings, both in natural regeneration and plantations. In order to evaluate the consequences of changes in the species composition of mycorrhizal fungi, it is necessary to compare the effectiveness of different fungal species in promoting tree growth.

The importance of maintaining a highly effective population was demonstrated in Colombia, where *Manihot esculenta* is produced in either

monoculture or rotational systems (Sieverding 1991). At one particular site, monoculture led to the build-up of a VAM spore population of which more than 50% were members of species considered to be inefficient, whereas, when *M. esculenta* was rotated with other crops, a smaller proportion of spores belonged to this group. Under monoculture, root yields were less than half those under rotation. Because chemical soil fertility was not a limiting factor, it was concluded that the composition of the indigenous VAM population was a crucial factor in determining the yield of cassava, which is obligately mycotrophic. Such observations have profound implications for forest management for both timber and non-timber species, and indicate that quantities of VAM propagules, the species composition, and their effectiveness need to be evaluated in much more detail.

Although it is possible to predict that those ecosystems which support a productive vegetation dominated by VAM plants, and which contain mycorrhizal spores in addition to other sources of inoculum, are more likely to maintain infectivity, even if disturbed, it is clear that many tropical ecosystems are likely to be highly vulnerable to damage, and therefore require careful management to ensure that mycorrhizal populations are maintained. The use of less destructive methods of site preparation to prevent damage occurring may be both economically and ecologically preferable to attempting to rectify the damage by inoculation or site manipulation.

## MANAGEMENT OF VAM FUNGI

With improved understanding of the damaging effects of site disturbance, it may be possible in many cases to reduce the amount of damage to the natural mycorrhizal population that occurs during site preparation by selecting less damaging methods. However, where disturbance is unavoidable, or where indigenous VAM populations are already damaged, action to correct mycorrhizal deficiencies may be advantageous.

Two methods can be used to correct VAM deficiencies:

- manipulation of indigenous VAM fungi;
- inoculation with selected VAM fungi.

Indigenous populations can be manipulated to enhance the overall levels of inoculum at a site, or to enhance a particular mycorrhizal species, and to increase or decrease VAM species diversity. Inoculation can be used to improve nursery or outplanting performance, or both, with either single isolates, or mixtures.

### Manipulation of indigenous VAM fungi

The use of suitable plant hosts to increase vegetation cover and restore VAM populations to their normal levels is a management practice

which could be used as an alternative to inoculation (Dodd *et al.* 1990a).

Several studies have examined the effects of pre-cropping and crop rotation on VAM populations in agricultural systems (Schenck & Kinloch 1980; Howeler, Sieverding & Saif 1987; Jeffries & Dodd 1989; Dodd *et al.* 1990a, b). They indicate that cropping history can substantially influence the abundance and composition of the fungal community, and can be used to manipulate mycorrhizal populations in favour of the target agricultural crop. Methods of land management can have a major impact upon VAM species diversity, which declines with increasing intensity of land management (Sieverding 1989). Studies in forest plantations in Côte d'Ivoire indicate that VAM species diversity was positively correlated with herbaceous plant species diversity (Lawson *et al.* 1991).

There is little information relating to the use of revegetation programmes for restoring mycorrhizal populations in non-agricultural tropical ecosystems. However, in a severely disturbed savanna in southern Venezuela, where spontaneous recolonisation was very poor, revegetation with a range of plant species enabled the recovery of the VAM inoculum to an extent adequate to enhance plant growth (Cuenca & Lovera 1992). As a result, native plants were able to colonise the revegetated areas at a higher rate than the non-revegetated areas. These results indicate that revegetation programmes may be used to promote the recovery of VAM inoculum in order to aid recolonisation by native plants.

