THE DISTRIBUTION OF GLOMEROMYCOTA IN CACAO RHIZOSPHERE IN INDONESIA

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ABSTRACT

KRAMADIBRATA, K. 2009. The distribution of *Glomeromycota* in cacao rhizosphere in Indonesia. *Reinwardtia* 12(5): 347–356. — A study on the distribution of *Glomeromycota* (AF) in cacao soils in several cacao plantations in Java and Bali showed that *Acaulospora walkeri* as a dominant species and *A. scrobiculata* as a predominant species.

Key words: Glomeromycota, cacao, Java and Bali.

ABSTRAK

KRAMADIBRATA, K. 2009. Persebaran *Glomeromycota* pada rizosfer kakao di Indonesia. *Reinwardtia* 12(5): 347–356. — Disajikan persebaran *Glomeromycota* (JA) pada beberapa perkebunan kakao di Jawa dan Bali. Jenis *Acaulospora walkeri* merupakan jenis yang dominan disusul oleh *A. scrobiculata*.

Kata kunci: Glomeromycota, kakao, Jawa dan Bali.

INTRODUCTION

Studies on Glomeromycota or arbuscular mycorrhiza fungi (AF) in agricultural soils and soils under natural vegetation in the tropical areas are relatively scarce, and only in some areas they are fairly well documented, such as in Brazil, Colombia, and Peru (Schenck et al., 1984; Schenck et al., 1986); Costa Rica, Mexico, and Panama (Janos & Trappe, 1982); Cuba (Ferrer & Herrera, 1981); India (Gerdemann & Bakshi, 1976; Bhattacharjee & Mukerji, 1980; Bhattacharjee et al., 1982; Mukerji et al., 1983); Indonesia (Widiastuti & Kramadibrata, 1992 & 1993; Kramadibrata et al., 1995; Setya et al., 1995; Silviana et al., 1999; Chairani et al., 2002; Muliawan et al., 2002, and Kramadibrata & Gunawan, 2006), Malaysia (Wastie, 1965; Nadarajah, 1980; Chulan & Ragu, 1986); Pakistan (Iqbal & Bushra, 1980); Phillipines (Baradas & Halos, 1980); Taiwan (Wu & Chen, 1986). Boedijn (1935) did describe Endogone tjibodensis from natural vegetation in West Java, a taxon later redefined by Gerdemann & Trappe (1974) as Glomus vesiculiferum. Boedijn (1935) did not define the mycorrhizal status of this species and until the 1980's the existence of these Indonesian studies remained unknown. Furthermore, detailed studies of Glomeromycota in soils under cacao plantation in Indonesia have not been carried out.

The aim of this study is to investigate the dis-

tribution of *Glomeromycota* in cacao rhizosphere throughout Java and Bali.

MATERIALS AND METHODS

Field sampling of soils under cacao plantation

About 2–4 kg of soil was taken from around each cacao trees. The soil was a combination of four sub-samples which were taken from four points at 0–15 cm depth, 40–50 cm from the tree trunk, using a small trowel.

Ten plantations in Java and one in Bali were selected (Table 1). Each plantation was divided into plots on the basis of the ages of trees, or topographical variations of the sites. Table 2 shows the abiotic factors in sampling sites. A cacao tree in the centre of each plot was selected.

Extraction of spores from soil samples

Spores were extracted from soil samples by use of a series of sieves (Gerdemann & Nicolson, 1963), following a modification of the technique of centrifugation (Walker *et al.*, 1982 and Gerdemann & Nicolson, 1963).

Taxa of *Glomeromycota* (AF) recovered from soil samples from Java and Bali

Table 3 presents a list of the taxa for which spores were recovered during sampling in 1987 for reasonably certain identification was possible.

