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Impact of Edapho-climatic Factors on the Dynamics of VAM Root Colonization and Spore Density in Three Forest Tree Species of Western Ghats, India

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ABSTRAK

Tinjauan telah dijalankan untuk menilai kepelbagaian kulat VAM yang disekutukan dengan tiga spesies pokok hutan eksotik, Eucalyptus grandis *Hill ex. Maid.,* Grevillea robusta *A. cunn dan* Tectona grandis *L. f. di ekosistem Ghat Barat, India Selatan. Contoh-contoh dikumpul daripada dua lokasi, Kodaikanal (1500 m A.S.L.) dan Siruvani (700 m A.S.L.) daripada Januari 1992 hingga Jun 1993. Faktor-faktor beriklim, harta kimia-psiko tanah rizosfera dan bilangan spota VAMF serta pengkolonian akar telah direkodkan. Pemencilan spesies adalah* Acaulospora, Gigaspora, Glomus, Sclerocystis *dan* Scutellospora *bersama* Glomus *menjadi 73% daripada jumlah spesies direkodkan. Densiti spora mikoriza adalah maksimum daripada Januari hingga Jun dalam semua contoh yang dikumpul melalui kesemua tiga spesies pokok pada kedua-dua bahagian. Pengkolonian akar yang tinggi direkodkan antara bulan September dan November. Bagi kedua-dua bahagian, densiti spota adalah berkaitan secara positif dengan suhu dan negatif dengan hujah dan lembapan tanah. Pembalikan direkodkan bagi pengkolonian akar. Wujud hubungan positif antara bilangan vesikal dan spora.*

ABSTRACT

A survey was carried out to evaluate the diversity of VAM fungi associated with three exotic forest tree species, Eucalyptus grandis *Hill ex. Maid,* Grevillea robusta *A. Cunn. and* Tectona grandis *L.f. in the Western Ghats ecosystem, South India. The samples were collected from two locations, Kodaikanal (1500 m A.S.L.) and Siruvani (700 m A.S.L.) from January 1992 to June 1993. Climatic factors, physico-chemical properties of rhizosphere soils and VAMF spore counts and root colonization were recorded. Species isolated were* Acaulospora, Gigaspora, Glomus, Sclerocystis *and* Scutellospora *with* Glomus *constituting 73% of the total species recorded. The mycorrhiza spore density was maximum from January to June in all samples collected from all three tree species at both sites. High root colonization was recorded between the months of September and November. In both sites, the spore density was positively correlated with temperature and negatively with rainfall and soil moisture. The reverse was recorded for root colonization. There was positive correlation between vesicle number and spore number.*

INTRODUCTION

A thorough understanding of the ecology of vesicular-arbuscular mycorrhizal (VAM) fungal species is needed to enable maximum manipulation of VAMF symbiosis for the benefit of minimum-input agricultural and forestry systems. Previous studies have assessed changes in total spore population under different ecosystems such as sand dunes (Koske and Halvorson 1981), tropical rain forest (Louis and Lim 1987), savannahs (Saif 1986). In nature VAMF multiply and survive by the formation of spores in and around the rhizosphere.

Spores of more than one species of VAMF may occur in the rhizosphere soil (Abbott and Robson 1977). The population composition and the activity of VAMF are affected by many factors; those affecting the symbiotic relationships between host and VAMF are well documented (Hayman and Tavares 1985). Inoculum and soil related factors are considered of primary importance. Other factors include the influence of soil pH (Hayman and Tavares 1985), soil moisture (Redhead 1975), soil fertility (Hayman 1982), organic matter (Hepper and Warner 1983), soil aeration (Saif 1981), soil clay content (Black and Tinker 1979), soil physical and chemical characteristics (Muthukumar *et al.* 1994), pesticides (Sugavanam *et al.* 1994; Udaiyan *et al.* 1995), season (Louis and Lim 1987) and biotic factors (Azcon-Aguilar and Barea 1985). The importance of these edaphic factors led Mosse (1972) to suggest that specificity may be strongly determined by interactions between fungal strain and soil rather than between fungus and its host plant. Changes in inoculum potential in soils have also been assessed using the 'most probable number' (MNP) techniques (Baltruschat and Dehne 1988). However, information on the number of VAM fungal species associated with respective tree species under natural ecosystems, and the influence of environmental factors on VAMF spore density, their distribution, establishment and survival over time is lacking. Such information is of prime importance in identifying and utilizing the most suitable mycorrhizal species for large-scale inoculation programmes. The present study was therefore conducted to (i) identify the mycorrhizal fungal species associated with three forest tree species from two different ecosystems in the Western Ghats, Tamil Nadu, India and (ii) evaluate the impact of edapho-climatic factors on the distribution and abundance of these fungi.

MATERIALS AND METHODS

Study Area

The study was conducted in plantation forests in Kodaikanal (Site 1) and Siruvani (Site 2) in the Western Ghats region. Kodaikanal is an offshoot of the Western Ghats located between 10° 12' and 10°15′ N latitude and 77°26′ and 77°38′ E longitude at an elevation of ca. 1500 m A.S.L. Siruvani is located at 76°37′ N latitude and 10°58′ E longitude at an elevation of ca. 700 m A.S.L. Soils at both sites were black loamy.

Climatic Data

Climatological data recorded from January 1992 to June 1993 included minimum and maximum temperature, relative humidity (RH) and rainfall (*Fig. 1* and *2*).

Sampling

Root and soil samples from three forest tree species, viz., *Eucalyptus grandis*, *Grevillea robusta* and *Tectona grandis* were collected at monthly intervals from January 1992 to June 1993. Five subsamples were collected from each species. The respective roots were carefully dug out, washed free of soil, cut into 1-cm sections, fixed in 50% formalic-acetic acid-ethanol (FAA). The rhizosphere soils from the respective tree species were mixed to form a composite soil sample, packed separately in polythene bags, and stored at 4°C for future analysis.

Analysis of Soil Physico-chemical Properties

Composite soil samples collected at monthly intervals were analysed for pH, total nitrogen, available phosphorus and potassium concentration. The total N and available P were determined respectively by the micro-Kjeldahl and molybdenum blue methods described by Jackson (1973). Exchangeable K was extracted from the soil in an ammonium acetate solution (pH 7) and measured with a digital flame photometer (Jackson 1973).