In the same vein, intercropping of perennials and annuals may possess the hidden advantage that woody perennials may maintain VAM populations of benefit to the annual crop. Studies of intercropping systems in Kenya have indicated that mycorrhizal infection of maize grown in soil taken from close (0.5 m) to *Cassia siamea* hedges is greater than when it is grown in soil taken from further away (2.0 m) (S McGreevy & K Wakanene Mbuthia, unpublished data), suggesting that trees may act as reservoirs of VAM inoculum. Whether the species of fungi maintained by the tree are beneficial to the crop remains to be investigated.

### **Inoculation with selected VAM fungi**

There are many examples in the literature which indicate that inoculation of both tropical crops and trees can be very successful in promoting the growth of the host plant in short-term experiments. The majority of studies on trees have been targeted at fruit trees and at nitrogen-fixing species. Mycorrhizal inoculation has been found to be an effective tool for improving tree performance in the *Citrus* industry (Menge 1983), and has reduced the

requirement for fertilizer. Sieverding (1991) lists studies by 28 authors in short-term nursery experiments in Central and South American countries. Practically all the tree species investigated responded positively to mycorrhizal inoculation.

Positive responses to VAM inoculation have been reported for seedlings of many leguminous tree species, many of which require effective VA mycorrhizas to supply P for nodulation and nitrogen fixation (Manjunath, Bagyaraj & Gopala-Gowda 1984; De la Cruz *et al.* 1988). *Acacia auriculiformis* (De la Cruz *et al.* 1988), *A. holosericea* (Cornet, Diem & Dommergues 1982), *A. mangium* (De la Cruz *et al.* 1988), *A. nilotica* (Michelsen & Rosendahl 1990; Reena & Bagyaraj 1990a), *A. scleroxyla* (Borges & Chaney 1988), *Albizia falcataria* (Ahmad & Maziah 1988; De la Cruz *et al.* 1988), *Calliandra calothyrsus* (Reena & Bagyaraj 1990a), *Cassia spectabilis* (Habte & Turk 1991), *Leucaena leucocephala* (Manjunath *et al.* 1984; Ahmad & Maziah 1988; Michelsen & Rosendahl 1990; Jagpal & Mukerji 1991), *Sesbania grandiflora* (Habte & Aziz 1985), *Sesbania sesban* (Jagpal & Mukerji 1991) and *Tamarindus indica* (Reena & Bagyaraj 1990b) have all been shown to be responsive to inoculation in short-term studies.

Reports among non-legumes are less frequent; however, several tree species from a wide range of tropical habitats have been found to respond positively to inoculation. They include species such as *Khaya grandifoliola* (Redhead 1975), *Terminalia superba* (Blal 1985) and *Theobroma cacao* (Chulan 1991). The list of Sieverding (1991) includes fruit trees such as *Citrus* spp., *Persea americana*, *Carica papaya*, *Psidium guajava*, *Annona muricata*, *Cyphomandra betacea*, *Passiflora* spp., *Solanum quitoense* and *Mangifera indica*, and forest trees such as *Hibiscus elatus*, *Cedrela mexicana*, *Ficus glabrata*, *Carludovica palmata*, *Terminalia oblonga*, *Genipa americana*, *Tabebuia* spp. and *Vitex cooperi*.

Results from a number of experiments in which different single-species inocula were compared demonstrate that there is considerable variation in effectiveness between fungal species and between isolates (eg Bagyaraj, Byra-Reddy & Nalini 1989; Reena & Bagyaraj 1990a, b). This evidence suggests that, where inoculation is required, there is the opportunity to screen and select those VAM fungi possessing greatest symbiotic efficiency. Criteria for selection include speed of colonisation, ability to take up nutrients and water, improvement of plant growth, persistence and competitiveness with indigenous fungi, and production of large numbers of resistant propagules (Abbott, Robson & Gazey 1992). Selection may be exploited particularly effectively in a tree domestication programme where high-performing clones of trees could be

matched with highly effective isolates of VAM fungi.

