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# ARBUSCULAR MYCORRHIZAL FUNGI DYNAMICS IN CONTRASTING CROPPING SYSTEMS ON VERTISOL AND REGOSOL SOILS OF LOMBOK, INDONESIA

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## SUMMARY

Arbuscular mycorrhizal fungi (AMF) may have a major role in phosphorus nutrition of crops in Lombok, where fertilizer use is low. As a start to understanding this role, AMF dynamics were monitored from the 1999 non-rice season to the end of the 1999/2000 rice season at 32 sites including dryland systems with no rice, upland rice and flooded systems with one or two rice crops per year in the rotation. Over all four systems, root colonization was greater in vertisol (22.3 % of roots) than in regosol (9.5 %) soil, possibly due to lower Bray-1 P content of the vertisol (6.2 v. 13.7 mg $\mathrm{kg}^{-1}$). Colonization was poor in flooded rice (3.1–5.1 %); at the same sampling times it was better in upland rice (10.6–13.4 %) and in non-rice crops growing in dryland systems (13.8–17.0 %). Therefore, the low colonization in flooded rice appeared to be the result of flooding, rather than the rice itself. Flooding also reduced transparent spore numbers, but sufficient inoculum appeared to survive flooding for plants in the following non-rice season to be well colonized (19–33 %) regardless of system. These non-flooded crops appear to replenish depleted AMF propagules.

## INTRODUCTION

Most soils used to produce rice (*Oryza sativa*) in Asia are deficient in phosphorus (P), and P fertilizer is needed for high yields (De Datta *et al.*, 1990). In Lombok, and elsewhere in Indonesia, fertilizer use on rice has fallen since the Indonesian economic crisis in 1998 that led to increased fertilizer prices. Farmers in Lombok (West Nusa Tenggara province) applied an average of 2.1 kg P $\mathrm{ha}^{-1}$ in 1999 compared with 4.7 kg $\mathrm{ha}^{-1}$ in 1997 (Diperta Tk.I NTB, 1999). With average rice yields of 4 t $\mathrm{ha}^{-1}$, P inputs as fertilizer are well below the P removed in grain. Although some P fertilizer is used on flooded rice in Lombok, no fertilizer is applied to non-rice crops following rice. Non-rice crops are normally grown as rainfed secondary food crops in the dry season, when irrigation water and/or rainfall are scarce and farmers are reluctant to invest in fertilizer.

In the absence of adequate P fertilizer, effective arbuscular mycorrhizal fungi (AMF) symbiosis has the potential to help crops access more soil P (Arihara and Karasawa, 2001; Solaiman and Hirata, 1995) and achieve higher yields. Integrating AM symbiosis

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into cropping systems appears to provide an alternative means of maintaining yield while reducing external P inputs (Miyasaka and Habte, 2001).

There is some evidence from the Philippines that AMF populations decline under flooded rice but increase again under the following maize and mungbean crops (Ilag *et al.* 1987). In Lombok, Indonesia, Parman (personal communication) reported that inoculation with AMF spores increased root colonization, spore production, P uptake and yield of non-rice crops (maize, soybean and mungbean) planted immediately following 'Gora' rice (i.e. dry sown then flooded). This work provided indirect evidence for depletion of AMF infective propagules during flooded rice and demonstrated the benefits of AMF inoculation for non-rice crops following a rice crop.

Given the evidence that AMF are important in crops where fertilizer-P inputs are limited, that flooded rice may deplete AMF inoculum in soil and that AMF inoculation may improve the performance of non-rice crops in rotation with rice, it follows that greater understanding of AMF dynamics in rice-based cropping systems is required. Lombok provided an ideal situation in which to study AMF dynamics in food crop production systems, because five broad types of systems are practised which vary greatly in cropping intensity, the presence of rice and alternative crops in the rotation, and the use of irrigation. Four of these systems are found on the two major soil types used in food crop systems: the regosols, which dominate in western Lombok, and the vertisols, which dominate in the south and south-east. Although rice is the preferred crop in irrigated areas, the local government enforces prescribed rotations to avoid a recurrence of the pest and disease outbreaks that occurred in the 1970s and 1980s. It is this that determines the repeatability of the four broad systems compared in this paper.

A field survey was conducted in Lombok over two cropping seasons, covering non-rice and rice-based cropping systems and the two main soil types. The aim was to quantify the dynamics of AMF colonization in roots and spore numbers in soil, and so provide a foundation for further studies to enhance the role of AMF in rice-based cropping systems.