Table 1. Origin of soil samples, no of soil samples and age of plant

Location	Site no	Site name	No of soil	Age of cacao plant	Remarks
***		WW DI	samples	4.5.0.10.11	37 1
West Java	1	XII Plantation State Company, Rajamandala, Cianjur	4	4, 7, 8 and 9 year old trees	No ground cover
	2	Batugajah Section, XIII Plantation State Company, Batulawang, Banjar	8	3, 4, 5 and five of 7 year old trees	No ground cover
	3	Putrapingan Section, XIII Plantation State Company, Batulawang, Banjar	12	two of 5, two of 6, 7, three of 8, 11, 12, 13 and 14 year old trees	No ground cover
	4	Pangandaran Section, XIII Plantation State Company, Batulawang, Banjar	8	2, 3, 6, four of 7 and 9 year old trees	
Central Java	5	Beji Barat Section, XVIII Plantation State Company, Beji, Jepara	5	14, 15, 16, 21 and 24 year old trees	No ground cover
	6	Beji Tengah Section, XVIII Plantation State Company, Beji, Jepara	12	1, 1.5, 2, 7, 8, 13, 15, 25, 27, 28, 30 and 31 year old trees	No ground cover
	7	Beji Timur Section, XVIII Plantation State Company, Beji, Jepara	6	3, 5, 6, 10, 29 and 30 year old trees	No ground cover
East Java	8	Kaliwining Experimental Station, Jember Plantation Research Centre, Jember	7	1.5, 2, 4, 9, 10 15 and 31 year old trees	No ground cover
	9	Small farm, Pancursari village, Malang	2	3 and 14 year old trees	No ground cover
	10	Small farm, Peniwen village, Malang.	2	Both 7 year old trees	No ground cover
Bali	11	Local Government Enterprise, Puluhan Plantation, Pekutatan, Jembrana	3	1 year 3 months, 1.5 and 4 year old trees	Mixed with banana, clove, coconut and cardamom

Table 2. Abiotic factors in sampling sites in Java and Bali

Location	Site	Site name	Soil pH ^a	Organic	Type of	Rainfall mm/yr	Altitude
	no			matter	soil		(metres)
				content +			
				(%)			
West Java	1	Rajamandala	5.3 (4.5-6.0)	7.20	Volcanic	> 3,000 (A)	<u>+</u> 300
	2	Batugajah	5.2 (4.5-6.1)	8.79	Volcanic*	> 3,000 (A)	<u>+</u> 300
	3	Pangandaran	5.8 (5.2-6.2)	5.96	Volcanic*	> 3,000 (A)	0-20
	4	Putrapinggan	5.8 (4.6-6.9)	7.40	Volcanic*	> 3,000 (A)	<u>+</u> 300
Central	5	Beji Barat	5.2 (4.6-5.8)	6.71	Volcanic*	2,000 (D)	0-20
Java		-					
	6	Beji Tengah	5.6 (4.9-6.0)	6.16	Volcanic*	2,000 (D)	0-20
	7	Beji Timur	5.6 (5.2-6.0)	6.97	Volcanic*	2,000 (D)	0-20
East Java	8	Kaliwining	5.3 (4.6-6.4)	8.96	Volcanic	2,000 (D)	<u>+</u> 45
	9	Pancursari	5.6	10.39	Volcanic	2,500-3,000 (B-C)	+ 400
	10	Peniwen	5.8 (5.6-6.1)	4.07	Volcanic	2,500-3,000 (B-C)	+ 400
Bali	11	Jembrana	6.0 (5-5-6.3)	6.86	Volcanic*	nd	<u>+</u> 45

Notes :

^a Mean pH with range indicated in parantheses

nd = no data

Organic matter content (%), only sample for each site was determined

^{*} Have significant recent volcanic material. According to the USDA classification most soils were Ultisols rather than Andisols. Analyses of soils were carried out by Dr. W Adams from Soil Science Unit, Dept of Biochemistry, Aberystwyth University.