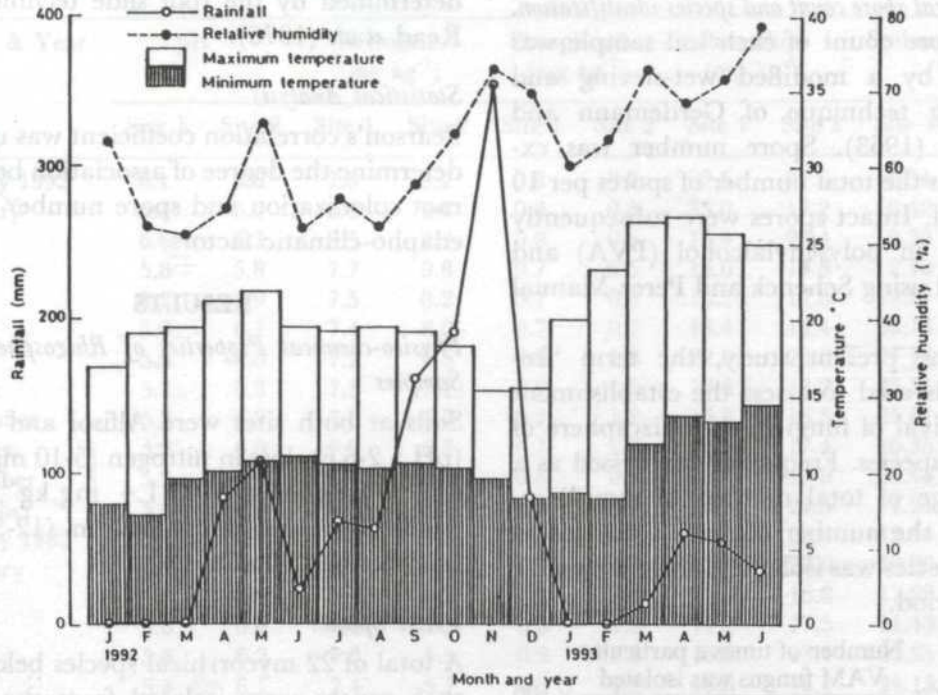

Fig. 1. Weather data at Kodaikanal (site 1) during the study period

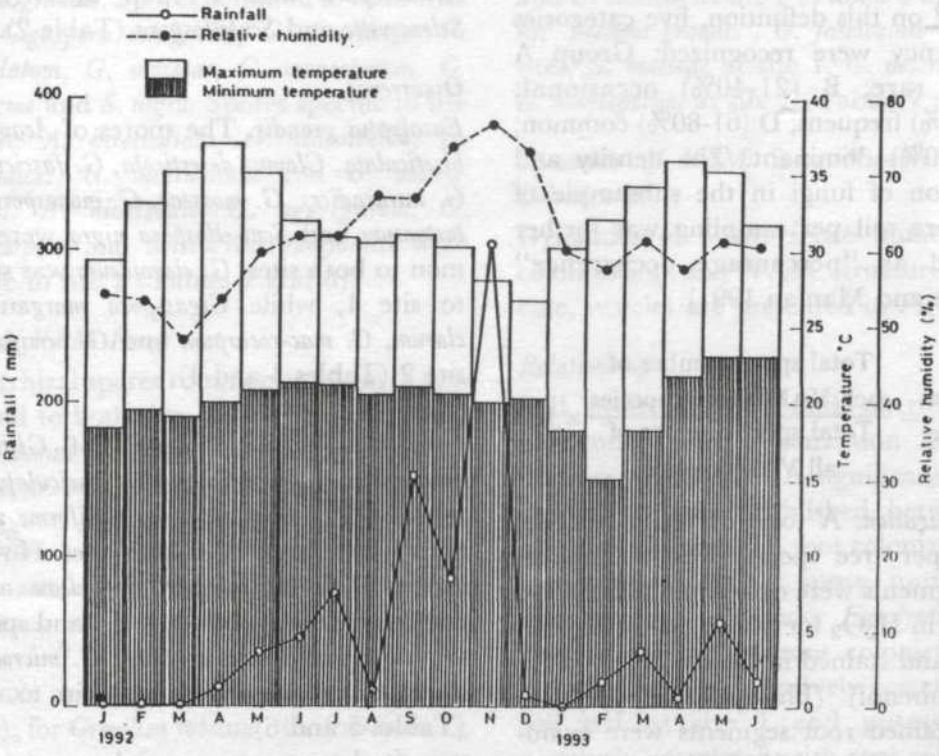

Fig. 2. Weather data at Siruvani (site 2) during the study period

Estimation of VAM

Mycorrhizal spore count and species identification. Total spore count of each soil sample was assessed by a modified wet-sieving and decanting technique of Gerdemann and Nicolson (1963). Spore number was expressed as the total number of spores per 10 g dry soil. Intact spores were subsequently mounted in polyvinylalcohol (PVA) and identified using Schenck and Perez Manual (1987).

In the present study, the term 'frequency' is used to assess the establishment and survival of fungi in the rhizosphere of the host species. Frequency, expressed as a percentage of total number of samplings, indicates the number of times a particular fungal species was isolated during the entire study period.

$$\text{Frequency} = \frac{\text{Number of times a particular VAM fungus was isolated}}{\text{Total number of samples observed (18)}} \times 100$$

Based on this definition, five categories of frequency were recognized: Group A (1-20%) rare; B (21-40%) occasional; C (41-60%) frequent; D (61-80%) common; E (81-100%) dominant. The density and distribution of fungi in the subsample of rhizosphere soil per sampling was further expressed as "percentage occurrence" (Udaiyan and Manian 1991).

$$\text{Percentage occurrence} = \frac{\text{Total spore number of each VAM fungus species}}{\text{Total spore number of all VAM species}} \times 100$$

Root colonization. A total of 100 1-cm root samples per tree species were examined. These segments were cleared in 10% KOH, bleached in H_2O_2 for 30 sec, acidified with 5N HCl and stained in trypan blue (0.05% in lactophenol) (Phillips and Hayman 1970). Stained root segments were examined for presence of VAM structures and the percentage of mycorrhizal infection determined by the root slide technique of Read *et al.* (1976).

Statistical Analysis

Pearson's correlation coefficient was used to determine the degree of association between root colonization and spore number to the edapho-climatic factors.

RESULTS

Physico-chemical Properties of Rhizosphere Soil Samples

Soils at both sites were Alfisol and acidic (pH 5.2-6.6), low in nitrogen (5-10 mg kg^{-1}) and phosphorus (0.5-1.4 mg.kg^{-1}) but medium to high in potassium (12-35 mg kg^{-1}) content (Table 1).

VAM Species

A total of 22 mycorrhizal species belonging to 5 genera were isolated from the study sites, of which 16 were *Glomus*, 3 were *Acaulospora* and 1 each of *Gigaspora*, *Sclerocystis* and *Scutellospora* (Table 2).

Occurrence

Eucalyptus grandis. The spores of *Acaulospora bireticulata, Glomus deserticola, G. fasciculatum, G. intraradices, G. mosseae, G. monosporum, G. tortuosum* and *Scut-ellospora nigra* were common to both sites. *G. claroideum* was specific to site 1, while *Gigas-pora margarita, G. clarum, G. mac-rocarpum* and *G. versiforme* to site 2 (Tables 3 and 4).

Grevillea robusta. Spores of *Gigaspora margarita, G. deserticola, G. fasciculatum, G. mosseae, G. monosporum, G. versiforme* and *S. nigra* were common to both sites. However, spores of *G. australe, G. claroideum* and *G. geosporum* were specific to site 1 and spores of *G. constrictum, G. invermaium, G. microcarpum* and *G. tortuosum* were specific to site 2 (Tables 5 and 6).