## MATERIALS AND METHODS

### *Description of farming systems*

Food-crop production systems in Lombok are either rainfed/dryland or wetland systems. Rainfed/dryland systems are further differentiated for the purposes of this paper by the inclusion of upland rice in the rotation. Thus we refer to 'dryland' cropping systems, which have a range of crops but no upland rice, and 'upland' systems that are rainfed but include one rice crop per year during the rainy season. Upland rice is grown on sloping, un-terraced lands at elevations less than 500 m above sea level. Wetland systems are either rainfed lowland, which is flooded during the rainy season for Gora rice, or irrigated. Gora rice is grown only on the vertisols of central Lombok and therefore is not considered further in this paper. In irrigated systems, paddy (flooded) rice is grown either once ('once-rice' system) or twice ('twice-rice' system) during the rainy season, followed by one or two non-rice food crops during the dry season. Irrigated areas are cropped three times per year, but rainfed/dryland systems may be cropped only once or twice, with weeds growing between crops during the driest months before the next rainy season.

### *Design of field survey and site selection*

AMF were monitored three times, on two soil types (regosol, vertisol), for four farming systems (dryland, upland rice, once-rice, twice-rice). Fields were sampled between August 1999 and April 2000, covering two crop seasons. The times were selected to follow AMF population dynamics from time 1, the dry (non-rice) cropping season of 1999, to time 2, the subsequent wet (rice) season of the 1999/2000 monsoon (early growth of rice crop), and time 3 (maturity or harvest of rice).

For each system on each soil type, four representative sites were surveyed (system replicates). The sites on the regosol soil were located in two districts of West Lombok Regency, while those on vertisol soil were in two districts of Central Lombok Regency. At each site, five replicates of field samples (site replicates) were taken at each sampling time, at random from a diagonal transect across the selected field, the location of each transect being randomly chosen for each sampling time. Every site was a farm operated by one farmer.

Farmers were randomly selected from a list of potential collaborators supplied by the local Agricultural Field Extension Officers ('PPL'), who know the general cropping history of fields operated by farmers they work with. Sites were finally selected following a survey conducted with the local PPL to check cropping patterns between rice and non-rice crops in the previous four years. Field sampling involved the local PPL. The sites are described in Table 1 (regosol) and Table 2 (vertisol).

### *Sampling and sample processing*

Each of the five field samples of 20 cm × 20 cm and up to 15 cm depth was taken from topsoil to include plant roots and rhizosphere soil. The roots from each field sample were separated from the soil for inspection of AMF colonization after staining in the laboratory using a modified clearing and staining procedure from Brundrett *et al.* (1996). The soil was air-dried and sieved using a 2-mm mesh sieve for spore counting and soil analysis. AMF colonization and spore numbers were quantified from each site replicate. Soil chemical analyses were performed on the bulked replicates of each site.

Spores were extracted from soil using a wet sieving and decanting procedure modified from Brundrett *et al.* (1996), by wet sieving 20 g air-dried soil for each site replicate. The data are reported as spore number $g^{-1}$ oven-dried soil (after conversion using moisture content of the air-dried soil samples). The sieves used had mesh sizes of 38, 105 and 750 $\mu$m, respectively, from bottom to top.

### *Variables and measurement*

The variables measured were AMF colonization in the roots of crops (or weeds) sampled from the field, number of spores extracted from soil samples, and soil properties including pH in water, organic carbon using the Walkley-Black method and extractable P using the Bray-1 method. Soil pH was measured at each sampling

Table 1. Field conditions of the sites on regosol soil at each sampling time.

| Site | Farming system | Crop and field conditions for each sampling time | | |
|---|---|---|---|---|
| | | Time 1 | Time 2 | Time 3 |
| 1 | Dryland | Peanut, maize, 5 WAS[†] | Peanut, 2 WAS | Peanut, maturity |
| 2 | Dryland | Cassava, 4 WAS | Cassava, vegetative | Cassava, maturity |
| 3 | Dryland | Cassava, 3 WAS | Cassava, vegetative | Weeds |
| 4 | Dryland | Cassava, 8 WAS | Cassava, maturity | Weeds |
| 5 | Upland rice | Weeds, rice ratoon, cassava | Rice, upland, 2 WAS | Rice, upland, maturity |
| 6 | Upland rice | Weeds, rice ratoon, pigeon-pea | Rice, upland, 2 WAS | Rice, upland, maturity |
| 7 | Upland rice | Weeds/maize near flowering | Rice, upland, near flowering | Rice, upland, maturity |
| 8 | Upland rice | Weeds, maize stubble, cowpea | Rice, upland, near flowering | Rice, upland, maturity |
| 9 | Once-rice | Maize 1 wk of emergence (direct-seeded after corn) | Rice, flooded, 3 WAT[‡] | Rice, grain-filling |
| 10 | Once-rice | Weeds, small chilli, harvest commenced | Rice, flooded, 3 WAT | Rice, grain-filling |
| 11 | Once-rice | Tobacco, start leaf harvest | Rice, flooded, 3 WAT | Rice, maturity |
| 12 | Once-rice | Tobacco, start leaf harvest | Rice, flooded, 3 WAT | Rice, maturity |
| 13 | Twice-rice | Peanut, 4 WAS | Rice, flooded, 4 WAT | Rice, just harvested |
| 14 | Twice-rice | Tomato (1 WAS), rice ratoon | Rice, flooded, 2 WAT | Rice, grain-filling |
| 15 | Twice-rice | Peanut, maturity | Rice, flooded, 6 WAT | Rice stubble |
| 16 | Twice-rice | Peanut, maturity | Rice, flooded, 2 WAT | Rice, just harvested |