When inocula are selected, the researcher must have a clear perception of the conditions for which the inocula are being screened – is the aim to achieve growth responses in potted plants in the nursery (where comparisons may be made with non-mycorrhizal control plants grown in sterile soil, or unsterile soil containing a mixture of indigenous mycorrhizal fungi) or in plants grown in the field with a more dispersed root system and a background indigenous inoculum, or is the researcher hoping for growth responses in both the nursery and the field, despite the widely differing conditions encountered? Selection for improved growth under nursery conditions is easily achieved, as demonstrated by the many papers on this subject, but selection for long-term effects poses a far greater challenge which agricultural mycorrhizal researchers do not have to meet.

Persistent effects of inoculation on growth in the field have not yet been demonstrated convincingly. Long-term successful symbiotic relationships with trees will need to be effective under a range of environmental conditions, from nursery to outplanting site and maturing plantation (Wilson & Coutts 1985; Janos 1988), and with a changing background of indigenous fungi, which may have been deficient at planting, but which will recover as vegetation is re-established. Because of the changing conditions, and the diversity in VAM physiology (Brundrett 1991), a mixture of VAM fungi (as in natural soil inoculum of undisturbed sites) may be a long-term advantage for trees, enhancing their performance under a range of conditions, and reducing the variation in host response. As fungal species diversity is lower in intensively managed systems, it may increase ecosystem instability because of the more limited physiological range of the VAM fungi present, and the more intensively managed forest plantations may be in greater need of mycorrhizal management than the less intensively managed, more mixed plantations.

While the performance of fungal mixtures in comparison with single isolates does not appear to have been tested in long-term experiments, short-term studies have demonstrated that a mixture of indigenous mycorrhizal fungi was as effective in promoting growth of *Albizia falcataria*, *Gmelina arborea*, *Intsia palembanica* and *Leucaena leucocephala* as the best of seven introduced VAM species used as single-species inocula (Ahmad & Maziah 1988).

An important gap in the literature is information relating to performance of inoculated trees after outplanting. Practically all studies have been restricted to short-term observations in tree

nurseries, where inoculation is frequently beneficial. The limited information that exists from field plantings indicates that inoculation can improve both survival and tree growth after outplanting, although this improvement has not been seen in all the experiments reported. Janos (1988) describes experiments in Costa Rica and Panama in which inoculated *Pithecellobium longifolium* seedlings had faster growth rates than non-inoculated seedlings in the nursery. After outplanting to over-grazed pasture, the inoculated seedlings maintained their superior growth rates for seven months before the growth rates of the non-inoculated plants caught up. In a further outplanting trial of non-inoculated and mycorrhizal seven-month-old *Inga edulis* planted on sites that had been cut three or 15 months previously and then allowed to regrow, the average height of mycorrhizal plants increased ten times faster than that of surviving non-inoculated individuals for eight months following transplanting on the more recently cleared land, and two times faster on land that had been cleared 15 months previously. The contrasting responses on these two sites may indicate the lower inoculum potential on the more recently disturbed site, compared with the older site where revegetation may have resulted in recovery of inoculum potential.

Dart, Umali-Garcia and Almendras (1991) have reported that *Acacia mangium* seedlings grew better in the nursery when inoculated with mycorrhizal fungi, and that all the non-inoculated seedlings had died two years after outplanting in the field. In Kenya, four tree species (*Acacia tortilis*, *Prosopis juliflora*, *Terminalia brownii* and *T. prunioides*) were pre-inoculated in the nursery with mixed VAM inoculants collected locally, and with rhizobia (Wilson *et al.* 1991; see also Milimo, Dick & Munro, pp210–219). Inoculated plants generally grew better in the nursery. Assessments made 30 weeks after outplanting to two different field sites indicated that inoculated plants survived better than non-inoculated plants, with the exception of *P. juliflora* at one site and *T. brownii* at the other. When averaged over the two sites, inoculated *Acacia tortilis*, *Prosopis juliflora*, *Terminalia brownii* and *T. prunioides* had survival rates at 30 weeks of 97%, 94%, 89% and 89% respectively, while those of non-inoculated plants were 79%, 88%, 81% and 57%. Further assessments two years after planting indicated that the beneficial effects of inoculation upon survival were sustained (Wilson *et al.*, unpublished data). However, while survival in the field was improved by inoculation, there were no substantial differences between treatments in the growth of surviving plants. Similarly, Cornet *et al.* (1982) found that, although inoculation improved the growth of *Acacia holosericea* in the nursery, and the absolute