TABLE 1
Physico-chemical properties of rhizosphere soil samples from Kodaikanal (site 1) and Siruvani (site 2)

Month & Year	pH		Nitrogen (mg kg^{-1})		Phosphorus (mg kg^{-1})		Potassium (mg kg^{-1})		Soil moisture (%)	
	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
January 1992	6.1	5.6	7.8	9.2	0.8	0.9	32.5	27.6	11.34	12.50
February	6.3	6.2	8.0	9.6	0.8	0.8	35.0	17.2	10.42	10.41
March	6.6	6.3	8.5	9.7	0.9	0.6	15.4	23.4	9.25	8.31
April	5.8	5.8	7.7	9.8	0.7	0.5	13.0	14.5	12.48	8.34
May	5.2	5.9	7.5	8.2	0.7	0.8	15.2	12.8	19.27	17.78
June	5.9	6.1	7.4	8.0	0.7	0.7	13.4	13.4	26.15	20.18
July	5.6	6.0	7.2	6.5	0.9	1.0	22.0	25.0	24.13	23.15
August	5.7	6.3	7.3	7.1	0.8	1.1	17.5	18.2	25.51	19.48
September	5.3	6.2	7.3	8.2	0.7	1.2	15.3	16.5	25.81	19.40
October	5.2	6.0	7.0	6.3	0.7	1.0	16.5	17.4	26.35	23.50
November	5.2	6.6	6.8	9.6	0.6	0.6	17.4	17.8	26.48	27.38
December	5.4	5.8	7.2	8.2	0.5	0.5	20.5	21.5	11.21	7.00
January 1993	5.8	5.3	7.8	7.3	0.6	0.7	26.0	23.6	12.34	8.52
February	6.0	6.1	8.2	6.4	0.7	1.3	15.3	27.0	10.00	10.26
March	6.2	6.3	8.3	6.3	0.8	1.4	12.4	16.8	17.28	7.27
April	6.0	6.0	8.0	5.2	0.8	1.2	14.2	17.5	21.43	15.25
May	5.3	6.2	7.8	5.5	0.9	1.0	15.3	13.4	23.25	18.75
June	5.4	6.1	7.4	5.7	0.6	1.2	13.8	16.2	24.15	26.32

Tectona grandis. Spores common to both sites were *Gigaspora margarita*, *G. deserticola*, *G. fasciculatum*, *G. mosseae*, *G. monosporum*, *G. versiforme* and *S. nigra*. Spores specific to site 1 were *A. bireticulata*, *G. claroideum*, *G. intraradices*, *G. invermaium* and *G. macrocarpum*. *A. nicolsonii*, *G. aggregatum*, *G. macrocarpum* and *Sclerocystis rubiformis* were specific to site 2 (Tables 7 and 8).

Common VAM Fungi

Mycorrhizal spores common to all three species and to both sites were: *Gigaspora margarita*, *Glomus deserticola*, *G. fasciculatum*, *G. mosseae*, *G. monosporum* and *Scutellospora nigra*.

Abundance

Dominant mycorrhizal species, i.e. with a frequency of 81-100% were for *Eucalyptus grandis* : *G. monosporum* at site 1 and *G. deserticola* and *G. mosseae* at site 2 (Tables 3 and 4); for *Grevillea robusta* : *G. deserticola*, *G. fasciculatum* and *G. monosporum* at both sites and *G. mosseae* at site 2 (Tables 5 and 6) and for *Tectona grandis* : *G. fasciculatum* at both sites, *G. mosseae* at site 1, *G. deserticola* and *G. monosporum* at site 2 (Tables 7 and 8).

Dynamics of VAM Spore Number and Root Colonization

Dynamics of VAM spore numbers, root colonization and VAM structures (arbuscule, vesicle) are presented in *Fig. 3 - 8*.

Relationship

Soil moisture, pH and nutrient levels influenced root colonization and spore number (Table 10). A significant negative correlation was established between root colonization and pH, root colonization and nitrogen at site 1; spore number and nitrogen at site 2 under *Eucalyptus grandis*. In *Grevillea robusta*, root colonization was significantly and negatively correlated with soil pH at site 1 and potassium was positively correlated with root colonization

TABLE 2
Spore types recorded from the rhizosphere of *Eucalyptus grandis*, *Grevillea robusta* and *Tectona grandis*

Sl. No.	VAM Fungi	Code
1.	*Acaulospora bireticulata* Rothwell & Trappe	ABTR
2.	*A. nicolsoni* Walker, Read & Sanders	ANCS
3.	*A. scrobiculata* Trappe	ASCB
4.	*Gigaspora margarita* Becker & Hall	GMRG
5.	*Glomus aggregatum* Schenck & Smith	LAGR
6.	*G. australe* (Berck.) Berch.	LAST
7.	*G. claroideum* Schenck & Smith	LCRD
8.	*G. clarum* Nicolson & Schenck	LCLR
9.	*G. constrictum* Trappe	LCST
10.	*G. deserticola* Trappe, Bloss & Menge	LDST
11.	*G. fasciculatum* (Thaxter Sensu Gerd.) Gerd. & Trappe	LFSC
12.	*G. geosporum* (Nicol & Gerd.) Walker	LGSP
13.	*G. intraradices* Schenk & Smith	LINR
14.	*G. invermaium* Hall	LIVM
15.	*G. macrocarpum* Tul. & Tul.	LMCC
16.	*G. microcarpum* Tul. & Tul.	LMRC
17.	*G. mosseae* (Nicol. & Herd.) Gerd. & Trappe	LMSS
18.	*G. monosporum* Gerdemann & Trappe	LMNS
19.	*G. tortuosum* Schenk & Smith	LTRT
20.	*G. versiforme* (Karsten) Berch.	LVSF
21.	*Sclerocystis rubiformis* Gerdemann & Trappe	SRBF
22.	*Scutellospora nigra* (Redhead) Walker & Sanders	CNGR

and spore number at site 2. For *Tectona grandis* pH was significantly and positively correlated with spore number at site 1 and root colonization at site 2.

DISCUSSION

Spores of VAMF were observed in the rhizospheric soil of all tree species, with the highest count for *Grevillea robusta*. However, compared to the cropland system (Abbott and Robson 1977) the spore count was comparatively lower. The viable mycorrhizal fungi persist in roots of perennial plants and are the main source of inoculum for further infection of new roots. This may be the reason for low spore production of the mycorrhizal fungi in forest land (Baylis 1969). The presence of *Gigaspora margarita*, *Glomus deserticola*, *G. fasciculatum*, *G. mosseae*, *G. monosporum* and *Scutellospora nigra* in the rhizosphere of all tree species indicates their broad host range.

Although a variety of VAMF species has been recorded in the rhizosphere of tree species from both sites, the species composition and their density, distribution and survival varied from host to host. Schenck and Kinloch (1980) observed that the incidence of VAM fungal species depend upon the plant species colonized. This influence of host plant on the incidence of VAMF has also been observed by Kruckelmann (1975) on a site where 6 crops were grown in monoculture for 16 years. It appears that the host plant can affect sporulation, and possibly the survival of VAMF.