[†] WAS: weeks after sowing.
[‡] WAT: weeks after transplanting.

Table 2. Field conditions of the sites on vertisol soil at each sampling time.

| Site | Farming system | Crop and field conditions for each sampling time | | |
|---|---|---|---|---|
| | | Time 1 | Time 2 | Time 3 |
| 17 | Dryland | Cassava, 8 WAS[†] | Soybean, 3 WAS | Soybean, just harvested |
| 18 | Dryland | Peanut/chilli, 5 WAS | Soybean, 3 WAS | Peanut, 1 WAS |
| 19 | Dryland | Weeds, fallow | Soybean, 3 WAS | Soybean, just harvested |
| 20 | Dryland | Cassava, 12 WAS | Soybean/Peanut, 3 WAS | ex-Soybean, weeds |
| 21 | Upland rice | Weeds, fallow | Upland rice, 3 WAS | Upland rice, just harvested |
| 22 | Upland rice | Sweet-potato, weeds | Upland rice, 3 WAS | Upland rice, just harvested |
| 23 | Upland rice | Weeds, fallow | Upland rice, 3 WAS | Upland rice, just harvested |
| 24 | Upland rice | Weeds, fallow | Upland rice, 3 WAS | Upland rice, just harvested |
| 25 | Once-rice | Rice-ratoon, Cowpea 2 WAS | Rice, flooded, 4 WAT[‡] | Rice, maturity |
| 26 | Once-rice | Peanut, 8 WAS | Rice, flooded, 4 WAT | Rice, just harvested |
| 27 | Once-rice | Soybean, 8 WAS | Rice, flooded, 4 WAT | Rice, maturity |
| 28 | Once-rice | Soybean, 7 WAS | Rice, flooded, 3 WAT | Rice, maturity |
| 29 | Twice-rice | Soybean, 10 WAS | Rice, flooded, 4 WAT | Rice, just harvested |
| 30 | Twice-rice | Soybean, 10 WAS | Rice, flooded, 4 WAT | Rice, just harvested |
| 31 | Twice-rice | Rice ratoon, fallow not flooded | Rice, flooded, 5 WAT | Rice, just harvested |
| 32 | Twice-rice | Rice ratoon, fallow not flooded | Rice, flooded, 3 WAT | Rice, just harvested |

[†] WAS: weeks after sowing.
[‡] WAT: weeks after transplanting.

time; the other variables were measured only at sampling time 1. These soil chemical analyses were performed by the Soil Biology and Chemistry Laboratory, Faculty of Agriculture at the University of Mataram, Lombok.

AMF colonization was measured as the percentage length of root colonized in each root sample observed under a compound microscope at 100× magnification, by putting 10–15 stained root fragments in a parallel position on a graticule slide. From 25 to 150 root fragments were observed per site replicate depending on the total stained root fragments obtained. The percentage of root colonization for that sample was obtained by averaging the percentage length of root colonized from all root fragments measured for that sample.

For spore data, both transparent (viable) and black (dead) spores were counted. All spores that were still transparent with colour varying from hyaline to dark brown were categorized as transparent spores. They were assumed to be viable because, when cracked open, they revealed translucent contents that contrasted with the black and dry contents of the so-called black spores that were assumed to be dead.

The techniques applied in counting the spores extracted from soil and captured on stamp-gridded filter papers using vacuum filtering differed between the two spore fractions obtained. Spores from the sieving-fraction of 105 $\mu$m were counted on the entire area of the filter papers while those from the sieving-fraction of 38 $\mu$m were counted using a sub-sampling technique developed using regression analysis.

