Appendix 1. Some timbers used by Kings Fourth Generation Woodworking Co.

By kind permission of Kings Fourth Generation Woodworking Co., Broadway, P.O. Box 194, Carterton, New Zealand, telephone +64-6-379 8812, fax +64-6-379 8919, email timbertops@generation-4.co.nz, web *www.generation-4.co.nz/timber.html*

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Generation IV TIMBER TOPS — Timber Gallery

New Zealand Native Timbers

NZ Plantation Timbers

Imported Timbers

Click on the samples to see a larger view and/or further details

---

"These images are true representatives of each species. Grains and colours can vary considerably."

New Zealand Native Timbers


Kahikatea


Matai


NZ Heart Kauri


NZ Kauri Pale


NZ Red Beech *


Rewarewa


Rimu Heart


Rimu Pale


Rimu Recycled


Southland Beech *


Tawa


Totara

* The only sustainably grown New Zealand native species

Black Totara

NZ Plantation Timbers

Lawson Cypress

Macrocarpa

NZ Ash

NZ Blackwood

NZ Elm

NZ Saligna

Radiata Pine

Silver Wattle

Imported Timbers

African Wenge

African Bubinga

African Padauk

African Anegre

Aust Blackwood

Aust Jarrah

Aust Silky Oak

Burmese Teak

Euro Beech

Fiji Kauri

Fiji Salu Salu


Fiji Yaka


Hondouras Sapele Mahogany


Victorian Ash (Aust)


USA Ash


USA Cherry


USA Maple


USA Oak


USA Black Walnut

Top

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Appendix 2. IUFRO Breeding theory and progeny testing: Eucalyptus and Acacia breeding programs in some Asian countries

Chris Harwood, Ensis, Private Bag 12, Hobart 7001, Australia.

At the IUFRO Conference "Eucalyptus in a Changing World" in Aveiro, Portugal, in October 2004, I was struck by a remark made in one of the sessions to the effect that little work on eucalypt breeding seems to be going on in Asian countries. While some of the work is under-reported in the international literature, many Asian countries in fact have well-advanced programs of domestication and genetic improvement for eucalypt species and other tree genera of Australian origin.

Australian tree genera are very prominent in tropical and subtropical plantation forestry (Evans and Turnbull 2004). In addition to their use in formal plantations, eucalypts and other Australian species are planted widely in rows or as individual trees on farms, around homesteads, and along canals and roadsides throughout much of the warmer regions of the world. Plantations of *Acacia* species of Australian origin are estimated to occupy about 2 M hectares, and continue to expand rapidly (Midgley and Turnbull 2003). Planting of Australian species as exotics began in the late 18th century, and has continued at an accelerating rate, despite some controversies over issues such as weediness, water use, social impacts and land ownership.

Commencing in the 1960s, with the support of FAO and IUFRO, international species and provenance trials based largely on seed collections made by CSIRO's Australian Tree Seed centre were established in many countries. The most productive species and provenances of *Eucalyptus* and *Acacia*, and other Australian genera prominent in tropical plantation forestry such as *Casuarina*, *Grevillea* and *Melaleuca* were identified. Important new plantation species such as *A. crassicarpa* were "discovered" and domesticated in this process. Over the past twenty years, *A. crassicarpa* has gone from a virtually unknown tree in the wilds of north Queensland and New Guinea to a major commercial plantation species for pulp and paper in Southeast Asia (Midgley and Turnbull 2003). China, Indonesia, Thailand and Vietnam all now have well-established progeny testing programs and seed orchards for this species.

Inbreeding and negative selection, often from a sub-optimal initial introduction, have caused severe genetic deterioration in many unmanaged land races of key Australian tree species, with resulting declines in the productivity of plantations based on informally collected seed (Harwood et al. 2004). Over the 1980s and 1990s, strong efforts were made to establish in-country mass-production of genetically improved planting stock based on superior provenances of key species, through seed orchards and clonal programs. Government research agencies and some private companies in many Asian countries now have well-established breeding populations based on appropriate provenances of their key species, and seed orchards and clonal programs delivering large quantities of improved planting stock, resulting in substantial gains in plantation productivity. A recent meeting in Bangkok, Thailand, sponsored by the Australian Centre for International Agricultural Research (ACIAR) and attended by lead scientists from national agencies charged with forest genetic research, documented the domestication status of Australian species in Asian countries. This information is summarised in Table 1 below.

Eucalyptus and Acacia breeding programs in some Asian countries.

It can be seen that countries such as China, India, Indonesia, Thailand and Vietnam are well-advanced in overall domestication of Australian species. Forest plantation companies have now established sophisticated tree improvement programs to support large scale industrial

plantings - *Acacia mangium*, *A. crassicarpa* and *E. pellita* in Indonesia and the programs to develop hybrid eucalypt clones in China are good examples. Genetically improved planting stock (relative to the best wild introductions) comprises a rapidly growing percentage of new plantations. In southern India, for example, seedling seed orchards established in the mid 1990s (Varghese et al. 2000) already provide about 20 kg of improved *E. camaldulensis* and *E. tereticornis* seed per year, sufficient to establish more than 2,000 ha of plantations. The breeding populations of these species established in southern India have also yielded a new series of highly productive clones for clonal forestry, and form a genetic base for hybrid breeding. Growth of the orchard seed in genetic gain trials is superior to that of local commercial seed sources (Mohan Varghese, pers. comm. 2004).

Table 1. Status of tree domestication programs in Asian countries

	China	India	Indonesia	Laos	Malaysia	Pakistan	Philippines	Sri lanka	Thailand	Vietnam
Key species identified for major planting regions	1 2 3	1 2 3	x	1 2	1 2	1	1 2	1	1 2 3	1 2 3 4
Superior provenances of key species identified	1 2 3	1 2 3	x	1 2	1 2	1	1 2	1	1 2 3	1 2 4
SPAs based on best provenances now delivering seed	1 2 3	1 2 3	x	1	(2)	(1)	1 2	(1)	1 2 3	1 2 4
Progeny trials of key species established	1 2	1 2 3	x		2	1	1 2	1	1 2	1 2
SSOs yielding seed	x	1 2 3	x			(1)	1 2	(1)	1 2	(1, 2)
Functioning national or regional tree seed centres		x							x	
CSOs based on index-selected material established	2	3								1 2
Clonal forestry operational with key species	1 3	(x)	2		-2		-1		1	1 2
Outgrower schemes for farmers to use clones	?	1							1	2
Clonal forestry with interspecific hybrids	1	(1 2)							1 3	2
2nd -generation breeding population (progeny trials)			2						1	1
Well-documented genetic improvement strategies	1,2	1 2 3	2		(2)		(1)	1	1	(1 2)
Wood quality incorporated into improvement objectives	(1, 2)							(1)	(1)	(1 2)
Controlled pollination used for key species/hybrids	1	(1)	1 2		(2)				1	1 2
Genetic gain trials testing improved seed/clones established	(1)	1 2					1 2	1	1	1 2

SPA = seed production area, SSO = seedling seed orchard, CSO = clonal seed orchard, 1 = *Eucalyptus*, 2 = *Acacia*, 3 = *Casuarina*, 4 = *Melaleuca*
x = all genera, 1 in cell of table = operational in this country, (1), etc. = impact not yet major, blank cell = not operational in this country

In China, which now has over 1.5 M hectares of eucalypt plantations, new plantings are delivering yields of around 20 m3 ha-1 year-1, almost three times that achieved with previously-used species and silviculture (Van Bueren 2004). The development of high-yielding trees has been at least partly responsible for the rapid expansion in planting area, and it was concluded that the eucalypt research and development supported by ACIAR and implemented by Chinese research institutes in partnership with Australian forest research agencies has almost certainly made a considerable contribution to improving the living standards of rural people in southern China. In Vietnam, the establishment of over 130,000 hectares of highly productive clonal plantations of the acacia hybrid A. mangium x auriculiformis is an outstanding achievement, considering that research on tropical acacias commenced in that country only in the late 1980s (Le Dinh Kha 2001; van Bueren 2005, in press).

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Appendix 3. Lists of arbuscular mycorrhizal plants suitable for windbreaks around truffières and unsuitable ectomycorrhizal plants.

There are several web sites that have lists of the types of mycorrhizas that are formed by various species of plants. Some good ones are:

www.ffp.csiro.au/research/mycorrhiza/ozplants.html#define

www.horticulturalalliance.com/Plant_Species_and_Type_of_Mycorrhizae.asp

www.mycorrhiza.org/EXPERTflat.PDF

www.nifg.org.uk/ecto.htm#Which%20trees

www.tandjenterprises.com/BioVam_Plant_List.htm

Table 1 is a short list of a few plants that form arbuscular mycorrhizas (AM or VAM) that can be grown near to a truffière. Incidentally with the exception of native beeches, manuka and kanaka almost all New Zealand natives form AM mycorrhizas. Table 2 is a list of some of the trees that form ectomycorrhizas. These harbour fungi that can compete with truffle fungi. Truffières should not be planted close to these and these trees should not be included in living windbreaks adjacent to a truffière.