The variations in spore number and mycorrhizal colonization were similar at both sites, i.e. when spore numbers were high, the percentage of mycorrhizal colonization was low and vice versa. A similar

TABLE 3
Percentage occurrence and frequency of VAM fungi isolated from the rhizosphere of *Eucalyptus grandis* at site 1

Sl. No.	VAM Fungi	Percentage Occurrence																		Percentage Frequency	Frequency Class
		1992												1993							
		Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June		
1.	*Acaulospora bireticulata*	4.6	5.7	0.0	0.0	0.0	8.2	3.5	0.0	2.6	0.0	0.0	0.0	11.0	9.1	0.0	0.0	0.0	5.0	44	*Frequent*
2.	*Gigaspora margarita*	8.4	11.3	17.8	0.0	0.0	30.1	35.2	17.2	9.4	38.6	42.5	48.1	0.0	0.0	0.0	0.0	10.4	24.6	72	*Common*
3.	*Glomus claroideum*	3.4	0.0	5.3	7.6	7.4	0.0	0.0	0.0	11.1	4.5	0.0	0.0	13.7	6.4	20.4	15.1	3.4	0.0	61	*Common*
4.	*G. deserticola*	32.1	17.0	24.1	35.0	26.2	24.1	0.0	0.0	5.2	12.1	15.5	10.2	25.1	0.0	27.8	20.6	19.1	15.9	77	*Common*
5.	*G. fasciculatum*	0.0	9.1	38.4	23.1	22.4	0.0	16.6	14.7	8.3	22.1	12.9	9.2	18.1	21.3	0.0	0.0	0.0	18.2	77	*Common*
6.	*G. invermaium*	7.7	6.7	0.0	8.1	0.0	3.1	5.1	4.6	0.0	6.0	0.0	0.0	4.3	3.2	7.3	5.4	0.0	0.0	61	*Common*
7.	*G. mosseae*	18.4	14.7	10.9	19.8	0.0	0.0	7.5	21.1	6.6	0.0	9.8	18.1	10.8	10.5	0.0	0.0	19.0	9.2	77	*Common*
8.	*G. monosporum*	15.8	35.3	0.0	0.0	36.1	24.3	13.0	27.4	8.2	12.7	19.2	14.3	12.7	41.0	44.0	42.4	10.6	8.6	83	*Dominant*
9.	*G. tortuosum*	9.4	0.0	3.3	6.4	2.3	0.0	0.0	0.0	4.5	3.8	0.0	0.0	4.0	4.0	0.0	0.0	8.7	0.0	55	*Frequent*
10.	*Scutellospora nigra*	0.0	0.0	0.0	0.0	5.4	10.1	19.0	14.8	43.8	0.0	0.0	0.0	0.0	4.3	22.3	16.5	28.6	18.2	55	*Frequent*

TABLE 4

Percentage occurrence and frequency of VAM fungi isolated from the rhizosphere of *Eucalyptus grandis* at site 2

Sl. No.	VAM Fungi	Percentage Occurrence																		
		1992											1993						Percentage Frequency	Frequency Class
		Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June		
1.	*Acaulospora bireticulata*	6.2	5.5	0.0	0.0	0.0	6.2	4.0	2.8	6.0	0.0	0.0	0.0	10.5	7.5	0.0	0.0	0.0	2.5	50	*Frequent*
2.	*Gigaspora margarita*	15.6	17.8	15.1	4.5	8.5	0.0	0.0	10.8	22.7	18.1	42.6	58.8	42.7	59.2	9.1	0.0	0.0	41.2	77	*Common*
3.	*Glomus claroideum*	0.0	0.0	3.9	3.1	4.0	4.2	3.5	0.0	0.0	0.0	5.1	1.8	0.0	0.0	2.8	2.5	2.9	4.6	61	*common*
4.	*G. deserticola*	28.9	14.6	14.1	13.9	19.8	0.0	0.0	32.7	25.4	12.1	6.8	7.9	8.5	8.4	36.0	31.2	41.4	0.0	83	*Dominant*
5.	*G. fasciculatum*	10.1	23.3	22.6	0.0	0.0	9.3	19.4	9.4	12.0	30.2	8.5	7.3	0.0	3.0	11.6	6.6	13.7	8.4	88	*Dominant*
6.	*G. intraradices*	0.0	0.0	5.9	2.4	2.7	2.5	0.0	0.0	0.0	7.4	4.5	3.1	5.2	0.0	0.0	1.7	1.8	2.1	61	*Common*
7.	*G. macrocarpum*	10.1	2.8	3.3	2.6	4.3	0.0	3.7	2.8	2.1	5.1	0.0	0.0	6.5	2.8	3.2	0.0	0.0	0.0	66	*Common*
8.	*G. mosseae*	7.8	12.5	10.5	17.0	25.5	34.2	23.1	13.9	11.2	0.0	0.0	4.3	11.8	9.1	14.2	13.3	15.2	8.0	88	*Dominant*
9.	*G. monosporum*	9.4	12.0	8.8	30.8	16.4	17.3	0.0	0.0	13.3	12.1	13.1	6.7	14.5	9.8	6.4	18.7	0.0	0.0	77	*Common*
10.	*G. versiforme*	11.7	11.2	11.5	10.1	0.0	0.0	43.9	27.2	7.0	14.8	12.5	6.1	0.0	0.0	14.4	16.7	13.6	17.5	77	*Common*
11.	*Scutellospora nigra*	0.0	0.0	4.2	15.4	20.2	16.3	2.1	0.0	0.0	0.0	6.8	3.7	0.0	0.0	1.9	9.2	11.2	15.5	61	*Common*

TABLE 5

Percentage occurrence and frequency of VAM fungi isolated from the rhizosphere of *Grevillea robusta* at site 1

Sl. No.	VAM Fungi	Percentage Occurrence																		
		1992											1993						Percentage Frequency	
		Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June	Frequency	Class
1.	*Gigaspora margarita*	25.6	10.3	9.2	10.1	0.0	0.0	4.9	17.7	15.0	19.6	0.0	22.2	29.6	18.5	0.0	0.0	12.4	17.1	72	*Common*
2.	*Glomus australe*	4.5	4.7	0.0	5.3	6.1	2.2	0.0	0.0	2.5	0.0	0.0	9.9	3.0	4.2	0.0	0.0	3.6	3.3	61	*Common*
3.	*G. claroideum*	3.9	4.1	3.1	0.0	1.5	5.1	1.0	2.4	0.0	0.0	0.0	13.4	5.3	6.6	14.9	3.9	0.0	0.0	66	*Common*
4.	*G. deserticola*	20.3	16.9	31.9	9.6	25.5	0.0	0.0	31.2	15.0	13.4	52.4	0.0	10.7	13.7	39.8	13.3	13.8	22.9	83	*Dominant*
5.	*G. fasciculatum*	14.4	32.1	18.5	34.8	35.0	20.1	14.8	0.0	0.0	14.7	15.2	42.6	18.5	23.5	14.6	18.1	0.0	9.3	83	*Dominant*
6.	*G. geosporum*	6.4	5.1	0.0	5.5	1.6	6.4	7.3	2.2	9.7	0.0	0.0	0.0	3.2	2.1	0.0	4.1	12.5	4.3	72	*Common*
7.	*G. mosseae*	0.0	0.0	9.4	22.7	11.8	30.4	31.7	3.7	18.6	25.4	10.3	0.0	5.1	7.3	0.0	12.4	15.3	13.8	77	*Common*
8.	*G. monosporum*	18.2	20.1	12.6	7.6	12.3	19.3	0.0	0.0	11.3	12.0	22.0	11.7	8.8	10.2	11.9	19.4	0.0	5.2	83	*Dominant*
9.	*G. versiforme*	6.5	6.4	14.1	0.0	0.0	5.1	27.7	12.5	22.7	14.7	0.0	0.0	12.3	11.2	16.7	28.7	42.2	9.6	77	*Common*
10.	*Scutellospora nigra*	0.0	0.0	1.1	4.3	6.0	11.1	16.8	16.2	0.0	0.0	0.0	0.0	3.5	2.5	0.0	0.0	0.0	14.3	50	*Common*