Table 3. List of *Glomeromycota* taxa recovered from cacao soils in Java and Bali

No	Glomeromycota taxa	Abbreviation
		of taxa use in
		Figures 1, 2, 3
		and 4
1	Acaulospora foveata	Af
2	A. rehmii	Ar
3	A. scrobiculata	As
4	A. tuberculata	At
5	A. walkeri	Aw
6	Gigaspora gigantean	Gig
7	Glomus aggregatum	Gag
8	G. albidum	Gal
9	G. diaphanum	Gdi
10	G. fasciculatum	Gfa
11	G. fuegianum	Gfu
12	G. invermaium	Gin
13	G. microaggreagtum	Gmi
14	G. multicaulis	Gmu
15	Paraglomus occultum	Poc
16	Scutellospora fulgida	Sfu
17	S. pellucida	Spe
18	Glomus rubiforme ex	Gru
	Sclerocystis pachycauluis	
19	G. sinuosum ex S. sinuosa	Gsi

Analysis of populations of *Glomeromycota* (AF) taxa present in sampling sites in Java and Bali

The methods of Koske (1987) were used to analyze the assemblages of spore types in each of the soil samples examined, to compare sites distributed throughout Java and Bali. For each sample examined and for each of the eleven sites the following calculations were made:

- 1. Species richness. It was used to determine whether there were differences in AF species diversity between samples taken at the same cacao sites as well as differences between sites distributed throughout Java and Bali. It was simply defined as the number of AF taxa recovered from each sample. Koske (1987) in his study of sand dune systems in eastern parts of the United States defines species richness of 'root zones' of Ammophila and other plants. However in the present study it was not possible to assign spores specifically to cacao root systems in all instances, although in most plantations few weed species occurred and it was highly probable that the taxa isolated were associated with the cacao root zone.
- 2. **Frequency of occurrence**. Koske (1987) used the percentage of samples from which particular taxa were recovered as an expression of their relative abundance. In the present study the total number of samples per site containing a taxon was divided by the overall number of samples per site

- to derive a percentage frequency of occurrence. The numbers of samples per site varied between 2 and 12 (see Table 1), which obviously affected the range of data points that could be derived.
- 3. **Population density**. Koske (1987) used the term 'density' to describe number of spores per 100 cm³ of soil. Here population density has been used to describe numbers of spores of AF per 1 kg fresh weight soil (1 kg of soil *ca*. 500 cm³ of soil) calculated from direct counts of samples. Data from samples for each site were averaged to give a site value.
- 4. **Spore biovolume**. Koske (1987) derived this concept from Dickman *et al.* (1984) in order to compensate for the differences in size between spores of AF species, pointing out that frequency of occurrence may not accurately reflect the inoculum potential of different species, since large spores have a capacity for multiple germination and are therefore more effective as inoculums than small spores (Koske, 1981). Spore biovolume was calculated by measuring the diameter of 10–50 spores for each taxon and then multiplying the average volume, calculated by 4/3 Πr³, by the average population density of a species at the site. Results were expressed per 1 kg fresh weight of soil (1 kg of soil *ca.* 500 cm³ of soil).
- 5. **Dominance index**. Koske (1987) derived this term from Southwood's 1968 description of dominance in ecosystems, in an attempt to determine the dominance of AF spore type in AF population of a soil sample in terms of its total volume, rather than numbers, as given by percentage frequency. Dominance for each site is expressed as the ratio between the biovolume of the species with greatest spore biovolume (biovolume max) and the overall biovolume of AF spores at that site (biovolume total).

D= Biovolume max
Biovolume total

6. Importance value. Koske (1987) adopted this terminology from Mueller-Dombois & Ellenberg (1974), who used it to describe the importance of a plant species in a community in terms of a summation of its relative frequency, relative population density and relative dominance, since in plant ecology this is measured as population density and basal area, *i.e.* the approximate 'volume' of the ecosystem filled by the plant species. The maximum values for each of the three components are 100 (100% frequency of occurrence of a species; 100% of the spore population the same species; 100% of the biovolume one species) giving a maximum IV of 300. Figures were thus calculated per site as follows:

Table 4. Species richness of AF spores in cacao soils in Java and Bali

Location	Site	Site name	Range of species	Average species	No of samples taken
	no		richness per sample	richness per sample	from each site
West Java	1	Rajamandala	7-10	9.00 ± 1.22	4
	2	Batugajah	3-9	5.75 ± 1.38	8
	3	Pangandaran	3-9	3.75 ± 1.29	8
	4	Putra pinggan	3-8	5.25 ± 1.59	12
Central Java	5	Beji Barat	4-8	4.80 ± 1.60	5
	6	Beji Tengah	3-9	4.16 ± 1.57	12
	7	Beji Timur	4-6	4.33 ± 0.47	6
East Java	8	Kaliwining	1-4	2.42 ± 1.05	7
	9	Pancursari	6-8	7.00 ± 1.00	2
	10	Peniwen	4-9	6.50 ± 2.50	2
Bali	11	Jembrana	5-8	6.33 ± 1.24	3

RESULTS

1. Species richness

The species richness found during the survey ranged between 1–10 for individual samples. The variation in species numbers for each site is shown in Table 4 together with average species richness for each of the sites in Java and Bali (see Figure 1). The variation in numbers of samples taken for each site seems to have little effect on the overall result of the species richness analysis. For example, in site 10 (Peniwen), East Java where only two samples were taken an average species richness of 6.50 ± 2.5 (range 4–9) was found, as against site 4 (Putrapinggan), West Java where 12 samples had an average species richness of $5.25 \pm$ 1.59 (range 3-8). However, some sites were definitely species poor, especially site 8 (Kaliwining), East Java with an average species richness of 2.42 ± 1.05 (range 1-4) based on 7 samples, whereas others are clearly species rich, for example site 1 (Rajamandala), West Java, with an average index of 9.00 ± 1.22 (range 7–10) based on 4 samples.

2. **Frequency of occurrence** (Figure 1).

The results of this analysis are shown in Fi-

gure 1 where the average values for each of the 2 species considered are shown as incrementally shaded squares, each increment being equivalent to a 20% increase in the value of the frequency of occurrence. The figure shows that the taxon Acaulospora walkeri was present throughout Java and Bali at an overall average frequency of 98%. A. scrobiculata (93% overall average) was only slightly less frequent. However an examination of figure 1 indicates that frequency of occurrence of some taxa did vary with the geographical location of the sites. West Java (sites 1-4) shows high frequencies for A. foveata (73% average) and Glomus fuegianum (50% average). Central Java (sites 5–7) was characterized by a high frequency of G. occultum (91% average). G. multicaulis and Gigaspora gigantea, with overall averages of 55% and 50% respectively, seemed to be most abundant in East Java (sites 8-10). The Bali site (11) was distinguished by a high frequency of A. tuberculata (100%) and G. sinuosum (67%).

Other taxa had lower frequencies of occurrence but a distribution pattern seems to emerge from the data presented in Figure 1 for *G. microaggregatum* and *G. rubiforme* which were found in West and Central Java. Other taxa seemed to be randomly distributed.

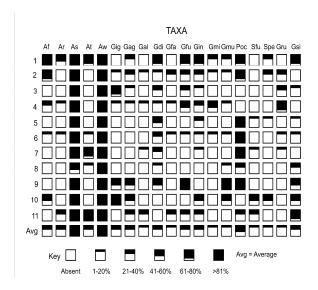


Figure 1. Frequency of occurrence of AF in Java and Bali. Key to sites is given in Table 2 and the full list of species is given in Table 3.

3. **Spore population density** (Figure 2).

Figure 2 shows spore population density for 19 of the AF spore types for the 11 sampling sites, using shading to illustrate numbers/kg fresh weight soil in increments of 20 up to 80 or more. The taxa showing the highest frequency of occurrence A. walkeri and A scrobiculata also had the highest spore populations (compare Figures 1 and 2). A. walkeri averaged of 440 spores per kg soil for all eleven sites, whilst A. scrobiculata averaged at 102.7 spores per kg. A. walkeri was very abundant at site 9 (Pancursari), East Java at 1278 spores/kg, at site 2 (Batugajah), West Java at 1015.7 spores/kg and at site 4 (Putrapinggan), West Java at 1204.5 spores/kg. A. scrobiculata was most abundant at Rajamandala (site 1), West Java at 693.6 spores/kg.