Table 1. Some arbuscular mycorrhizal plant species

Common name	Botanical name	Plant family
Akeake	*Dodonaea viscosa*	Sapindaceae,
Akiraho	*Olearia paniculata*	Asteraceae
Almond	*Prunus dulcis*	Rosaceae
Apple	*Malus*	Rosaceae
Apricot	*Prunus armeniaca*	Rosaceae
Angelica tree	*Aralia*	Araliaceae
Ash	*Fraxinus*	Oleaceae
Avocado	*Persea americana*	Lauraceae
Bamboo	*Bambusa*	Pooideae
Banana	*Musa*	Musaceae
Barberry	*Berberis*	Berberidaceae
Bayberry	*Myrica*	Myricaceae
Black locust	*Robinia*	Fabaceae
Blackberry	*Rubus eubatus*	Rosaceae
Box elder	*Acer negundo*	Aceraceae
Broadleaf	*Griselinia*	Griseliniaceae
Boxwood	*Buxus*	Buxaceae
Buckeye	*Aesculus*	Hippocastanaceae
Burning bush	*Euonymus*	Celastraceae
Cacao	*Theobroma cacao*	Sterculiaceae
Camellia	*Camellia*	Theaceae
Catalpa	*Catalpa*	Bignoniaceae
Cherry	*Prunus avium*	Rosaceae
Chinaberry	*Melia azedarach*	Meliaceae
Coral tree	*Erythrina indica*	Fabaceae
Crabapple	*Malus*	Rosaceae
Cryptomeria	*Cryptomeria japonica*	Taxodiaceae
Cucumber tree	*Magnolia acuminata*	Magnoliaceae

Dogwood	*Cornus*	Cornaceae
Fig	*Ficus carica*	Moraceae
Flax, New Zealand	*Phormium tenax*	Agavaceae
Fuschia	*Fuchsia*	Onagraceae
Gingko	*Ginkgo biloba*	Ginkgoaceae
Gorse	*Ulex europaeus*	Fabaceae
Grapes	*Vitis*	Vitaceae
Hackberry	*Celtis*	Ulmaceae
Hibiscus	*Hibiscus rosa-sinensis*	Malvaceae
Holly	*Ilex*	Aquifoliaceae
Horse chestnut	*Aesculus*	Hippocastanaceae
Juniper	*Juniperus*	Cupressaceae
Kamahi	*Weinmannia racemosa*	Cunoniaceae
Karamu	*Coprosma robusta*	Rubiaceae
Kauri	*Agathis*	Araucariaceae
Korokia	*Corokia buddleoides*	Cornaceae
Kowhai	*Sophora spp.*	Papilionaceae
Lacebark	*Hoheria populnea*	Malvaceae
Lawson cypress	*Chamaecyparis lawsoniana*	Cupressaceae
Lemonwood	*Pittosporum*	Pittosporaceae
Leyland cypress	*X Cupressocyparis leylandii*	Cupressaceae
Macrocarpa	*Cupressus macrocarpa*	Cupressaceae
Magnolia	*Magnolia*	Magnoliaceae
Mahoe	*Melicytus ramiflorus*	Violaceae
Maples	*Acer*	Aceraceae
Marbleleaf	*Carpodetus serratus*	Carpodetaceae
Mulberry	*Morus*	Moraceae
Olive	*Olea europaea*	Oleaceae
Palms	*Cycad*	Cycadaceae
Papaya	*Carica papaya*	Cariceae
Paulownia	*Paulownia*	Paulowniaceae
Peach	*Prunus persica*	Rosaceae
Pear	*Pyrus communis*	Rosaceae
Persimmon	*Diospyros*	Ebenaceae
Plum	*Prunus*	Rosaceae
Podocarp	*Podocarpus*	Podocarpaceae
Pohutukawa	*Metrosideros excelsior*	Myrtaceae
Privet	*Ligustrum*	Oleaceae
Rain tree	*Koelreuteria elegans*	Sapindaceae
Rata	*Metrosideros*	Myrtaceae
Redwood, coastal	*Sequoia sempervirens*	Taxodiaceae
Redwood, giant	*Sequoiadendron giganteum*	Taxodiaceae
Ribbonwood	*Plagianthus betulinus*	Malvaceae
Rowan	*Sorbus*	Rosaceae
Sycamore	*Acer*	Aceraceae
Tree-of-heaven	*Alianthus altissima*	Simaroubaceae
Tulip tree	*Liriodendron*	Magnoliaceae
Viburnum	*Viburnum*	Caprifoliaceae
Yew	*Taxus spp*	Taxaceae

Table 2. Some ectomycorrhizal plants (may also form arbuscular mycorrhizas).*

Common name	Botanical name	Plant family
Alder	*Alnus*	Betulaceae
Strawberry tree	*Arbutus*	Ericaceae
Aspen	*Populus* *	Salicaceae
Beech	*Fagus*	Fagaceae
Birch	*Betula*	Betulaceae
Cedars	*Cedrus*	Pinaceae
Chestnut	*Castanea*	Fagaceae
Cherry, bird	*Prunus padus*	Rosaceae
Cherry, dwarf	*Prunus cerasus*	Rosaceae
Cherry, wild	*Prunus avium*	Rosaceae
Douglas fir	*Pseudotsuga menziesii*	Pinaceae
Eucalyptus	*Eucalyptus* *	Myrtaceae
Fir	*Abies*	Pinaceae
Hawthorn	*Crataegus*	Rosaceae
Hazels	*Corylus*	Betulaceae
Hemlocks	*Tsuga*	Pinaceae
Hickory	*Carya*	Juglandaceae
Hornbeam	*Carpinus*	Betulaceae
Ironwood	*Casuarina*	Casuarinaceae
Kanuka	*Kunzea ericoides* *	Myrtaceae
Larch	*Larix*	Pinaceae
Lime	*Tilia*	Tiliaceae
Manuka	*Leptospermum scoparium* *	Myrtaceae
Oak	*Quercus*	Fagaceae
Pine	*Pinus*	Pinaceae
Poplar	*Populus* *	Salicaceae
Redbud	*Cercis canadensis*	Fagaceae
Rock rose	*Helianthemum*	Cistaceae
She-oak	*Casuarina* *	Casuarinaceae
Spruce	*Picea*	Pinaceae
Walnut	*Juglans*	Juglandaceae
White leaved rock rose	*Cistus*	Cistaceae
Wild service tree	*Sorbus torminalis*	Rosaceae
Wild pear	*Pyrus pyraster*	Rosaceae
Willows	*Salix* *	Salicaceae

Appendix 4 Gilmore's 1958 paper on Douglas fir

Gilmore, J.W. 1958. Chlorosis of Douglas-fir. *New Zealand journal of forestry* 7: 94-106. The full article can be downloaded free of charge from: http://www.nzjf.org/free_issues/NZJF07_5_1958/35E128E8-C36C-4432-8296-4E60B097564A.pdf

CHLOROSIS OF DOUGLAS FIR

J. W. GILMOUR*

Summary

Chlorosis followed by stagnation of up to 80% of the newly established Douglas fir at Akatore, Berwick, and Herbert State Forests is described. Field investigations indicated that this condition was caused by the poor development of a particular type of mycorrhiza in the heavy clay soils occurring in these forests and in Milton nursery. Only stands established with Milton raised seedlings have been severely affected. Interim results from planting trials showed that Tapanui seedlings and Milton seedlings treated with duff in the field, were far superior to untreated Milton seedlings in transplantability and survival. Lack of mycorrhizal development in Milton nursery appeared to be due to the absence of proper inoculation, certain unfavourable nursery practices and possibly periodic anaerobic soil conditions.

INTRODUCTION

The development of a chlorotic moribund condition in young Douglas fir (*Pseudotsuga taxifolia* (Poiret) Britton) has been alarmingly evident in the establishment of a number of plantations in the South Island of New Zealand.

In 1939, at Golden Downs State Forest, early chlorosis was reported by Forest Ranger R. E. Lawrence. He believed that this condition was caused by the absence of all the appropriate mycorrhizal fungi in certain nurseries. He also saw similar symptoms in newly established Douglas fir grown at Ashley State Forest in 1940. Here it was supposed to have been corrected by the addition of duff collected from under established stands of Douglas fir at Hanmer. Unfortunately his ideas and observations were not adequately recorded or investigated at the time.

In 1954 a similar chlorotic condition of Douglas fir was reported from Berwick, Herbert and Akatore State Forests, near Dunedin in the South Island.