### *Data analysis*

The survey design had four factors (time, soil type, farming system and site) that could potentially be included in an analysis. However, a site mean was calculated from the five site replicates, and these site mean data were used as replicates in a 3-way ANOVA with times, soil type and farming system as fixed, orthogonal factors. When pre-analysed using Minitab 13 for Windows, all data were found to be normally distributed based on the Kolmogorov-Smirnov test, or they became normally distributed with homogeneous variances after being transformed, based on the F-max test of Fowler *et al.* (1998). Analysis of variance (ANOVA) was undertaken using Statistica for Windows. For the presentation of mean values and standard errors, calculations were based on Riley (2001).

Based on the pre-analyses, site mean data were transformed into hyperbolic arcsine [$\mathrm{Asinh}(x + 0.5)$] for root colonization, $\mathrm{Ln}(x)$ for transparent spore number and $\mathrm{Ln}(x + 1.3)$ for extractable P. Percentage black-to-total spores did not need transformation. Soil pH and organic C data were not normally distributed, but the F-max test showed homogeneous variances between samples. Therefore, according to Fowler *et al.* (1998), analysis of variance was also valid on these soil properties.

## RESULTS

### *Soil properties*

The ANOVA (not shown) of soil pH, which was analysed at each sampling time, revealed significant ($p < 0.05$) main effects for soils and systems and a significant interaction between soil and system, but only at sampling time 2, which was at the stage of early rice growth in the systems with rice. Regosol soils had lower pH than the vertisol soils overall (6.04 v. 6.62, $p < 0.05$), but the difference between the soil types

Table 3. Mean soil pH (±*s.e.*) in water at sampling time 2 for each combination of soil type and farming system in Lombok.

| | Farming systems | | | | |
|---|---|---|---|---|---|
| Soil type | Dryland | Upland rice | Once-rice | Twice-rice | Mean[†] |
| Regosol | 6.34 (0.23) | 6.51 (0.16) | 6.27 (0.12) | 5.03 (0.50) | 6.04 (0.20) |
| Vertisol | 6.73 (0.22) | 6.76 (0.30) | 6.40 (0.20) | 6.61 (0.18) | 6.62 (0.11) |

[†] The main effects of soil type and system and their interaction were significant ($p < 0.05$).

Table 4. Available soil P and organic carbon for each combination of soil type and farming system at sampling time 1 in Lombok. Values for P are means of transformed ($\log_e [x+1.3]$) (±*s.e.*) data and means of the untransformed data (in bold).

| | Farming systems | | | | |
|---|---|---|---|---|---|
| Soil type | Dryland | Upland rice | Once-rice | Twice-rice | Mean[†] |
| Available P (untransformed data, mg P $kg^{-1}$ soil) | | | | | |
| Regosol | 1.53 (0.09) **13.4** | 1.62 (0.16) **18.0** | 1.40 (0.16) **10.3** | 1.44 (0.20) **13.2** | 1.51 (0.07) **13.7** |
| Vertisol | 1.03 (0.16) **3.4** | 1.31 (0.24) **10.1** | 1.35 (0.16) **8.7** | 1.05 (0.04) **2.5** | 1.18 (0.08) **6.2** |
| Organic C (%) | | | | | |
| Regosol | 2.00 (0.48) | 1.93 (0.18) | 3.29 (0.21) | 2.76 (0.85) | 2.49 (0.27) |
| Vertisol | 1.67 (0.08) | 3.00 (1.42) | 2.11 (0.41) | 2.95 (0.23) | 2.43 (0.36) |

[†] The main effect of soil type for available P was significant ($p < 0.05$).

at sampling time 2 was greatest in the twice-rice system where pH in regosol was 5.03 (*s.e.* 0.50) and the vertisol was 6.61 (*s.e.* 0.18) (Table 3).

Available P and organic C, measured only at sampling time 1, are reported in Table 4. Over all systems, vertisol soil had significantly ($p < 0.05$) lower concentrations of available P (6.2 mg $kg^{-1}$) than regosol soil (13.7 mg $kg^{-1}$). The available P concentrations varied amongst system-soil combinations in the range of 2.5–18.0 mg $kg^{-1}$. There was no difference in the concentration of organic C (2.49 % in regosol and 2.43 % in vertisol soil).