Figure 2 shows that spores of most other taxa were present but in much lower numbers, mostly in the range 1-20 spores per kg soil with the exception of Paraglomus occultum at sites 1 (Rajamandala) and 2 (Batugajah) in West Java and 9 (Pancursari) in East Java, and all sites in Central Java. Some taxa were only found as 11 spores in 1 subsample for some sites, giving a spore population of less than 1 per kg for the site. They do appear in the figure as spores per kg soil, for example, A. rehmii at site 6 (Beji Tengah, Central Java), G. diaphanum, G. albidum and G. gigantea in site 4 (Putrapinggan) in West Java and G. invermaium in site 6 (Beji Tengah) in Central Java. Clearly these taxa are widely distributed but their spore populations are low.

A comparison of Figures 1 and 2 shows that some species which had frequency of occurrence, and were found in a large proportion of

subsamples, nevertheless had low spore populations. For example, *A. foveata* at sites 1 (Rajamandala) and 2 (Batugajah) in West Java had 60–100% occurrence, but 8–11 spores/kg, *A. tuberculata* at site 1 (Rajamandala) in West Java had 100% frequency, 10 spores/kg and *G. sinuosum* at site 1 (75% frequency, 2 sporocarps/kg).

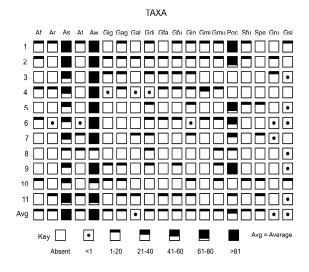


Figure 2. Population density of spores (per 1 kg soil) of AF in Java and Bali. Key to sites is given in Table 2 and the full list of species is given in Table 3.

4. **Spore biovolume** (Figure 3)

Figure 3 illustrates biovolumes of spores for AF taxa in µm³ per kg fresh weight soil. Squares are shaded in steps from $1.0 \times 10^5 \mu m^3$ to $1.0 \times 10^5 \mu m^3$ $10^9 \mu m^3$. Biovolume of the spore population e.g. A. walkeri at 6.93 x 10⁹ µm³ at site 9 (Pancursari) in East Java and A. scrobiculata at 2.23 x 10⁹ µm³ per kg at site 2 (Batugajah) in West Java. The value of this method of analysis is shown by G. sinuosum dan G. rubiforme. The sporocarp of these AF were always less than 20 per kg soil (see figure 2 spore population density). Yet the biovolume of G. sinuosum exceeded 1.0 x 10⁷ µm³ per kg at site 1 (Rajamandala) and site 3 (Pangandaran) in West Java, site 6 (Beji Tengah) and site 5 (Beji Barat) in Central Java, site 8 (Kaliwining), site 9 (Pancursari), site 10 (Peniwen) in East Java and site 11 (Jembrana in Bali). At site 9 (Pancursari) the biovolume of G. sinuosum (1.67×10^7) exceeded that of G. fuegianum (6.65×10^6) even though the latter had a spore population of 12.50 spores/kg whereas G. sinuosum occurred at a density of less than 1 sporocarp per kg soil.

Other taxa with large spores illustrate the same point, for example *G. gigantea* occurs at less than 1 spore per kg soil in site 4 (Putrapinggan) in West Java, at 1–20 spores/ kg at site 2

(Batugajah) and site 3 (Pangandaran) in West Java and site 9 (Pancursari) and site 10 (Peniwen) in East Java (see figure 2), yet had biovolume of 1 x $10^7 - 1 \times 10^8 \mu \text{m}^3$ per kg soil for all these sites (see Figure 3).

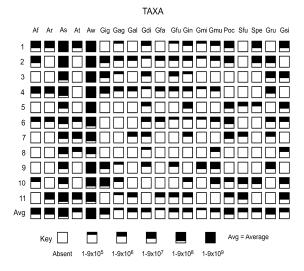


Figure 3. Spore biovolume (µm³ per 1 kg soil) of AF in Java and Bali. Key to sites is given in Table 2 and the full list of species is given in Table 3.