TABLE 6
Percentage occurrence and frequency of VAM isolated from the rhizosphere of *Grevillea robusta* at site 2

Sl. No.	VAM Fungi	Percentage Occurrence																		
		1992												1993					Percentage Frequency	Frequency Class
		Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June		
1.	*Gigaspora margarita*	22.6	44.0	12.5	0.0	0.0	0.9	16.5	40.3	28.6	13.5	34.7	14.6	25.0	8.5	0.0	0.0	2.9	8.7	77	*Common*
2.	*Glomus constrictum*	0.0	0.0	3.1	3.8	1.7	1.7	2.9	0.9	0.0	0.0	1.4	1.8	3.9	7.9	1.8	2.1	0.0	0.0	66	*Common*
3.	*G. fasciculatum*	12.6	2.1	14.1	0.0	0.0	20.7	26.9	17.9	15.3	12.2	5.9	13.7	3.4	3.9	9.4	16.6	0.0	14.6	83	*Dominant*
4.	*G. invermaium*	2.8	1.6	1.2	0.9	2.6	0.0	0.0	1.3	1.3	1.7	1.9	0.0	0.0	0.0	4.4	2.6	1.6	2.1	72	*Common*
5.	*G. deserticola*	7.1	9.7	15.6	16.6	27.7	25.9	0.0	0.0	25.1	12.8	17.5	14.15	8.6	5.2	7.3	7.9	13.1	0.0	83	*Dominant*
6.	*G. microcarpum*	4.3	0.0	0.0	1.7	2.4	3.1	2.7	2.5	5.5	5.9	3.3	7.6	8.9	9.8	0.0	0.0	2.8	1.7	77	*Common*
7.	*G. mosseae*	36.0	10.4	8.5	10.7	11.4	13.8	13.8	0.0	0.0	8.7	17.5	34.5	9.8	8.5	19.1	14.3	22.4	0.0	83	*Dominant*
8.	*G. monosporum*	10.7	8.3	29.6	35.1	21.2	0.0	0.0	6.9	8.1	29.4	11.8	6.3	10.9	10.5	7.3	12.3	35.1	14.4	88	*Dominant*
9.	*G. versiforme*	0.0	0.0	11.2	18.5	21.8	18.2	24.1	22.4	11.5	12.9	0.0	0.0	15.9	19.1	25.3	0.0	0.0	46.9	66	*Common*
10.	*G. tortuosum*	1.3	2.0	0.0	0.0	1.4	1.8	3.2	1.7	1.3	0.0	1.0	1.3	2.2	6.6	0.0	2.7	8.2	0.0	72	*Common*
11.	*Scutellospora nigra*	0.0	0.0	4.1	12.4	9.6	13.5	10.0	4.5	1.9	0.0	0.0	1.3	3.6	4.6	25.3	41.3	13.7	9.8	77	*Common*

TABLE 7

Percentage occurrence and frequency of VAM fungi isolated from the rhizosphere of *Tectona grandis* at site 1

Sl. No.	VAM Fungi	Percentage Occurrence																		Percentage Frequency	Frequency Class
		1992												1993							
		Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June		
1.	*Acaulospora bireticulata*	7.5	10.6	0.0	0.0	5.6	3.6	8.8	0.0	0.0	0.0	0.0	0.0	9.4	13.8	0.0	0.0	9.5	8.8	50	*Frequent*
2.	*Gigaspora margarita*	20.8	28.5	22.7	11.1	0.0	0.0	11.7	8.1	8.8	20.0	0.0	0.0	7.3	6.8	13.3	47.7	0.0	13.7	72	*Common*
3.	*Glomus claroideum*	5.1	6.2	0.0	0.0	3.9	4.7	11.2	0.0	0.0	0.0	0.0	0.0	3.4	2.8	3.8	0.0	0.0	2.3	50	*Frequent*
4.	*G. deserticola*	11.7	8.3	10.7	14.6	25.2	0.0	0.0	12.8	0.0	0.0	38.8	54.1	5.9	10.8	28.9	4.6	0.0	5.9	72	*Common*
5.	*G. fasciculatum*	10.0	4.8	12.7	11.4	13.4	17.5	14.8	0.0	17.9	14.5	21.5	12.2	0.0	14.0	15.5	6.7	11.9	0.0	83	*Dominant*
6.	*G. intraradices*	0.0	0.0	4.8	2.5	8.8	5.0	6.2	9.3	29.9	8.6	0.0	0.0	6.9	4.2	5.9	9.4	0.0	5.6	73	*Common*
7.	*G. invermaium*	9.1	2.7	4.1	5.4	4.2	0.0	0.0	27.5	0.0	0.0	0.0	0.0	4.5	5.1	3.3	5.5	6.8	7.6	66	*Common*
8.	*G. mosseae*	14.9	16.4	9.9	24.5	16.7	32.3	5.7	0.0	11.3	9.8	19.0	22.4	33.6	0.0	0.0	4.2	18.0	4.8	83	*Dominant*
9.	*G. monosporum*	11.9	15.3	17.5	11.5	0.0	0.0	25.4	16.4	7.0	36.0	20.6	11.2	5.6	25.2	13.1	0.0	0.0	9.1	77	*Common*
10.	*G. versiforme*	0.0	0.0	9.1	12.6	8.7	14.6	11.7	9.6	10.9	10.9	0.0	0.0	7.1	9.6	6.2	6.8	31.6	28.5	77	*Common*
11.	*G. macrocarpum*	8.6	6.9	2.9	0.0	0.0	6.6	4.4	7.8	0.0	0.0	0.0	0.0	9.4	7.4	9.6	7.0	22.1	0.0	61	*Common*
12.	*Scutellospora nigra*	0.0	0.0	5.3	6.2	13.4	15.5	0.0	0.0	14.0	0.0	0.0	0.0	11.8	0.0	0.0	7.9	0.0	13.3	44	*Frequent*

TABLE 8
Percentage occurrence and frequency of VAM fungi isolated from the rhizophere of *Tectona grandis* at site 2