All areas of this species established since 1949 in these forests, using seedlings raised in Milton nursery, showed many sickly yellow, stagnating trees scattered at random among apparently healthy fast growing trees. The purpose of this paper is to describe this early chlorotic moribund condition of Douglas fir in newly established areas, to discuss its probable cause and remedy, and to present interim results of two field trials.

* Forest Mycologist, Forest Research Institute, Rotorua.

Appendix 5. A review of older papers on growth responses to arbuscular mycorrhizal inocula

Reprint of: Hall, I.R. 1988. Potential for exploiting vesicular arbuscular mycorrhizas in agriculture. *In*: Biotechnology in Agriculture, Ed A. Mizrahi, Advances in Biotechnological Processes 9: ARL, New York, 141-174. See, in particular pages 142 and 152 of the reprint for typical examples of growth responses to inoculation by arbuscular mycorrhizal fungi.

Biotechnology in Agriculture, pages 141–174

Potential for Exploiting Vesicular-Arbuscular Mycorrhizas in Agriculture

I.R. Hall

Invermay Agricultural Centre, Ministry of Agriculture and Fisheries, Private Bag, Mosgiel, New Zealand

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Vesicular-arbuscular mycorrhizas (VAM) can improve plant growth by stimulating the uptake of nutrients, especially phosphorus (Fig. 1) [43, 97,168], suppressing the detrimental effects of root pathogens [18,35,36,78] (Table I) and possibly by having beneficial effects on plant hydration (see Table XV:ii for references). However, the beneficial effects isolates and species of VAM fungi have on plant growth can vary [4,5,6,50,58,61,

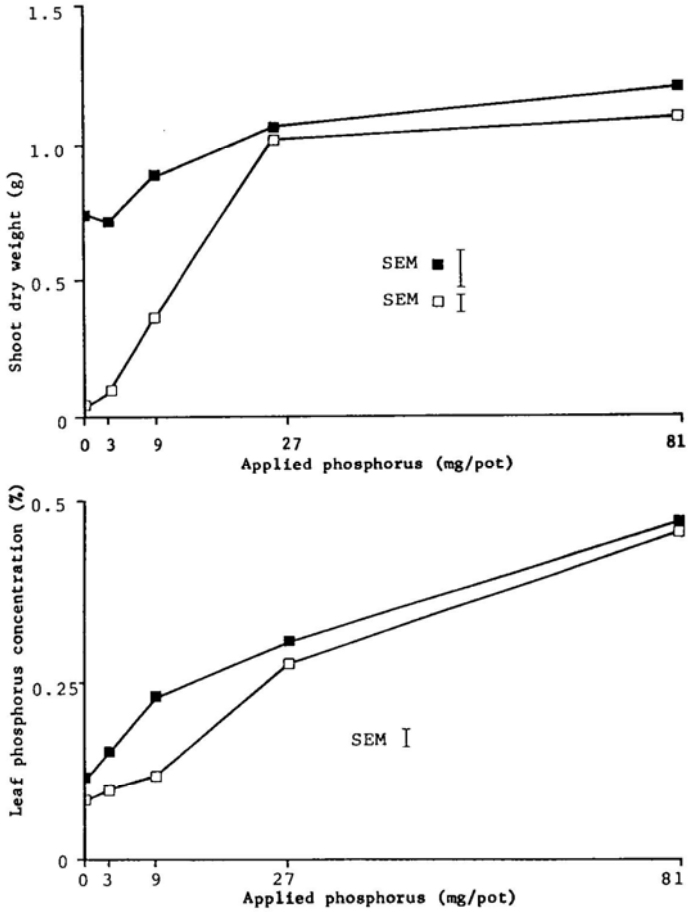

Fig. 1. Effect of a mixed inoculum of *Glomus fasciculatum* and *Gigaspora margarita* on Grasslands Huia white clover (*Trifolium repens* L.) growth in a phosphorus-deficient steamed soil in a greenhouse pot experiment. □, uninoculated; ■, inoculated [from 86].

62,74,118,125,131,133,163,166,185,203,223]. This plus the demonstration that some soils contain few or no VAM fungi, or are populated by VAM fungi less effective than those which can be introduced (Table II; see sections I and II.A for references) has attracted the attention of applied research workers. This paper reviews this applied research and discusses the possi-

TABLE I. Effect of a Mixed VAM Inoculum, *Meloidogyne hapla* Chitwood and Applied Phosphate on Shoot Dry Weight of Wairau Alfalfa (*Medicago sativa* L.) and Number of Nematodes Per Gram of Root [From 78—VAM and Nematodes Added at Transplanting]

Inoculum		Added phosphorus (kg P/ha)			
VAM	Nematodes	0	8	30	120
Shoot dry weight (g—square-root transformed)					
−	−	4.24	4.69	9.27	13.71
+	−	10.95	10.77	12 .77	17.44
−	+	3.16	3.46	5.83	11.49
+	+	11.31	9.70	13.82	16.73
			LSD (5%) 1.08		
Nematodes/g fresh weight of root (square-root transformed)					
−	+	44 .72	37.42	46.90	44.72
+	+	14.14	14.14	28. 28	24.49
			LSD (5%) <9.14		

TABLE II. Effect of Two VAM Inocula on Soybean [*Glycine max* (L.) Merrill cv. Tainon 4] Seed Yield (g/pot) Grown for 84 Days in Four Lowland Subtropical Soils in the Greenhouse [From 230: Experiment 1]

	Soil			
Inoculum	Taichung	Pingtung	Changhua	Tainan
Glomus fragile	4.7	8.9	6.5	4.9
G. fasciculatum	4.2	10. 0	6.9	5.3
None	3.9	7.5	4.8	3.7
		LSD (5%) 0.8		

bilities and practicalities of exploiting VAM symbiosis in agriculture. It has therefore been written more from an agriculturalist's point of view than a mycologist's, and readers who would prefer a different emphasis are referred to Harley and Smith [97], papers in the book edited by Powell and Bagyaraj [184], and papers by Mosse [157] and Smith and Gianinazzi-Pearson [211].*

*This chapter was prepared before the 7th North American Conference on Mycorrhizas. There are a number of papers presented in the Proceedings which are relevant to this review.

I. POT EXPERIMENTS

Pot experiments in sterilized soil have proved valuable by providing much useful information, for example, on the role VAM play in the mineral nutrition (Fig. 1) [8,43] and carbon economy [98,220] of plants, and by demonstrating apparent differences in the effectiveness of VAM fungi (Table II; see above for references). Partial or complete soil sterilization, however, can change its nutrient status and structure [116,142,160,195], as well as removing some or all of the microbiota [30,160], while VAM fungi appear to be adapted to such specific soil conditions. The results of experiments in sterilized soils which purport to show that a soil's indigenous VAM fungi differed in effectiveness from others with which it was compared [e.g., 175,180] are therefore questionable because the indigenous fungi may no longer be well adapted to the changed soil conditions. The same criticisms do not apply to similar greenhouse pot experiments which used unsterile soils containing their normal complement of VAM fungi [2,38,91,135,156, 176,230]. However, these experiments too are open to question. For example, Young and co-workers' [230] (Table II) data could be interpreted as showing that both *Glomus fragile* (Berk. & Broome) Trappe & Gerd. and *G. fasciculatum* (Thaxter sensu Gerd.) Gerd. & Trappe were superior VAM fungi to the indigenous ones in the four soils. It is conceivable, however, that the inoculum potential of the four soils may have been naturally low or depressed by prolonged storage (see section II.A.1). This could have resulted in the delayed onset and benefits of infection in the controls, which could have been particularly marked in relatively short-term experiments.

Another limitation of pot experiments is that greenhouse environments usually differ from those in the field. For example, water is not usually allowed to become limiting in greenhouse studies [cf. 32], but tolerance to drought may be the most important factor to which a VAM fungus may have to be adapted [3]. Plants raised in containers in the greenhouse and then placed in or on the soil surface in the field offer some compromise, but where the effects of VAM in agriculture are under study there is no substitution for field experiments conducted using standard agricultural practices and with soil and climatic conditions, etc., as close as possible to those to which a crop/pasture is normally exposed.

II. FIELD EXPERIMENTS

Despite all the work that has been done on VAM over the past two decades regrettably only a limited amount has been directly aimed at exploiting the

symbiosis in agriculture and relatively few researchers have attempted field experiments. There are a number of reasons for this omission:

- There are only a limited number of establishments where VAM research is being conducted which have the facilities and expertise for conducting field experiments.
- Ph.D. and M.Sc. supervisors are unwilling to let their students conduct risky field investigations and have therefore steered them towards greenhouse and laboratory work.
- Many institutions involved in VAM research would find the cost of extensive field experiments prohibitive. For example, I estimate that the current cost of my own series of field experiments and preliminary experiments [89,90] would be in excess of $200,000.
- Much VAM research is conducted simply to further our scientific understanding of the symbiosis, and commercial values have little relevance.