*AMF variables: colonization, transparent spore numbers, percentage black (dead) spores*

Based on the ANOVA (not shown), the main effects of soil type and sampling time were significant ($p < 0.05$) for AMF colonization and transparent spore number, whilst that of farming system was significant for the three AMF variables. The interaction between soil type and farming system was significant only for AMF colonization and transparent spore number, whilst the interaction between soil type and time was significant only for transparent spore number. The farming system × sampling time interaction was significant only for AMF colonization. There was no significant three-way interaction for the AMF variables measured. Thus, levels of AMF colonization in plant roots and total transparent spore numbers in soil showed similar responses to differences in soil types, farming systems and sampling times, except for the

Table 5. Root colonization with AMF in each combination of soil type and farming system, and sampling time and farming system, in Lombok.[†]. Values are means (± s.e.) of transformed data for colonization (%) (hyperbolic arcsine [x + 0.5]), and means of untransformed data in bold.

| Soil or sampling time (T) | Farming system | | | | Mean |
|---|---|---|---|---|---|
| | Dryland | Upland rice | Once-rice | Twice-rice | |
| Regosol | 3.05 (0.22) **15.2** | 2.19 (0.18) **5.3** | 2.05 (0.23) **6.9** | 2.84 (0.30) **10.5** | 2.44 (0.13) **9.5** |
| Vertisol | 3.64 (0.22) **27.2** | 3.42 (0.21) **23.4** | 2.83 (0.42) **23.0** | 2.57 (0.32) **15.5** | 3.11 (0.16) **22.3** |
| T1 | 3.92 (0.25) **32.7** | 3.07 (0.32) **19.1** | 3.71 (0.40) **36.7** | 3.61 (0.35) **30.6** | 3.58 (0.17) **29.8** |
| T2 | 3.02 (0.31) **17.0** | 2.57 (0.41) **13.4** | 1.60 (0.21) **3.1** | 1.85 (0.21) **3.7** | 2.26 (0.17) **9.3** |
| T3 | 3.09 (0.21) **13.8** | 2.77 (0.24) **10.6** | 2.01 (0.23) **5.1** | 2.11 (0.18) **4.6** | 2.50 (0.13) **8.5** |

[†] The main effects of soil type, farming system and sampling time, and the interactions between farming system and soil type and farming system and time, were significant ($p < 0.05$).

soil × time and system × time interactions, in which colonization and transparent spores showed opposite responses.

The percentage of roots colonized in vertisol soil was higher than in regosol soil in all farming systems, with the difference in mean colonization (22.3 % v. 9.5 %, or transformed values of 3.11 and 2.44 in Table 5) being statistically significant ($p < 0.05$). Colonization was highest in all systems at sampling time 1, i.e. during the dry, non-rice season (Table 5). The subsequent decline in colonization was similar for the two soil types, with no significant interaction between soil type and sampling time ($p \geq 0.05$). With respect to differences in colonization between farming systems, the most notable effect was the interaction ($p < 0.05$) between system and sampling time. The decline in colonization over time was greater in the flooded lowland systems (once- and twice-rice) than in the rainfed systems (dryland and upland), with this interaction being significant ($p < 0.05$). The greatest decline was between times 1 and 2, which was the transition from the non-rice season to the beginning of the subsequent rice season. Although upland rice had the poorest colonization at sampling time 1, it suffered the least reduction in colonization over time.

Mean transparent spore numbers were significantly higher in vertisol soil than in regosol soil (19.3 v. 15.4 spores $g^{-1}$ soil, or the transformed values of 2.91 v. 2.62 in Table 6). Among the systems, the number of transparent spores was on average highest in the dryland system (24.2 spores $g^{-1}$) and lowest in the twice-rice system (13.2 spores $g^{-1}$). In relation to sampling time, transparent spores were most abundant at sampling time 1 (22.9 spores $g^{-1}$) and least so at time 3 (12.0 spores $g^{-1}$).

When the means for transparent spore numbers were considered according to the soil-system interaction (Table 6), the means were greatest in the upland rice system on vertisol soil (28.5 spores $g^{-1}$) and the dryland system on regosol and vertisol (25.0, 23.4 spores $g^{-1}$ respectively) (Table 6), each of which is rainfed. The lowest figures were in the flooded, twice-rice systems on the vertisol (17.2 spores $g^{-1}$) and regosol (9.2 spores $g^{-1}$).

Table 6. Transparent spore numbers in each combination of soil type and farming system, or sampling time and farming system, in Lombok[†]. Values are the means (± s.e.) of spore number $g^{-1}$ soil ($\log_e$ transformed), and means of untransformed data in bold.