Sl. No.	VAM Fungi	Percentage Occurrence																	Percentage Frequency	Frequency Class
		1992											1993							
		Jan.	Feb.	Mar.	Apr.	May.	June	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June		
1.	*Acaulospora bireticulata*	7.1	3.4	2.8	1.3	3.8	0.0	0.0	0.0	3.4	1.9	3.6	0.0	4.0	8.4	7.8	3.9	3.0	0.0	72	*Common*
2.	*Gigaspora margarita*	12.5	17.9	43.5	0.0	0.0	4.9	19.0	33.1	29.4	19.9	27.7	14.0	14.1	22.2	0.0	0.0	8.4	15.3	77	*Common*
3.	*Glomus aggregatum*	0.0	0.0	2.3	2.8	3.2	2.8	3.2	0.0	0.0	0.0	2.3	7.4	0.0	0.0	6.7	2.6	2.0	1.4	61	*Common*
4.	*G. deserticola*	10.7	11.2	11.2	26.7	17.6	0.0	0.0	14.2	16.8	18.8	12.6	45.6	6.4	8.4	56.5	33.8	21.8	15.4	58	*Dominant*
5.	*G. fasciculatum*	11.6	32.0	14.3	18.9	25.3	11.1	24.1	14.7	0.0	0.0	3.6	8.8	33.5	17.8	19.9	13.3	25.8	22.8	88	*Dominant*
6.	*G. microcarpum*	0.0	0.0	2.8	3.2	2.2	2.4	4.7	0.0	2.4	1.9	2.8	0.0	0.0	0.0	3.1	1.8	1.2	1.4	66	*Common*
7.	*G. mosseae*	9.8	6.0	4.6	9.5	15.5	0.0	0.0	15.1	18.6	0.4	18.3	0.0	4.0	8.7	15.4	19.1	12.3	0.0	77	*Common*
8.	*G. monosporum*	24.1	6.7	6.5	7.6	8.2	14.6	0.0	0.0	23.9	31.2	18.8	16.2	41.7	8.7	0.0	0.0	13.3	14.5	88	*Dominant*
9.	*G. versiforme*	24.1	6.7	6.5	7.6	8.2	14.6	0.0	0.0	23.9	31.2	18.8	16.2	41.7	8.7	0.0	0.0	13.3	14.5	77	*Common*
10.	*Scutellospora nigra*	0.0	0.0	1.0	13.6	13.8	20.9	11.9	7.0	4.4	3.1	2.1	0.0	0.0	5.1	3.3	11.6	0.0	15.1	72	*Common*
11.	*Sclerocystis rubiformis*	11.6	4.3	0.9	0.0	0.0	0.0	1.8	1.4	1.1	2.7	1.1	0.0	10.1	7.0	2.0	0.0	0.0	0.0	61	*Common*

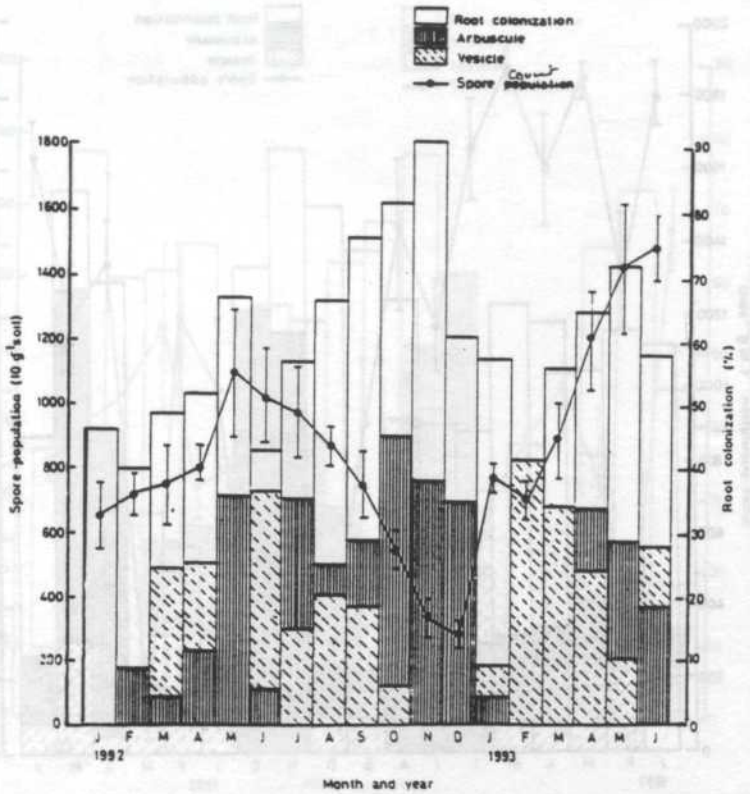

Fig. 3. Dynamics of the VAMF spore count and root colonization in Eucalyptus grandis *at site 1*

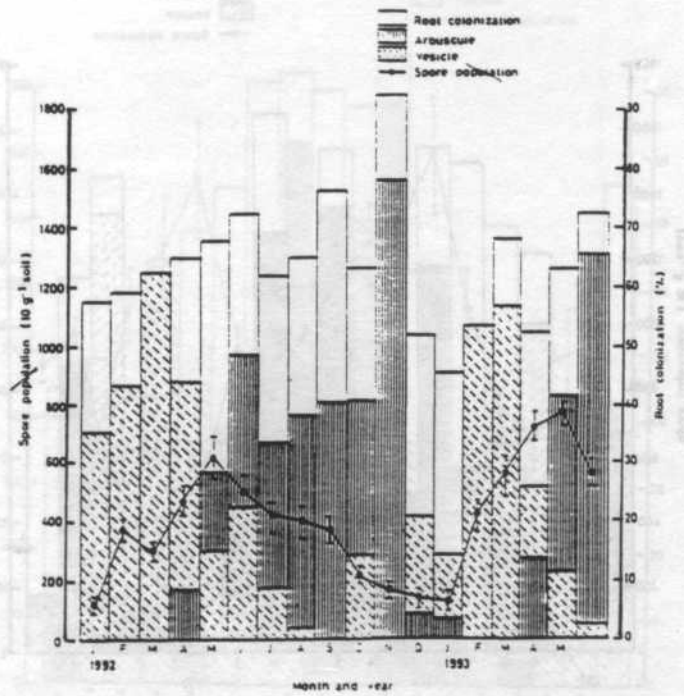

Fig. 4. Dynamics of the VAMF spore count and root colonization in Eucalyptus grandis *at site 2*