A. Field-Sown Crops and Pastures

In some pot and field experiments dealing with normally field-sown crop and pasture species, a comparison of the effectiveness of indigenous and introduced VAM fungi was made by transplanting from the glasshouse to the field uninoculated seedlings (controls) or seedlings inoculated with an "elite" strain of a VAM fungus and then comparing subsequent plant growth [17,101,105,113,115,123,124,197]. Such experiments have two inherent errors:

1. Plants inoculated before transplanting would benefit from mycorrhizas for the period from inoculation to transplanting, while the uninoculated controls would not. For example, in Khan's [123,124] experiments this time advantage was from 18% to 20% of the total experimental period and in Islam and colleagues' [112] from 20% to 43%. At transplanting this advantage may not have been apparent, but by the end of the experiment it would have at least contributed to significant differences in treatments.
2. Work by Hall [83] suggests that as uninoculated seedlings get older they respond to VAM infection more slowly, and hence the controls would have been further disadvantaged.

In other experiments using pre-inoculated transplant techniques these criticisms were overcome by inoculating the controls with a culture of the indigenous fungi from the soil into which the seedlings were later to be transplanted [e.g., 176,178,179]. However, even in these experiments

TABLE III. Effect on Plant Height (Square-Root Transformed) of Inoculating Pelletted Field Grown *Lotus pedunculatus* Cav. cv. Grasslands Maku With *Glomus fasciculatum* [From 88]

	Applied P (kg/ha)	
Inoculum	10	50
Non-VAM-infested pellet	2.28	2.81
VAM-infested pellet	2.95	3.52
	LSD (5%) 0.34	

competition among the indigenous VAM fungi, the soil flora and fauna, and the inoculant fungus develops only after transplanting. All the phases of growth and competition that an inoculant VAM fungus might otherwise have encountered from the initiation of hyphal growth from a resting propagule, growth through the soil to a root, and the formation of pre-infecting structures followed by infection are bypassed [3]. Also, transplanting infected seedlings to inoculate field-sown crops and pastures with VAM fungi is not a practical technique (see section IV), and consequently the results of experiments which employed these techniques for normally field-sown crops and pastures must be interpreted with some caution.

Two field techniques which have been used to investigate the effects of VAM on the growth of crops in the field are comparing the growth of plants in unfumigated soil with that in fumigated soil [171,222,229], and removing the indigenous fungi with soil fumigation followed by re-inoculation of half of the plots [33,34,115,117,192,201]. However, in the former the beneficial (removal of pathogens and release of nutrients) and detrimental (e.g., bromine residues) effects of fumigation can be confounded, with the loss of the potential benefits of VAM fungi [also see 229]. In addition, neither type of experiment can determine whether inoculant fungi were any more effective than the indigenous ones under normal soil conditions. To study this it is necessary to conduct field experiments in which normal agronomic practices have been followed and, preferably, inocula applied using techniques which could be adapted to agriculture.

1. Soils with low VAM inoculum potentials. Subsoils, eroded soils, fumigated soils, and mine spoils can contain low VAM fungal populations [10,71,82,93,116,153,189,191,225]. It also seems likely that those VAM fungi which are present in these soils would have been derived from miscellaneous accidental natural introductions and therefore may not be those best suited to the conditions. The beneficial effects of VAM inocula on plant growth demonstrated in Hall's [89] (Table III) experiment on an eroded soil, Haas and co-workers' [82] on a methyl bromide fumigated soil,

TABLE IV. Effect of *Glomus macrocarpum* and Fertilizer Phosphorus on Yield and VAM Infection of Potato (*Solanum tuberosum* L.) Growing in the Field in a Fallowed Soil [From 28]

	Triple superphosphate application (kg/ha)	Tuber yield (t/ha)	VAM infection in July (%)
Inoculated with *G. macrocarpum*	0	8.07	24.3
	481	9.62	2.6
Not inoculated	0	6.72	4.6
	481	10.37	1.6
		<1.54	<19.7
		LSD (5%)	

TABLE V. Effect of VAM Inocula on Mean Shoot Dry Weights (g/m Row; Log_e Transformed) of Lucerne cv. European, Onion (*Allium cepa* L. cv. Ailsa Craig) and Barley (*Hordeum vulgare* L. cv. Ark Royal) Grown in Unsterile Field Soil [From 167]

	Crop		
Inoculum	Lucerne	Onion	Barley
Glomus mosseae + other VAM fungi	0.858	−0.139	2.178
Glomus c. caledonium	2.145	0.972	2.213
None	0.031	−1.663	1.665
		LSD (5%) 0.748	

Swaminathan and Verma's [216] on Phagu reclaimed terrace soil, and Hashim-Chulan [99] and Lambert and Cole's [138] on mine spoils were therefore not unexpected. In Hall's [88] experiment the soil was also very deficient in phosphorus and had a very high phosphorus sorbing capacity; and the host plant, *Lotus pedunculatus* Cav. cv. Grasslands Maku, was one known to be reliant on the formation of VAM for vigorous growth in phosphorus-deficient soils [93,181]. Similarly, the experiments of Haas et al. [82] on *Capsicum* (bell pepper) were conducted in a very high phosphorus sorbing soil which had been fumigated to control pepper collapse disease and therefore contained a low VAM fungal density.

The fallowed soil used by Black and Tinker [28] in their study on potatoes was also clearly deficient in VAM fungi, as evidenced by the low infection levels in the uninoculated plots (Table IV). This accounted for the observed responses to inoculation in the absence of applied phosphorus. Similarly in Owusu-Bennoah and Mosse's [167] experiment (Table V), even though by the end of the experiment infection levels were high in the uninoculated controls, the responses to inoculation were surprisingly large, suggesting that the previously fallowed soil either was deficient in VAM fungi or was populated by relatively ineffective species. Also, the response to inoculation

TABLE VI. Effect of *Glomus fasciculatum* Inoculum on Soybean (cv. Hardee) Growing in a Fallowed Soil [From 19]

						45 days after inoculation	
Inocula	Shoot dry wt/ plant(g)	Grain yield/ 1.2 m^2 plot(g)	Shoot N content (mg)	Shoot P content (mg)	Nodule dry wt/ plant(g)	VAM infection level(%)	VAM spores/ 50ml soil
Rhizobium alone	2.83	85.0	93.4	11.3	0.24	65	226
Rhizobium + *G.fasciculatum*	4.65	100.7	198.1	26.6	0.41	82	274
LSD(5%)	<1.82	>15.73	<104.7	<15.38	<0.17	na	<48

na = not analyzed

TABLE VII. Response of Field Grown Subterranean Clover (*Trifolium subterraneum* L. cv. Seaton Park) to Inoculation With *Glomus fasciculatum* [From 9—Site 2, Harvest 1]

Inoculum	Individual plant weight (g)	Total infection (%)
None	0.24	10
G.fasciculatum	0.42	42
LSD(5%)	<0.08	<10

(Table VI) produced in soybean [19] and in barley [179] in fallowed soils could have been due to a low VAM fungal density.

2. Pastures. The primary aim in the experiments of Abbott et al. [9] was not to determine if growth could be stimulated by introducing more effective strains of VAM fungi but to investigate the possibility of establishing inoculant fungi in soils which were already well populated by indigenous VAM fungi. Two inoculant fungi, *Glomus fasciculatum* and *G. monosporum* Gerd. & Trappe, were compared at four experimental sites chosen on the basis of the infectivity of their indigenous VAM fungi. The soils ranged from severely phosphorus deficient to well fertilized and not responsive to phosphorus. The *G. monosporum* inoculum failed, but *G. fasciculatum* did establish and raise infection levels at two sites. At the less fertile of these two sites this increase in infection level was accompanied by a transitory growth response at early harvests (Table VII).