| | Farming system | | | | |
|---|---|---|---|---|---|
| Soil or sampling time (T) | Dryland | Upland rice | Once-rice | Twice-rice | Mean |
| Regosol | 3.04 (0.19) **25.0** | 2.53 (0.20) **16.1** | 2.80 (0.14) **18.2** | 2.10 (0.16) **9.2** | 2.44 (0.13) **9.5** |
| Vertisol | 3.07 (0.12) **23.4** | 3.25 (0.14) **28.5** | 2.69 (0.21) **19.2** | 2.65 (0.19) **17.2** | 3.11 (0.16) **22.3** |
| Mean | 3.05 (0.11) **24.2** | 2.89 (0.14) **22.3** | 2.74 (0.13) **18.7** | 2.37 (0.14) **13.2** | |
| T1 | 3.06 (0.24) **25.4** | 3.09 (0.30) **28.0** | 3.24 (0.19) **29.0** | 2.59 (0.35) **18.5** | 3.00 (0.14) **25.2** |
| T2 | 3.18 (0.16) **26.5** | 2.89 (0.27) **22.8** | 2.68 (0.16) **15.8** | 2.52 (0.13) **13.1** | 2.82 (0.10) **19.6** |
| T3 | 2.92 (0.16) **20.6** | 2.69 (0.15) **16.0** | 2.31 (0.18) **11.3** | 2.01 (0.14) **8.0** | 2.48 (0.10) **14.0** |

[†] All main effects, and the interactions between soil type and farming system and soil type and sampling time were significant ($p < 0.05$). The interaction between farming systems and sampling time was not significant ($p \geq 0.05$).

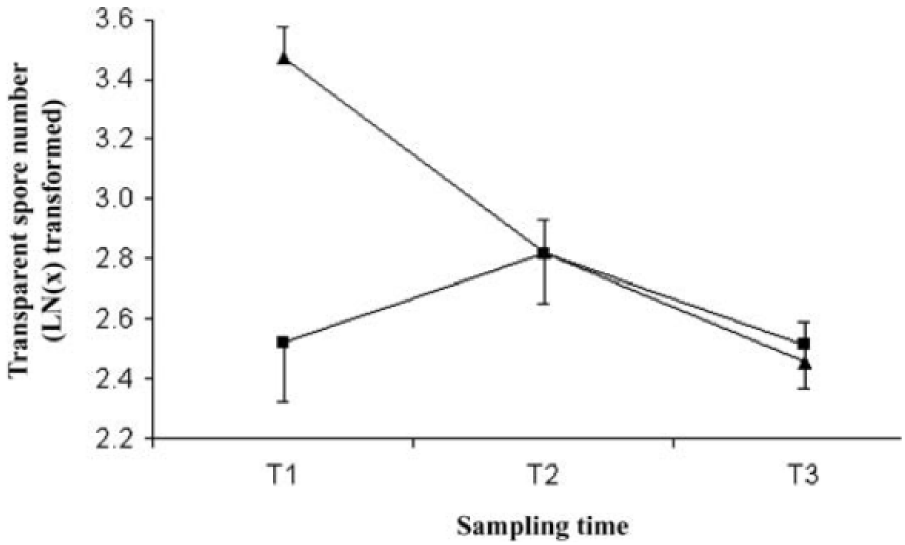

Figure 1. Means of transparent spore number across sampling times, between soil types (–■– regosol, –▲– vertisol), with −*s.e.* for regosol and + *s.e.* for vertisol.

From the trend in transparent spore numbers averaged over systems (Figure 1), the lowest transparent spore numbers were recorded during sampling 3 on both soil types. The vertisol had higher transparent spore counts than the regosol at time 1, but there was a strong interaction between soil type and sampling time. The vertisol suffered a large reduction in transparent spores in the transition from the pre-rice crop to the beginning of the subsequent rice crop.

The averages of percentage black-to-total spores are presented in Table 7. Unlike the other two AMF variables, the only significant effect was that of farming system, where the dryland system had the highest mean value (69.5 %) and the twice-rice system the lowest (57.3 %). Both of the irrigated lowland rice systems (once- and twice-rice)

Table 7. Means (±*s.e.*) of percentage of black-to-total spores in each combination of soil type and farming system, or sampling time and farming system, in Lombok†.

| | | Farming systems | | | | |
|---|---|---|---|---|---|---|
| | | Dryland | Upland rice | Once-rice | Twice-rice | Mean |
| Soil type† | Regosol | 68.7 (2.11) | 68.4 (2.50) | 59.4 (4.98) | 58.0 (2.79) | 63.6 (1.75) |
| | Vertisol | 70.3 (1.90) | 66.1 (2.18) | 62.1 (2.51) | 56.6 (3.60) | 63.8 (1.47) |
| | Mean | 69.5 (1.40) | 67.3 (1.64) | 60.8 (2.74) | 57.3 (2.23) | |
| Sampling time | T1 | 67.6 (2.80) | 66.2 (3.43) | 60.1 (5.07) | 54.6 (2.49) | 62.1 (1.94) |
| | T2 | 69.5 (2.42) | 66.9 (2.27) | 62.4 (6.16) | 54.0 (3.86) | 63.2 (2.18) |
| | T3 | 71.4 (2.14) | 68.8 (3.02) | 59.7 (3.10) | 63.4 (4.47) | 65.8 (1.76) |

† The only significant effect was that of farming system ($p < 0.05$).

had substantially lower percentages of black-to-total spores than the rainfed systems (dryland and upland rice systems). Values appeared to increase with sampling time although the main effect of time was not statistically significant. When comparisons were made within each farming system, the increase in percentage black spores with time was especially marked in the twice-rice system from sampling 2 to sampling 3.