5. Dominance Indices (DI)

These are shown in Table 5 together with the biovolumes of the spores of the 'dominant' species and the total volume of spores of all AF species.

Table 5. Dominance Indices of AF in cacao soils from Java and Bali

Sites	Site	Bio-	Identity of	Bio-	DI
	name	volume	dominant	volume	
		max.		all taxa	
1	Rajaman- dala	2.55 x 10 ⁹	Acaulospora walkeri	4.54 x 10 ⁹	0.56
2	Batu gajah	5.51 x 10 ⁹	Acaulospora walkeri	7.92 x 10 ⁹	0.69
3	Pangan- daran	1.06 x 10 ⁹	Acaulospora walkeri	1.11 x 10 ⁹	0.95
4	Putra- pinggan	6.54 x 10 ⁹	Acaulospora walkeri	6.77 x 10 ⁹	0.96
5	Beji Barat	1.66 x 10 ⁹	Acaulospora walkeri	1.82 x 10 ⁹	0.91
6	Beji Tengah	4.76 x 10 ⁸	Acaulospora walkeri	5.93 x 10 ⁸	0.80
7	Beji Timur	9.28 x 10 ⁸	Acaulospora walkeri	1.09 x 10 ⁹	0.85
8	Kaliwi- ning	8.29×10^7	Acaulospora walkeri	1.28 x 10 ⁸	0.64
9	Pancursa- ri	6.93 x 10 ⁹	Acaulospora walkeri	7.19 x 10 ⁹	0.96
10	Peniwen	1.38 x 10 ⁸	Acaulospora walkeri	4.40×10^8	0.31
11	Jembrana	3.83 x 10 ⁸	Acaulospora walkeri	6.68 x 10 ⁸	0.57

In most cases the bulk of the biovolume was made up of the two *Acaulospora* species, *A. scrobiculata* and *A. walkeri*. The values of 0.5–0.6

reflect high biovolumes of more than one species *e.g.* site 1 (Rajamandala) in West Java (see Figure 3). Site 10 (Peniwen) in East Java shows the lowest value, due to high biovolumes of *A. scrobiculata* and *G. gigantea*.

6. **Importance Values** (IV see Figure 4)

In the preceding presentation of the results it has been made clear that assessment of frequency (Figure 1), population density (Figure 2) and biovolumes (Figure 3) give conflicting pictures of the relative importance of different AF species in the spore populations at the different sites throughout Java and Bali. The idea of the Importance Value is to bring these three aspects together. The results are illustrated in Figure 4.

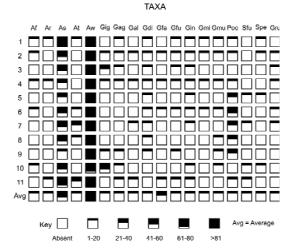


Figure 4. Importance values of AF in Java and Bali. Key to sites is given in Table 2 and the full list of species is given in Table 3.

The overall averages for all the sites in Java and Bali confirmed the importance of A. walkeri, with an average IV of 155.99 including values as high as 204.99 for site 4 (Putrapinggan) in West Java, 198.83 for site 9 (Pancursari) in East Java and 192.96 for site 3 (Pangandaran) in West Java. A. scrobiculata had an average IV of 51.43 and its importance in the AF community was more site variable, with importance values as high as 98.7 on site 1 (Rajamandala) in West Java but a trend to greatest importance value in East Java and Bali at site 8 (Kaliwining), site 10 (Peniwen) and site 11 (Jembrana). P. occultum had the highest average IV at 19.53, again emphasizing the effect of biovolume measurement, as against spore numbers, in assessing relative importance. G. diaphanum was another taxon which proved to be important using the indices, with an average value of 13.56, and values of 14.83 on site 5 (Beji Barat) in Central Java and 11.05 on site 8 (Kaliwining) perhaps indicated East Java and Central Java distribution.

By themselves, the data on frequency of occurrence can only roughly indicate distribution, however, the data do emphasize the almost universal presence of the two *Acaulospora* species in cacao soils throughout Java into Bali.