Other experiments conducted by Azcon-Aguilar and Barea [16], Hall [90], Hayman [102,103], Newbould and Rangeley [162], and Rangeley et al. [188] were designed specifically to determine if pasture growth could be

TABLE VIII. Effect of VAM Inoculation on the Yield of Grasslands Huia White Clover (kg Dry Matter/ha) in an Acidic Brown Earth [From 188]

	Applied P(kg/ha)	
Inoculum	0	40
None	1,070	841
Glomus etunicatum	598	1,930
	LSD (5%) 572	

TABLE IX. Effect of VAM Inocula on Pasture Dry Matter Yields (t/ha) on a Soil With 15 μg Olsen Available P/ml Meaned Over Four Levels of Applied P [From 90: Experiment 3]

	Year 1			
Inoculum	Harvest 1	Harvest 2+3	Year 2	Year 3
Glomus mosseae	0.80	1.12	6.32	6.15
Glomus macrocarpum	0.91	1.16	6.08	6.01
Glomus tenue + *G. pallidum*	0.93	1.14	5.78	5.92
None	0.92	1.02	5.56	5.59
5% LSD	0.10	0.07	0.35	0.40

stimulated by inoculant VAM fungi. The soils on which their experiments were conducted ranged from very infertile hill country soils to high-fertility alluvial flats. In some of the experiments, rate of applied phosphorus was a treatment factor and some were carried on for more than 1 yr. The most widely used inoculant fungus was *Glomus mosseae* (Nicol. & Gerd.) Gerd. & Trappe, but a number of others were also employed. Proportionately the largest responses to inoculation were detected in the less fertile soils (Tables VIII, IX). For example, in Rangeley and co-workers' [188] (Table VIII) experiment on an acidic brown earth in Roxburghshire, United Kingdom, clover yields were doubled (ca. 1,000 kg dry matter/ha), providing 40 kg/ha phosphorus was also applied, while in Hall's experiment on a high-fertility alluvial soil [90: experiment 4], the maximum increase was only 5% (640 kg dry matter/ha). On this highly fertile soil, responses to inoculation occurred in the only year there was also a response to fertilizer phosphorus. Similarly, in an experiment on another fertile site which was accidentally top-dressed with about 50 kg/ha phosphorus on two occasions, no response to phosphorus or inoculation could be detected (Hall, unpublished data). A reduced response to VAM inocula with increasing soil phosphorus levels is in keeping with the results of VAM/phosphorus response curve pot experiments (Fig. 1) [1,29,86,181]. Even so, the tissue phosphorus levels at which responses

TABLE X. Effect of Applied Phosphorus and *Glomus mosseae* Inoculation on Growth and Seed Yield of Broad Bean (*Vicia faba* L.) Grown in Buried Cylinders in the Field [From 136 With Site Used as the Replication Factor]

	Applied phosphorus (μg P/g soil)		
Inoculum	0	Medium (5.5 to 9)	High (11 to 18)
Shoot dry weight (g/cylinder at 8 weeks)			
Glomus mosseae	17.3	21.4	22.5
None	13.6	20.4	18.8
		LSD(5%) (inoculum) 2.67	
		LSD(5%) (phosphorus) 3.27	
Seed dry weight (g/cylinder at harvest)			
Glomus mosseae	8.3	14.0	16.3
None	6.2	10.8	12.4
		LSD(5%) (inoculum) 2.64	
		LSD(5%) (phosphous) 3.23	

occurred on Hall's [90: experiment 4] most fertile site were very high (0.4%), indicating that the beneficial effects of the inoculant VAM fungi may not have been restricted to merely utilizing fertilizer phosphorus more efficiently.

3. Field-sown crops. Field inoculation experiments on field-sown crops on apparently normal agricultural soils have been conducted on soybean [*Glycine max* (L.) Merr. [63,137], cereals [33,34,39,187], faba beans [136], onions [183], and cotton [190]. In these experiments, maximum responses to inoculation were up to 35% (Table X) [136], but in none of these experiments had there been any preselection of fungi likely to produce the maximum growth responses under the conditions of the experiments. Had this been done, it is conceivable that the responses to inoculation would have been greater. In those experiments where rates of phosphorus had been applied, proportional responses to inoculation generally decreased with increasing level of applied phosphorus (Fig. 2).

B. Transplanted Crops—Seedlings Raised in "Sterile" Media

Many horticultural crops and ornamental species are raised in fumigated or heat-treated soil or in essentially sterile soilless potting media. The principal reasons for this are that losses from pests and pathogens are reduced and plant growth rates can be more predictable. Also, seedlings of some species can be raised aseptically using tissue culture techniques [228]. But the growth of plants in these media can be very poor owing to the detrimental effects heat and fumigants can have on VAM or the absence of VAM from

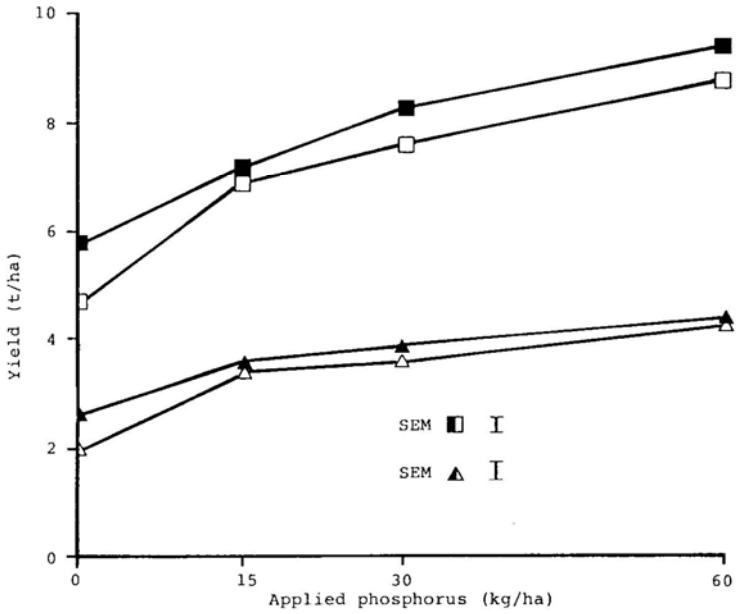

Fig. 2. Effect of *Glomus mosseae* inoculum applied below the seed on spring wheat (*Triticum aestivum* L.) grain (triangles) and total (squares) yields. □ △, uninoculated; ■ ▲, inoculated [from 33].

soil-less potting mixes [144,148,170]. The problem can therefore be rectified either by inoculating with VAM fungi or relieving the limiting factor that VAM would normally help correct, for example, by the application of phosphorus. Some species in which poor growth in media devoid of VAM fungi has been remedied either by inoculating with VAM fungi or by applying nutrients are—

- Apple [65,108,172]
- Avocado [146]
- Bell pepper [130]
- Cassava [109]
- Citrus [77,147]
- Grapes [151]
- Onions [212]
- Peach [141]
- Raspberry [154]

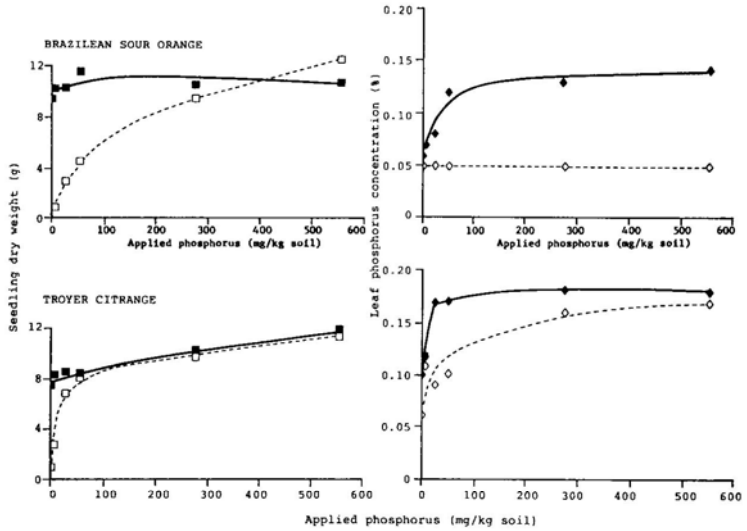

Fig. 3. Effect of *Glomus fasciculatum* inoculum and fertilizer phosphorus on seedling dry weight (squares) and percent phosphorus (diamonds) in leaves of Brazilean sour orange (*Citrus aurantium* L.) and Troyer citrange [*Poncirus trifoliata* (L.) Raf. X *Citrus sinensis* (L.) Osbeck] growing in phosphorus-deficient (4.6 μg/g bicarbonate extractable) autoclaved soil. □ ◇, uninoculated; ■ ◆, inoculated [from 149].

- Tamarillo [42]
- Forest species and ornamentals [13,23,27,45,46,120,127,129,143, 182,215]

For some plant and soil combinations and where VAM normally stimulates phosphorus uptake, the amount of phosphorus which has to be applied to nonmycorrhizal plants in order to get them to grow as well as mycorrhizal ones can be very large. For example, when Brazilian sour orange was grown in a low-fertility soil (4.6 μg available phosphorus/ml soil) approximately 8 t/ha of single superphosphate had to be applied to uninoculated plants to stimulate growth and tissue phosphorus concentrations to the level of unfertilized inoculated ones (Fig. 3) [149]. Similarly, Howeler et al. [109], working on cassava, found that nonmycorrhizal plants had to be fertilized with 1,600 kg phosphorus/ha for their growth rate to reach that of mycorrhizal plants receiving no additional phosphorus. But it should be realized that these are extreme examples resulting from the use of hosts highly dependent on VAM and soils very deficient in available phosphorus.