differences in height growth observed at planting were sustained for at least seven months after planting in the field, the relative differences between inoculated and uninoculated plants diminished. Ducouso and Colonna (1992) have also reported that, although inoculation improved the growth of *Acacia holosericea*, *A. senegal* and *A. raddiana* in the nursery, the beneficial effects of inoculation diminished after one or two years in the field. As mycorrhizal inoculation in the nursery often produces larger plants, differences in survival between inoculated and uninoculated treatments may result from the initial differences in plant size, from differences in mycorrhizal infection, or a combination of both, and data need to be interpreted with care. Furthermore, differences in growth rate can be misleading, when initial plant size is different.

The effects of inoculation on field performance will depend upon the quantity and efficacy of naturally occurring inoculum, which needs to be assayed at the time of planting and at intervals thereafter to interpret the performance of inoculated and control plants. Likewise, assessments of the extent of mycorrhizal infection on root systems before planting and at intervals after planting are desirable, although observations on field material are very difficult. Responses to inoculation are most likely to be found on sites which have low background availabilities of inocula, and with mycorrhizal-dependent tree species.

## SYNOPSIS

Many tropical trees are highly dependent upon their mycorrhizal associations for growth and survival. Mycorrhizal fungi are major intermediaries between plant and soil, of particular importance in adverse environments, yet their role in tree domestication, and in developing sustainable forestry systems in the tropics, has been neglected.

Site preparation can have a great impact upon indigenous mycorrhizal populations, particularly those communities in which spore inocula have been relatively unimportant. The use of less damaging methods of site preparation results in less disturbance to mycorrhizal populations, and limited studies indicate that this factor is more favourable to mycorrhizal infection on the roots of planted tree seedlings. Where there is a choice in the method of site preparation to be applied, consideration should be given to using methods which retain much of the ecological diversity of the indigenous mycorrhizal flora, and which do not lead to its depletion, thereby providing a good source of inocula for planted trees and potential benefits in long-term sustainability. When sites are deficient in mycorrhizal fungi, they may be manipulated to enhance mycorrhizal populations, and, where

specific tree/VAM fungal isolate combinations are to be exploited, plants may be inoculated in the nursery. Methodology is available for assessing the mycorrhizal status of sites, and the mycorrhizal dependency of plant species. These tools should be applied to determine appropriate strategies for the treatment of different sites and tree species.

Short-term studies of the effects of VAM fungi upon plant growth have demonstrated that the use of inoculants to improve seedling growth in the nursery is readily achievable for a wide range of tree species. The use of selected isolates of inocula can considerably enhance growth, and opportunities exist for the exploitation of tree clone/symbiont interactions, so that the domestication of trees could run in parallel with the domestication of mycorrhizal fungi. However, the use of fungal mixtures as inoculants may be preferable to the use of single isolates.

Inoculation can be used to improve survival rates during the establishment phase after tree planting. Longer-term effects on post-planting performance have yet to be realistically evaluated. The development of longer-term effects will depend upon the selection of inocula that are appropriate for the site conditions (which may not necessarily be those that are most beneficial in the nursery), and the availability of effective indigenous inocula on-site. Plants destined for disturbed, nutrient-poor sites, with low levels of background inocula, are most likely to benefit from the application of inoculants in the nursery. Results so far indicate that expectations of long-term cumulative effects on most sites should not be raised too high: the advantages of inoculation are most likely to occur during the establishment phase.

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