DISCUSSION

A particular feature of the Indonesian soil samples was the abundance of A. walkeri. It was not found in association with cacao in Ecuador (Kramadibrata, 2009). Geographical speciation may be the explanation for this difference, but as yet there is little evidence as to how AF speciate and what are the relative effects of geographical isolation, temperature and rainfall differences, soil characteristics and host range. Janos (1980) argued that poor dispersal of AF fungi probably constrained host specificity by limiting the ability of the fungi to encounter specific host, especially in diverse tropical forests. Pirozynski (1968) did note that temperature was the most important climatic factor regulating distribution and occurrence of fungi and Koske (1987) agreed that the structure of the AF community was affected by temperature; but he also noted that for most species, variation in frequency, spore density or spore biovolume could not be related to any abiotic factors. He argued that one reason could be the aggregated type of distribution of AF fungi spores in soil.

Cacao plantations are managed vegetation stands and man's activity has been one of the most important single factors affecting the geographical distribution of fungi (Pirozynski, 1968). Thus the distribution of spore types collected in cacao plantations could have been brought about on their hosts through man's activity.

However, the argument of Janos (1980) about poor dispersal of AF, could also be applied to speciation due to geographical separation (allopatric speciation). As yet there have been too few studies of spore populations to provide much data, but the present evidence of the abundance A. walkeri in Java and Bali with cacao, and its complete absence from Ecuador, may indicate a geographical factor. However, in contrast, A. scrobiculata seems to be a taxon with worldwide distribution, including sand dunes in the USA (Koske, 1987), tropical rain forest in Mexico and agricultural soils in the USA (Trappe, 1977), sand dunes in Australia (Koske, 1975), agricultural soils (Widiastuti & Kramadibrata, 1992 & 1993;

Silviana *et al.*, 1999; Haerida & Kramadibrata, 2002; Chairani *et al.*, 2002; Muliawan, *et al.*, 2002), managed ecosystem or in the Bogor Botanic Garden (Setya *et al.*, 1995) and under forest trees (Kramadibrata, 1993). Koske (1975) stated that he could find no evidence that this spore type was associated with a particular host or pH value in the sand.

There is a large literature on the distribution on AF spore types, most of it fragmentary, as in the example of *A. scrobiculata* quoted above. Few attempts have been made to make consistent investigation of spore assemblages under the same plant community over a wide geographical range, as was attempted here in the survey of Java and Bali. One exception was Koske (1987) who used the Atlantic seaboard of the USA to determine latitudinal differences in spore assemblages.

Koske (1987) concluded that temperature was the main factor in determining AF community in these sand dune systems. However, in Indonesia, with regular temperature throughout the year, it would not have affected distribution.

pH, organic matter and other soil properties have also been recorded as positive factors in recent publications such as by Schenck et al. (1984), Morton (1986), Sieverding (1987), Sieverding & Toro (1987 a & b) and soil pH was also mentioned by Wang et al. (1985) in connection with AF. Plant vigour may affect spore production of AF fungi as has been reported by Chilvers & Daft (1982), Daft & Nicolson (1972), Furlan & Fortin (1972), Hayman (1974) and Pugh et al. (1981). It was difficult to ascertain the vigour of the cacao trees under field conditions. Although the age of cacao trees were recorded, the many herbaceous plants surrounding them could not be ignored, and the AF spores associated with cacao trees were possibly also associated with these other plants. Thus whether the age of trees was a major factor in AF pattern of distribution, or pattern of association cannot be determined.

The determinants of the distribution patterns found in Indonesia remain unclear and indeed it was not anticipated that the study could reveal them. However, the evidence presented here has shown that the approaches to the analysis of the data provided by the spore sampling program, namely that based on a descriptive approach, which differentiated geographical distribution (following Koske, 1987) did provide useful ways of looking for patterns of distribution. A major difficulty in the analysis of the data was that the original sampling program was not designed with the final analytical method in mind, so that the processing of the data was made more difficult.