TABLE XI. Effect of *Glomus mosseae* and Applied Phosphorus on the Shoot Dry Weight of Apple (*Malus domestica* Borkh.) Seedlings Grown in Fumigated Soils [From 108]

		Soil				
	VAM inoculum	Okanogan loam	Taunton fine silty loam	Magallan fine sandy loam	Chelan gravelly sandy loam	Esquatzel silt loam
Extractable phosphorus (μg/g soil)		1.6	11.5	12.2	19.4	60.6
pH		6.0	7.8	6.2	6.4	7.3
Applied phosphorus (mg P/ kg soil)[a]						
0	−	0.6	0.4	0.7	0.5	3.9
	+	1.6	2.7	1.0	1.5	3.9
50	−	3.2	1.4	2.1	1.9	3.8
	+	3.5	3.6	2.0	2.1	4.1
LSD(5%)		0.08	0.09	0.5	0.07	>0.3

[a]When calculated from the surface area of soil in the pots and assuming 1.6 kg soil/pot, 50 mg P/ kg soil is approximately equivalent to 72 kg P/ha.

In contrast, Hoepfner et al. [108] found that inoculating apple had no effect on growth in a very fertile soil without added phosphorus; and in relatively less fertile soils, inoculation had no significant beneficial effects when more than 70 kg/ha phosphorus was applied (Table XI).

Most of the studies in the above list were conducted in the nursery, and subsequent growth after transplanting either was not monitored or has not been reported. However, Barrows and Roncadori [23], Biermann and Linderman [27], Cooper [42], Cornet et al. [45], Menge et al. [146], Morandi et al. [154], and Plenchette et al. [172] showed that when inoculated and uninoculated seedlings of the same size were raised in sterile media and transplanted into soils containing a normal complement of VAM fungi, the inoculated seedlings had improved transplant survival and regrowth, and subsequently produced plants which were less variable than the uninoculated ones. As far as I am aware it has not been convincingly demonstrated why these benefits occurred. One possibility is that the mycorrhizal seedlings had been pre-inoculated with more effective endophytes than those present in the soil into which they were being transplanted. Another possibility is that as with pre-infected transplanted crops (see section II.C) the lag between transplanting and the establishment of VAM infections limited the growth of the nonmycorrhizal seedlings after transplanting. In contrast to these experiments, Snellgrove and Stribley [212] failed to detect any benefit on onion

TABLE XII. Effects of Pre-Inoculating With VAM on Peat Module Raised Onions (cv. Balstora) Transplanted to the Field With a Soil Containing 31 μg/g Bicarbonate-Extractable Phosphorus [From 212—Without Dazomet Treatments]

		At transplanting		At harvest	
Module type	VAM inoculum	Shoot fresh wt (mg)	Shoot phosphorus content (%)	Harvestable yield (t/ha—$\log_{10}$ transformed)	Root length infected (%)
Commercial blocking compost	−	550	1.22	1.59	15
Modified low phosphorus compost	−	348	0.53	1.39	24
Modified low phosphorus compost	+	363	0.58	1.60	15
				0.085 LSD(5%)	

yields from inoculation prior to transplanting into a field soil where water but not phosphorus was limiting (Table XII). Unfortunately, in order to ensure that the inoculated seedlings were well infected they used a potting mix for these seedlings which was less fertile than the commercial potting mix the controls were raised in. Consequently, at transplanting the inoculated seedlings were smaller and had much lower shoot phosphorus concentrations than the controls. The inoculated seedlings were therefore disadvantaged when transplanted to the field, and conceivably this could have affected their final yields.

C. Transplanted Crops—Seedlings Raised in Unsterile Soils

In developing countries, where labor is relatively cheap, seedlings of crops which might otherwise be field-sown can be raised in nurseries and then transplanted to the field after a previous crop has been harvested. The advantages of this are that the length of time a crop is growing in the field is reduced, as is the gap between one crop and the next, more crops can be harvested per year, and food production per unit area is increased. In these regions the soils are often particularly low in available phosphorus [22,198], but the cost of fertilizer is relatively high, which restricts its use. Crops are therefore often grown in soils containing inadequate phosphorus for maximum growth and VAM make a major contribution to their phosphorus nutrition. Simply by broadcasting 1.25 kg inoculum/m^2 of pre-selected VAM fungi over the surface of nursery beds at sowing prior to transplanting to the field, Bagyaraj and Sreeramulu [20] (Table XIII), Govinda Rao et al. [72], and Sreeramulu and Bagyaraj [213] (Table XIII) have obtained increased

TABLE XIII. Effect of Preinoculating Chilli (*Capsicum annum* L.) Transplants With *Glomus fasciculatum* and *G. albidum* on Fruit Yield and VAM Infection Level in Two Soils [From 20,213]

		Applied P (kg P/ha)		
	Inoculum	0	37.5	75
Fruit yield ($kg/4.05m^2$)				
Site 1[a]	None	1.23	1.30	1.81
	G. fasciculum	1.33	1.56	—
	G. albidum	1.76	2.14	—
		LSD (5%):P 0.14	Inoculum 0.22	
Site 2[b]	None	0.27	0.37	0.43
	G. fasciculatum	0.40	0.52	—
	G. albidum	0.38	0.42	—
		LSD (5%):P 0.036	Inoculum 0.057	
Infection level (%)				
Site 1[a]	None	71	75	80
	G. fasciculatum	77	91	—
	G. albidum	100	100	—
		LSD (5%):P 5.89	Inoculum 9.31	
Site 2[b]	None	66	80	80
	G. fasciculatum	100	100	—
	G. albidum	89	97	—
		LSD (5%):P 5.71	Inoculum 9.03	

[a]Site 1 was at Chikkaballapur with a red sandy soil, pH 6.0, 6μg/g of $NH_4F + HCl$ extractable phosphorus. The chilli cultivar was Jwala.
[b]Site 2 was at Rattinhalli with a black clay soil, pH 7.2, and 12 μg/g of $NH_4F + HCl$ extractable phosphorus. The chilli cultivar was Byadigi.

yields of chilli and finger millet. Bagyaraj and Sreeramulu [20] and Sreeramulu and Bagyaraj [213] (Table XIII) also found that *Glomus fasciculatum* was superior at one site, while *G. albidum* Walker and Rhodes was superior at another. Unfortunately, different host cultivars were used at the two sites, and consequently it is not possible to distinguish whether these differences in fungal effectiveness were due to adaption of the fungi to soil conditions or host cultivar, both of which are known to influence responses to VAM inoculation (Table XIV).

D. Persistence of Responses to VAM Inocula

In soils naturally containing no VAM fungi or VAM fungi less effective than those which can be introduced, a response to inoculation could be expected to persist indefinitely provided the fungi in the inocula were well adapted to the soil and host, and were able to compete [227] with the

TABLE XIV. Factors Shown to Play a Differential Role in Determining the Effectiveness of Individual Inoculant VAM Fungi

i)	Soil P status [89,204,205,218].
ii)	Ability to compete with other VAM fungi [11,49,52,177,194,227].
iii)	Temperature [52,203,209,221].
iv)	Adaption to soil [25,73,74,121,139,155,165,174,204,213].
v)	Adaption of fungus to host (or vice versa) [25,49,51,53,68,79,80,97,129,134,163].
vi)	Resistance to heavy metals [69,70].
vii)	Soil aeration [196].
viii)	Susceptibility to organisms parasitic on VAM fungi [18,132,194,207,217].
ix)	Ability to counteract the effects of pathogens of the host [18,54,55,202].

TABLE XV. Some Factors Which May Affect the Effectiveness of Individual Inoculant VAM Fungi

i)	Ability to stimulate uptake of nutrients other than P [4,43,44,97,126].
ii)	Ability to stimulate uptake of soil water [12,14,43,52,75,96,97,110,161,206,214].
iii)	Ability to produce plant growth regulators [21,43].
iv)	Dependency of host on VAM formation [15,24,26,31,76,87,94,128,134,140,149, 150,171,173] .

indigenous soil microbiota. However, if a soil's natural inoculum potential was low, for example, perhaps by precropping with a nonmycorrhizal species [but see 164] such as a brassica [66] and the indigenous VAM fungi were as effective as those in the inocula, inoculation would merely produce a transitory increase in infection level. The size of the growth response would then be determined by the length of the delay between germination and the establishment of good infections in uninoculated plants compared with inoculated ones.