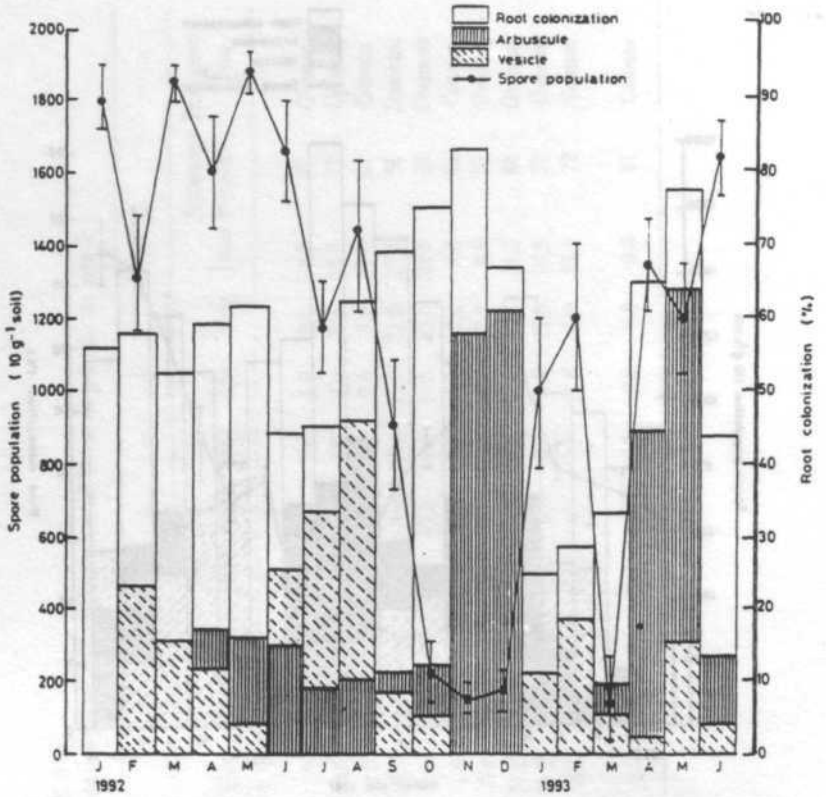

Fig. 5. Dynamics of the VAMF spore count and root colonization in Grevillea robusta *at site 1*

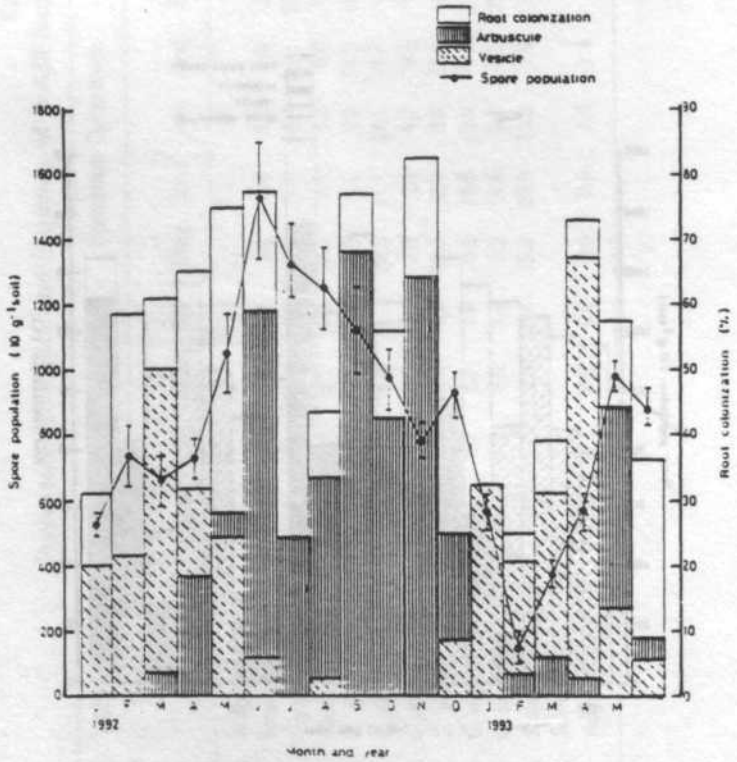

Fig. 6. Dynamics of the VAMF spore count and root colonization in Grevillea robusta *at site 2*

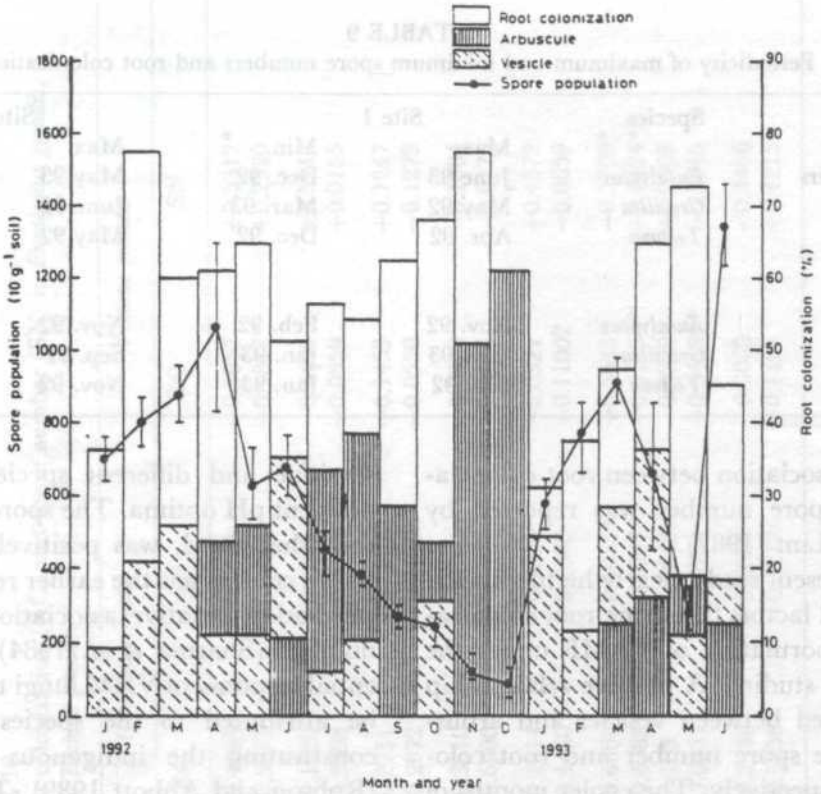

Fig. 7. Dynamics of the VAMF spore count and root colonization in Tectona grandis *at site 1*

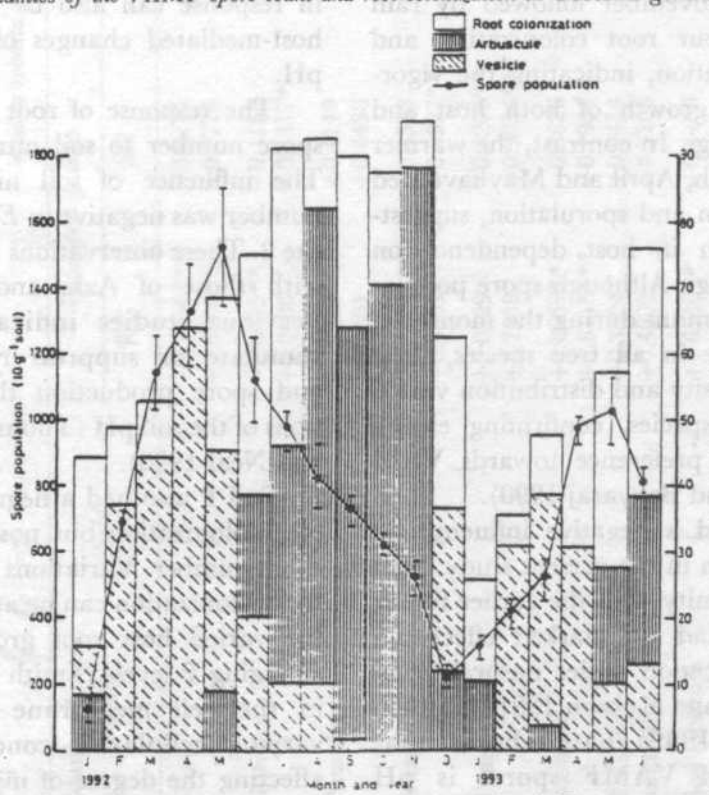

Fig. 8. Dynamics of the VAMF spore count and root colonization in Tectona grandis *at site 2*