Temperature was mentioned earlier as a factor in AF distribution and a final point can be made about the overall significance of this study of a tropical crop. In Indonesia air temperature, day time is around 25–30° C and, although many fungi have a broad latitudinal range (Bisby, 1943; Pirozynski, 1968), so that it is difficult to identify a tropical species distribution, it might be speculated that spore types recorded in the survey were of taxa with a tropical or subtropical distribution.

Examination of the literature showed that a number of taxa found in this study have a very wide geographical range, for example G. fasciculatum (Molina, 1985; Walker & Koske, 1987). Other taxa found seem to have a distribution in the northern or southern temperate latitudes, for example S. calospora, Scotland, Illinois, Pacific Northwest and New Zealand (Nicolson & Gerdemann, 1968; Gerdemann & Trappe, 1974; Mosse & Bowen, 1968). Koske (1987) found in a study of the spore density of this species in sand dunes that it was favoured by cooler soil temperatures and, together with G. gigantea, it was not found in sand dunes in Florida (Sylvia, 1986). Both of these species, although found in the present study, occurred in very low numbers. A similar explanation may be offered for the low numbers of G. mosseae, which has been found in northern latitudes (Gerdemann, 1961; Koch, 1961; Gerdemann & Trappe, 1974) and southern latitudes i.e. Australia and New Zealand (Mosse & Bowen, 1968). A similar hypothesis could be put forward for a number of the spores found infrequently during the study, but the greater number of studies carried out in the northern latitudes may well influence this data.

Other taxa which were found did have previous evidence of a tropical distribution. A. rehmii and A. tuberculata seem to occur together in the Javan soils and were described from the tropical zones of South and Central America (Sieverding & Toro, 1987; Janos & Trappe, 1982). S. fulgida was found in Indonesia and also in Ecuador (Kramadibrata, 2008). Koske & Walker (1986) described this species from sand dunes in the eastern north of the USA. Later Koske (1987) concluded that S. fulgida in the sand dune system in the east coast of the USA has a significant linear increase in frequency of occurrence and spore density with more southern latitudes, and proposed that it preferred warmer temperatures. This spore type was found from quite a wide area in Java and Bali. Its higher frequency and the higher spore density compared to S. calospora in

Java and Bali (see Figures 1 and 2) makes an interesting comparison. Other taxa with a probable tropical distribution which were found regularly in the survey in Indonesia included G. multicaulis (described by Gerdemann & Bakshi, 1976 from India). G. sinuosum (formerly Sclerocystis sinuosa or S. pakistanica) also from India (Gerdemann & Bakshi, 1976) and from Pakistan (Iqbal & Bushra, 1980) was another taxon with a possible tropical origin which was found in the survey. Most former *Sclerocystis* may have a tropical origin. Up to 1974 only three species of Sclerocystis were known; two of them S. coremioides and S. dussii have been previously found only in the tropics or subtropics or in tropical greenhouses (Gerdemann & Trappe, 1974; Janos, 1975). G. rubiforme (formerly known Sclerocystis pachycaulis or S. rubiformis) was originally described temperate (Gerdemann & Trappe, 1974) but than reported from subtropical zone in Taiwan (Wu & Chen, 1986) under bamboo vegetation, it is also widely distributed under bamboo vegetation (Setya et al., 1995), durian (Chairani et al., 2002), cacao, cogon grass and corn (Widiastuti & Kramadibrata, 1992), forest trees in Indonesia (Kramadibrata unpublished data). An interesting feature was that in the 1987 survey G. sinuosum and G. rubiforme never occurred together in the same sample. The former species occurred in wide soil pH range (pH 4.6-6.9) compared to the latter (pH 5.2-6.3).

The distribution of other taxa is less capable of environmental interpretation. G. fuegianum was first described from southern temperate (Spegazzini, 1887), then New Zealand (Hall, 1977) and England (Godfrey, 1957). In spite of such previous records in temperate zones, it was found widely in the present study in Indonesia and it was also reported from under cogon grass, corn and cacao (Widiastuti & Kramadibrata, 1992). G. invermaium is a similar case. It was firstly described from New Zealand (Hall, 1977) associated with Trifolium repens but was widespread in Java and Bali associated cacao root.

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