## DISCUSSION

Across 32 sites sampled in this study, soil P (Bray-1) concentrations ranged from 3 to 18 mg kg$^{-1}$. Regosol soils on average had higher P concentrations than vertisols (13.7mg kg$^{-1}$ v. 6.2 mg kg$^{-1}$), with the highest P being in regosols used for upland rice (18 mg kg$^{-1}$). Olsen and Sommers (1982) classified soils as very low (<3), low (3–7), medium (7–20) and high (>20 mg kg$^{-1}$) for Bray-1 P. On this basis, most soils in Lombok would be classified as low in available P. From this, and the fact that little P fertilizer is used on Lombok, it seems that AMF could play an important role in P nutrition, especially in the vertisol soils.

The most obvious difference in AMF colonization and transparent spore numbers amongst the 32 sites was between soil types; both were on average higher in vertisol than regosol soil. This may be related to differences in available P concentrations in the soil. Many researchers have reported that AMF colonization is reduced by higher plant-available P concentration (e.g. de Miranda and Harris, 1994). Soil P concentration was related negatively to colonization at sampling time 1 by the exponential equation:

$$Y = 69.975e^{-0.1063X} \qquad (r^2 = 0.512,\ p < 0.05),$$

where Y and X were soil-system means of colonization and available P respectively.

The differences in colonization and spore count between soil types might also be related to soil texture and structure. The vertisol soil is high in clay and strongly aggregated, whilst the regosol is sandier and less well-structured. Land and Schonbeck (1991) found higher colonization in a clay vertisol soil than in silty sand.

Apart from the effect of soil type, colonization and transparent spore numbers also varied between the four farming systems. These systems differed markedly in the intensity of annual flooding and rice cropping. At the first sampling time, which was at the end of a season when the soil is not flooded and only non-rice crops or weeds were growing, sites in the upland system had the lowest colonization (19.1 %). The high P status of upland regosol soils (18 mg $kg^{-1}$) may have been a factor in this result, tending to reduce colonization on this soil type and lower the average colonization of plants growing in the two soils. Low colonization at upland sites at the first sampling may also be related to the plants sampled. Weeds mostly dominated the upland regosol sites at the time of sampling 1 (no crops because of the dry season), while on the twice-rice systems half the sites had leguminous crops. Sites in the dryland system mostly had cassava (*Manihot esculenta*) and legumes, and those sites with cassava had the highest spore number during sampling time 1. Many reports show that crop species affect colonization and spore production by AM fungi (Arihara and Karasawa, 2001).

Sampling times 2 and 3 were in the rainy season, which coincided with the rice season in three of the farming systems. The irrigated systems (once-rice and twice-rice) had low colonization, with less than 5 % of roots being colonized. Both the upland and particularly the dryland farming systems had substantially greater colonization at both sampling times. The poor colonization of flooded rice appears to be related directly to the flooded conditions (Ilag *et al.*, 1987; Solaiman and Hirata, 1995; 1997) rather than any effect of the rice host, since rice was effectively colonized in the upland system. Ilag *et al.* (1987) suggested that lower numbers of infective AMF propagules in rice-rice rotations than in rice-corn-mungbean rotations in the Philippines was due to prolonged inundation during the wet season rice. Although upland rice was more extensively colonized than rice in either of the flooded systems, colonization was poorer than any non-rice crop at sampling 1 (as noted above), or at any time in the dryland system. This relatively low level of colonization compared with crops in other non-flooded conditions could reflect the high soil P in this system, as previously discussed, rather than any possible negative effect of the rice host.

Despite clear evidence for low colonization in flooded rice, the field survey could not conclusively differentiate between the effect of flooding on colonization and that of the host. However, Solaiman and Hirata (1997) found that inoculation with *Glomus* sp. in a wet (flooded) nursery resulted in all seedlings being colonized at about 22 % of root length at transplanting, compared with about 55 % in a dry nursery. This shows that rice is a host for the AM fungi, even if flooding reduces colonization. In another experiment, inoculation with *Glomus* sp. resulted in about 5 % colonization in continuously flooded pots v. about 34 % colonization in non-flooded pots at 60 days after seeding (Solaiman and Hirata, 1995). Thus, it seems almost certain that the poor colonization of flooded rice in this field survey is related to the flooded conditions, rather than the rice host, as Ilag *et al.* (1987) and Solaiman and Hirata (1995; 1997) have suggested.