Hall [89] has argued that where there have been relatively recent major changes to vegetation and soils perhaps it is to be expected that the indigenous VAM fungi may no longer be those which are best suited to the new conditions. But in VAM field and pot experiments in unsterile soil it is not even necessary to have to assume that this situation preexisted, as the soil conditions and/or host species were often changed at the start of the experiments. If these changes were relatively transitory—for example, the effects of a single application of lime on pH—then responses to inoculation might also be transitory. Indeed, some pot experiments on unsterile soil do appear to demonstrate that responses to inoculation decrease with time (Fig. 4) [47,89,186,198]. However, the sizes of the responses to inoculation Hall [89] and Powell and Daniel [186] detected at early harvests were very large (Fig. 4), while at later harvests the responses to inoculation fell to much more

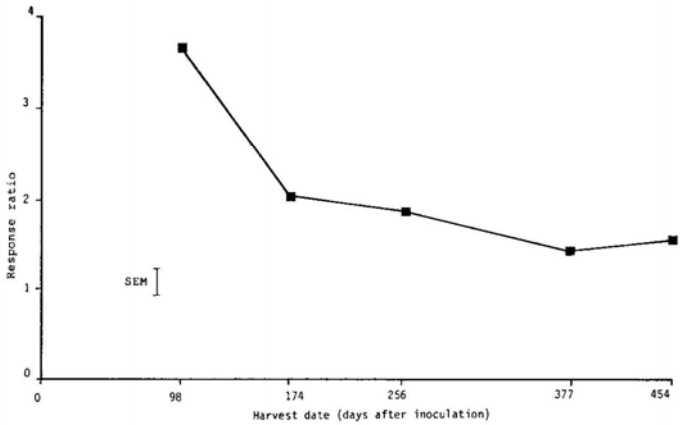

Fig. 4. VAM response ratios (means of eight different inocula and three levels of applied phosphorus—2.2, 6.6, and 19.8 mg P/pot) of Grasslands Huia white clover growing in unsterile phosphorus-deficient soil cores with five sequential harvests [from 89].

modest levels on a par with those later detected in the field [90]. Consequently, the extrapolation to the field of the fall in response to inoculation with time detected in pot experiments must be regarded as questionable. Furthermore in some of Hall's [90] (unpublished data) pastoral field experiments, responses to inoculation continued for more than 3 yr, which suggests that if there is likely to be a loss of response with time, in the field its onset is not rapid.

E. Failures of VAM Inocula to Produce Growth Responses

Within their experiments on poor soils, Rangeley et al. [188] (Table VIII) and Hall [90: experiments 1 and 2 in the second year] detected responses to inoculation only if phosphorus was applied. Indeed, in one of Rangeley et al.'s experiments, *Glomus etunicatum* Becker and Gerd. actually depressed growth unless 40 kg phosphorus/ha was also applied (Table IX). As both Hall's and Rangeley and colleagues' most effective fungi originated from relatively fertile soils, it is conceivable that their endophytes were not adapted to functioning symbiotically in soils with a very low phosphorus status. Early attempts to stimulate clover growth in the field by Hall (unpublished data) also failed because the isolate of *G. fasciculatum* used was no more effective than the indigenous fungi at a low level of available soil phosphorus. Jensen's [119] and Ross and Harper's [193] failure to detect

responses in unsterile soil could also have been because the inocula were either not effective or no more effective than the indigenous ones. Indeed, in both Jensen's and Ross and Harper's studies, the inocula contained fungi derived from the experimental sites, and apparently no attempt had been made to select for effectiveness. There are, however, many reasons—other than that the inoculant fungi were no more effective than the indigenous ones—that responses to inoculant fungi may not be detected. For example, Bolan et al. [29] and Pairunan et al. [169] detected little or no response to inoculation in subterranean clover at very low levels of available soil phosphorus as well as at very high levels. Similarly, Black and Tinker [28] (Table IV) probably failed to get a response to inoculation in their plus-phosphorus treatment because this raised the soil phosphorus status to a level where VAM had no beneficial effects (Fig. 1). Newbould and Rangeley [162] also failed to get a response to inoculation on a brown earth. But they had poor nodulation of their clovers, and as nitrogen was probably the principal factor limiting growth, it would have masked any beneficial effects a more effective VAM fungus may have had on plant phosphorus uptake.

III. SELECTION OF VAM FUNGI

An excellent discussion of the selection of VAM fungi for possible use in agriculture has been published by Abbott and Robson [3], and consequently I have tended to restrict my comments to those papers which have appeared since their paper was written in 1980.

The variations in VAM fungal effectiveness may be due to differences in the ratio of hyphae a fungus produces in the soil to the amount of mycelium in the root which supports it [3,74,200]. Abbott and Robson [6] also speculated that the distribution of hyphae in the soil and a number of other factors [4] may also be important. Whatever the reasons for these differences it is known that a variety of factors can or might modify the subsequent effectiveness of a VAM fungus and may have to be taken into account when selecting VAM fungi for a specific purpose. For example, pH can affect the germination of VAM fungal spores, hyphal growth, and the effectiveness of endophytes [7,58,79,81,106,122,135,208,219,224]. Other factors known to, or which might, have similar effects are listed in Table XIV and XV along with references to pertinent papers.

Govinda Rao et al. [72], Gianinazzi-Pearson et al. [67], Hall [89], Powell [180], and Schubert and Hayman [204], for example, have outlined procedures for comparing the effectiveness of VAM fungi. Govinda Rao and co-workers' [72] technique was designed specifically to select fungi for the pre-inoculation of transplanted crops raised in unsterile soils (section II.C).

Seedlings were first raised in unsterile nursery soils containing a normal complement of indigenous mycorrhizal fungi to which either VAM cultures on guinea grass (*Panicum maximum* Jacq.) or a similar amount of an uninfected grass root and soil mixture had been added. Once infections had developed, the seedlings were transplanted to experimental field plots and plant growth monitored. This technique follows precisely the procedures used by farmers in India and therefore cannot be criticized.

The selection of fungi using pre-inoculation transplant techniques, however, is probably of little value for normally field-sown crops and pastures as the ability of the fungi to survive in inocula suitable for field use has not been taken into account—a criticism which can also be made of the experiments of Gianinazzi-Pearson et al. [67], Hall [89], and Schubert and Hayman [204]. These experiments can also be faulted because fungi were screened in greenhouse pot experiments and consequently all the criticisms of pot experiments outlined in section I apply. Unfortunately Schubert and Hayman [204] also compared VAM effectiveness in sterile soil, which ignores the ability of the fungi to function with a competing soil flora. Gianinazzi-Pearson and co-workers' [67] techniques can also be criticized because they used sievings of field soils as the VAM inocula instead of pure cultures. They may therefore have estimated the confounded beneficial effects of the VAM fungi and deleterious components in the inocula [41,89,199]. Most of these faults are, however, avoided in the technique devised by Powell [180]. In this, VAM fungi were first isolated from unsterile soil by baiting [85,91] with sterile perennial ryegrass (*Lolium perenne* L.) seedlings. The seedlings were then transplanted into sterile soil, and the ability of the endophytes to stimulate growth was compared by weighing harvested herbage. Those fungi which stimulated growth most were then evaluated in several unsterile soils in a shadehouse and in the field. Unfortunately his field comparisons involved inappropriate pre-inoculated transplant techniques. However, in his shadehouse study, soils infested with *Glomus fasciculatum,* or the initial fungal selections or an uninfested control soil were each made into pellets containing two white clover seeds. These were then sown onto a number of unsterile soils in pots; and after 13 wk, plant growth was measured and the effects of the VAM fungi compared. This is an approach which has much to recommend it. The inoculant fungi were introduced into the soil in soil pellets which may have some practical value (section IV), and once the seedling has passed through the pellet the inoculant fungus has to compete with the indigenous VAM fungi and soil flora and fauna before establishing an infection.

It is conceivable that some fungi with potentially desirable characteristics such as a superior ability to persist in the soil [3] may have been discarded

during Powell's initial selection, but he has argued (personal communication) that this is a risk one might have to take to reduce the number of fungi being further assessed to a manageable level. The effectiveness of VAM fungi can vary with soil phosphorus level (Table II), and hence screening of VAM fungi should be conducted with several levels of applied phosphorus [e.g., 72,89] instead of the one level Powell used [180]. Powell's experiments could also have been extended to screen for ability to counteract the deterimental effects of pathogens and various other factors listed in Tables XIV and XV. Obviously experiments incorporating these additional factors would be very large and quite unmanageable unless confounded designs or resolvable balanced incomplete blocking designs were employed [40].

Daft and Hogarth [49] showed that inocula containing more than one endophyte gave more consistent results than those containing a single species. They therefore suggested mixtures of VAM fungi be used for field inoculations. But there would be no value in including a species in a mixed inoculum which had no redeeming features, and therefore screening would still have to be carried out to eliminate these. Moreover, as competition between VAM can occur [11,177,227] careful consideration would have to be given to the composition of mixed inocula to avoid the inclusion of one which might oust the others.