TABLE 9
Periodicity of maximum and minimum spore numbers and root colonization

Parameters	Species	Site 1		Site 2	
		Max.	Min.	Max.	Min.
Spore numbers	*Eucalyptus*	June 93	Dec. 92	May 93	Jan. 92
	Grevillea	May 92	Mar. 93	June 92	Feb. 93
	Tectona	Apr. 92	Dec. 92	May 92	Jan. 92
Root colonization					
	Eucalyptus	Nov. 92	Feb. 92	Nov. 92	Jan. 93
	Grevillea	May 93	Jan. 93	Sep. 92	Feb. 93
	Tectona	Feb. 92	Jan. 93	Nov. 92	Jan. 93

negative association between root colonization and spore number was reported by Louis and Lim (1987).

The present study clearly highlights the periods and factors favouring root colonization and sporulation of VAMF under the tree species studied. A positive relationship was observed between vesicles and arbuscules to the spore number and root colonization respectively. The cooler months of September – November followed by rain seemed to favour root colonization and arbuscule formation, indicating the vigorous vegetative growth of both host and mycorrhizal fungi. In contrast, the warmer months of March, April and May favoured vesicle formation and sporulation, suggesting a reduction in host dependence on mycorrhizal fungi. Although spore populations were maximum during the months of January – June in all tree species, their occurrence, density and distribution varied with the host species, confirming earlier reports of host preference towards VAM fungi (Reena and Bagyaraj 1990).

Soil pH had a negative influence on root colonization in the present study. This is not in conformity with the earlier report that soil pH had no marked effects on mycorrhizal infection under natural vegetation (Abbott and Robson 1991). Robson and Abbott (1989) have shown that germination of VAMF spores is pH sensitive and different species may have different pH optima. The spore number, on the other hand, was positively correlated, which contradicts the earlier report that soil pH had a negative association with spore number (Sharma *et al.* 1984). The differential response of VAM fungi to soil pH can be attributed to the species and strains constituting the indigenous VAM flora (Robson and Abbott 1989). The variation in response can also be attributed to the host-mediated changes of the rhizosphere pH.

The response of root colonization and spore number to soil nitrogen also varies. The influence of soil nitrogen on spore number was negative in *Eucalyptus grandis* at site 2. These observations are in accordance with those of Aziz and Habte (1989). Previous studies indicate that N can stimulate or suppress root colonization and spore production through modifications of the soil pH (Thompson 1986; Sylvia and Neal 1990).

Soil P also had a negative influence on root colonization but positively influenced spore number. Variations in the response of root colonization can be attributed either to the varied host root growth response to changing P levels (Smith 1982) or changes in the cell membrane permeability of varying cellular P concentrations, thus affecting the degree of mycorrhizal coloni-

TABLE 10
Correlation matrix between edapho-climatic factors, mycorrhizal root colonization (RC) and spore number (SN) in *Eucalyptus grandis*, *Grevillea robusta* and *Tectona grandis*

Edapho-climatic Factors	Site	*Eucalyptus grandis*		*Grevillea robusta*		*Tectona grandis*	
		RC	SN	RC	SN	RC	SN
pH	1	−0.7664***	−0.0216	−0.4695*	+0.3454	−0.3057	+0.5312*
	2	+0.6906**	+0.2726	+0.3971	+0.1498	+0.4817*	+0.2320
Nitrogen	1	−0.6675**	−0.1188	−0.1020	+0.1023	−0.3449	+0.3413
	2	+0.2486	−0.5317*	+0.3398	+0.0069	+0.0859	+0.0155
Phosphorus	1	−0.2231	+0.4149	−0.3751	−0.3852	+0.1453	+0.1247
	2	−0.0101	+0.4430	−0.2972	−0.2123	−0.0550	−0.1279
Potassium	1	−0.3221	−0.3303	−0.3610	+0.0762	−0.0870	−0.1004
	2	−0.4869*	−0.5927**	−0.6900**	−0.4474	−0.3376	−0.6176
Temperature	1	+0.0329	+0.8205**	−0.1611	+0.1690	−0.0321	+0.4572
	2	+0.2558	+0.9054***	+0.4460	+0.2088	+0.11002	−0.0659
Rainfall	1	+0.8659**	−0.3826	+0.6869**	−0.5055*	+0.5633*	−0.5709*
	2	+0.8115***	−0.1934	+0.4783	+0.2097	+0.6105**	+0.8424**
Relative humidity	1	+0.3824	+0.2414	+0.103	−0.3642	−0.0299	+0.0508
	2	+0.4202	−0.3265	+0.0877	+0.3764	+0.6438**	−0.3545
Soil moisture	1	+0.6716**	+0.3160	+0.2438	−0.2036	0.3069	−0.3466
	2	−0.2161	+0.2318	+0.1256	+0.3212	−0.1361	+0.4215

*,** and *** significant $P < 0.05$, 0.01 and 0.001 respectively

zation (Ratnayake *et al.* 1978). It has also been established that soil P can reduce infections by directly inhibiting the external hyphal growth (Sanders 1975).

The role of K in root colonization and spore number of VAMF is little known compared to P and N. Potassium has previously been reported to have no effect on VAMF (Daniels and Trappe 1980), but K positively influenced spore number in all the plants at site 2 and negatively influenced root colonization in *Eucalyptus* and *Grevillea* at site 2.

Fluctuations in temperature can affect both root growth and survival and infectivity of the mycorrhizal fungi. In the present study temperature had a positive influence on *Eucalyptus*. Previous workers have shown that temperature may influence VAMF spore germination, root colonization and spore production (Tommerup 1983). The spore number was positively related to temperature in *Eucalyptus* at sites with different temperature ranges (23-30°C and 13-21°C). The occurrence of certain species common to both sites for this species indicates that the VAMF species may have multiple optimum temperatures for sporulation. Similar multiple optimum temperatures for colonization have been reported for isolates of VAMF by Schenck and Smith (1982).

The relative humidity was negatively correlated with spore number and positively with root colonization. This emphasizes that the environmental factors can strongly influence VAM fungal infection (Hayman 1974).

Percentage of root colonization was positively correlated to soil moisture which is one of the factors that determine plant growth in natural soils. An adequate moisture for plant growth may favour mycorrhizal formation due to an increase in host nutrient demand. Soil moisture optimum for plant growth has also been reported to be suitable for VAM colonization and sporulation (Redhead 1975).

CONCLUSION

The findings of this study emphasize the need for an understanding of the ecology of VAM fungi in various agroclimatic zones for the successful selection and introduction of VAM fungal species for a particular agroclimate.

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