IV. INOCULA AND INOCULUM PRODUCTION

A number of pot investigations have shown that inoculant VAM fungi can spread through VAM fungus infested soil at 300 to >1,000 mm per year [11,159,177]. Also Jakobsen [115] has detected a rate of spread of 300 mm in 96 days through fumigated soil in the field. If similar rates of spread for inoculant VAM fungi can be demonstrated through unsterilized field soils, then it should be possible to reduce the amount of pelleted whole soil inoculum to just a few tens of kilograms per hectare [90]. However, lighter and possibly more potent inocula such as mass-produced spores [152] or those produced using the nutrient film technique [59,60,145,158], root organ cultures [37], in expanded clay [56] or peat cultures (Mosse, personal communication) [226] might prove more attractive than whole soil for field use.

In most field experiments conducted to date the inoculum was whole soil containing VAM spores, hyphae, and infected roots (see ref 145 for a review of pot culture methods for the production of inocula). In some cases it was pelletized using clay binding agents [90,95,103] which made it more convenient to apply, and by placing it in the seeding furrows, i.e., in the immediate vicinity of the seed, made it more effective than broadcast

inoculum [104]. VAM have also been successfully introduced into soils by inoculating seed or seedlings with fresh or lyophilized VAM fungal spores [64,100], fresh roots [e.g., 84,89], dried whole inocula [137], lyophilized roots [48], and by fluid-drilling soil sievings or homogenized spores, hyphae, and roots [57,63,104].

The first roots of VAM hosts which have relatively small seeds containing limited quantities of phosphorus are quickly infected by VAM fungi [e.g., 210]. However, species with relatively large seeds can contain considerable stores of phosphorus, which seems to make their seedling roots uninfectable and hence inoculation is more successful if the inoculum is placed a few centimeters below the seed (e.g., soybean, corn, sorghum [114]; peach [141]; citrus—Menge, personal communication).

Some VAM fungi can be adversely affected by other microorganisms (see Table XIV: viii for references), and obviously it is important that inocula should be free of such hyperparasites. But perhaps even more importantly it should be ensured that inocula produced for commercial purposes are free of oragnisms pathogenic to the host; and to achieve this it may be necessary to go to considerable lengths [145,150]. Commercially produced inocula must also maintain their integrity and not be subject to drift in their effectiveness [47] or to contamination with other, perhaps less desirable VAM fungi [3,85].

V. CONCLUSIONS AND FUTURE RESEARCH

Research funding bodies are often populated by individuals who are not scientists themselves but who have specialist skills in other directions. To extract money from these bodies against competition it is sometimes necessary to make a case outlining the most favorable outcome of a research program. Unfortunately, when this is written by an overenthusiastic researcher or similarly modified by a well-meaning head of a department, it can lead to more optimism than is really justified. I can think of one example at least where this has occurred and which resulted in a suggestion that farmers would be using VAM inocula by the end of the decade—a prediction made in 1977! The result was predictable: a loss of confidence in the research, a withdrawal of funding, and the collapse of the research program. Of the papers which have been published on VAM, those which deal with field applications are very much in the minority. Far more, however, expound the potentials for exploiting the symbiosis either in their introductions or discussions, and I believe that this too along with spectacular responses in greenhouse pot experiments has added to perhaps unjustified optimism.

A. Field-Sown Crops and Pastures

Whether VAM technology will ever be used in the production of field-sown crops and pastures will depend on the economics of employing it as compared with, for example, stimulating growth with fertilizers. But in past field experiments (see section II.A) the primary consideration was to gauge the effects inoculant fungi had on growth. Whether the method of inoculation was economically justifiable or had any agronomic value was of secondary interest. All that really mattered was that the host plant had as good a chance as possible of picking up the inoculant fungus and that the experiment did not founder for want of inoculum potential. The levels of inocula applied in the experiments were therefore very high, generally in the range 0.8 t/ha [111] to 25 t/ha [9] although 100 t/ha was used by Lambert and Cole [138], all of which were well beyond what could be considered practical. Consequently, before an economic appraisal of the value of inoculating field-sown crops and pastures with VAM inocula can be made, more information is needed on the minimum quantity of inocula that has to be applied and the most cost-effective way of producing it. Additional work is also required on identifying very effective endophytes, the soil/host combinations to which they are best suited, and how long responses to inoculation are likely to last. Of these, I think the most important is our inability to produce large quantities of cheap, reliable inocula, for without this, research on the effects of inoculating field-sown crops and pastures becomes little more than a stimulating academic exercise. Dehne and Backhaus's [56] technique of growing inocula inside expanded clay in pot cultures and the peat cultures of Warner et al. [226] appear to be suited to commercial use. However, I believe that the production of large quantities of inocula in pure axenic culture [107] is the only way that inocula will become cheap enough to be employed as rhizobial inocula are currently used in agriculture.

B. Transplanted Crops

From the work of Bagyaraj and co-workers (see section II.C) and, for example, the research on citrus (see section III.B) there can be little doubt that VAM inocula can produce worthwhile and economic growth responses for those transplanted species which are raised in unsterile or sterile soil in nurseries, are transplanted into relatively phosphorus-deficient soils, and where the cost of phosphatic fertilizers is a severe economic constraint. At the other extreme, where VAM have no detectable effects other than with the phosphorus nutrition of a crop and the cost of phosphatic fertilizer is negligible compared with the value of the crop [212], VAM can be ignored.

Between these two ends of the scale—where either the cost of fertilizer phosphorus is an important consideration or where VAM have some beneficial effect, other than with the phosphorus nutrition of a crop, which cannot otherwise be achieved cheaply—is an area where there is insufficient information at present to predict the future importance of VAM. Clearly this is an area which requires an additional research input.

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Biotechnology in Agriculture

Editor
Avshalom Mizrahi
Israel Institute for Biological Research
Ness Ziona, Israel

Alan R. Liss, Inc., New York

Appendix 6. Effects of fungicides on containerised plants in Finland.

Tarja Laatikainen Side effects of nursery fungicides on ectomycorrhiza of Scots pine seedlings. *In*: EUROSOIL 2004, September 04 to 12, Freiburg, Germany. www.bodenkunde2.uni-freiburg.de/eurosoil/abstracts/id771_Laatikainen.pdf

Abstract (abridged)

About 150 million forest tree seedlings are annually produced in Finnish forest nurseries. During last two decades container seedlings have extensively replaced barerooted seedlings. In containers seedlings are growing as dense moist mats, which is favourable to pathogenic fungi. Furthermore, in Finland seedlings are usually stored over winter outdoors under the snow cover, which allow some fungi, like scleroderris canker (*Gremmeniella abietina* Lagerb.), and snow blights, to spread from one container to another. Therefore, routine controls for fungal diseases with fungicides are considered to be a necessary forest nursery practice, and there is practically no seedling production in Finland without fungicide treatments.

Fungicides chlorothalonil and propiconazole have become common forest nursery practice for control of scleroderris canker and snow blights of conifers (e.g. *Phacidium infestans* P. Karst. and *Herpotrichia juniperi* Duby) during over winter cold storage. The repeated and long-term use of fungicides has raised the concern of the side effects of pesticides on soil microorganisms, especially on ectomycorrhizal infection of seedlings after outplanting.

In the preset study the side effects of the fungicides, chlorothalonil and propiconazole, on ectomycorrhizal fungi on Scots pine (*Pinus sylvestris* L. Karst.) seedlings have been evaluated both in laboratory and field experiments. Toxicity tests were performed with pure culture tests on agar petri dishes, where the fungal growth was measured as colony diameter, and in liquid pure cultures, where the growth was determined as mycelium biomass and ergosterol concentration. Fungicide effects on nutrient uptake and allocation by mycorrhizal fungi to symbiont seedling were studied both in allocation tests in pure cultures, and in laboratory microcosms with Scots pine seedlings inoculated with *Paxillus involutus* or *Hebeloma* cf. *longicaudum*, as well as, in a field experiment in a forest nursery.

Both chlorothalonil and propiconazole had a clear inhibitory effect on the growth of almost all tested mycorrhizal fungi. Allocation tests showed that ectomycorrhizal fungi have differential capability to take up ammonium, and propiconazole might influence on these processes depending on a species of ectomycorrhizal fungus. Propiconazole induced free amino acid arginine synthesis both in pure culture tests with *P. involutus* mycelium, and in shoot of inoculated Scots pine seedling. Noteworthy was the accumulation of arginine in samples both from non-mycorrhizal and mycorrhizal seedlings. Chlorothalonil caused growth reduction and a retarded frost hardening in forest nursery container seedlings. The effect can be seen still two years later as changes in concentrations of total nitrogen and total free amino acids. Results of this study may indicate a stress-related influence of both fungicides in Scot pine seedlings.