In the field, infection may be low during flooded conditions because oxygen tension in the bulk soil is low. However, flooded rice crops oxygenize and acidify their rhizosphere (Hinsinger, 2001). Acidification was detected in the twice-rice system on vertisol soil in this study. It is possible that only selected species or isolates that are adapted to low pH are able to start infection in the rice rhizosphere.

Transparent spore numbers declined with sampling time between the non-rice (dry) season and the subsequent rice season, especially when crops were flooded (the once- and twice-rice systems). Ilag *et al.* (1987) and Solaiman and Hirata (1995; 1997) similarly reported that flooded rice reduced the numbers of infective propagules in soil. There was also a tendency for the percentage of black, dead spores to increase during flooded conditions in the twice-rice system between sampling time 2 (the early stage of rice crop) and sampling time 3 (maturity), although the data are quite variable. Flooding may increase spore mortality, a factor worth further investigation.

In addition to any effect of flooding, all irrigated systems are puddled before transplanting rice, requiring intensive tillage that may damage the hyphal network of AM fungi built up during the preceding non-rice crops. However, the seedlings in puddle rice had comparable colonization to seedlings in upland rice.

Despite the poor colonization of roots in flooded rice, the reduced number of transparent spores during flooded conditions and a possible increase in dead spores, it does not follow that subsequent crops in the rotation will necessarily be poorly colonized. Although sampling did not continue until the next crop in the cycle, it is significant that, at the end of the previous cropping cycle (sampling time 1), all crops were extensively colonized. This included non-flooded crops following flooded rice. Whilst continuous flooded rice may seriously deplete inoculum levels in soil, it appears that sufficient viable inoculum survives at least two cycles of flooded rice for subsequent non-rice crops to colonize. These non-rice crops then have the potential to rebuild inoculum levels.

P-fertilizer is not used on non-rice crops in Lombok. Given this, and that drying flooded soil for growing non-rice crops in rotation increases P sorption and reduces P availability for non-rice crops (Brandon and Mikkelsen, 1979) and that available soil P was low at many sites, it can be expected that non-rice crops will suffer from P deficiency. Thus, AM association is likely to be very important for the non-rice rotation crops to achieve relatively high yields.

Although non-rice crops in the dry season were satisfactorily colonized in this study, they were only observed late in their development. The high levels of colonization in the non-rice season may have resulted from a rapid build up late in the season due to reinfection by runner hyphae. If so, this could explain why Parman (personal communication) found in Lombok that inoculation with AMF spores increased root colonization, spore production, P uptake and yield of non-rice crops (maize, soybean and mungbean) planted after rice. Further work is needed to determine if crops in the non-rice season are infected early enough to benefit from the association. They may behave principally as a host to rebuild inoculum depleted by flooding.

In rice, AMF are known to improve nutrient uptake (Solaiman and Hirata, 1995; 1997), although it is commonly thought that rice is relatively unresponsive to P-fertilizer because of its ability to solubilize fixed phosphates in the soil from the non-labile pool (Hinsinger, 2001). However, with soil P concentrations being so low in some soils in Lombok (e.g. 2.5 $\mathrm{mg\,kg^{-1}}$ in twice-rice systems on vertisol soil), and with consistently poor colonization of flooded rice by AMF, there is a strong possibility that rice is also deficient in P.

## CONCLUSIONS

Colonization and transparent spore numbers were generally higher in vertisol than regosol soils, possibly due to the lower available P concentration in the vertisols. With respect to AMF dynamics, this field survey has shown that rice seedlings are well colonized soon after transplanting under flooded conditions, but subsequent colonization and transparent spore numbers are reduced by prolonged flooding. The effect of flooding on transparent spore numbers, which provide the inoculum for later crops, appeared to be greater in cropping systems which include two rice crops per year rather than one. Non-rice crops in the rotation were well colonized, and appear to play an important role in cropping systems by restoring AMF populations that have been depleted by flooded rice.

Future research should establish if non-rice crops following flooded rice benefit from the AM association found in this survey. This seems likely, given that the available P was very low at most of the sites sampled, and that drying flooded rice soil for growing non-rice rotation crops reduces P availability to subsequent non-rice crops. However, experiments are needed to establish if the colonization of non-rice crops, from the depleted inoculum source following flooded rice, develops sufficiently early for the crops to benefit from the association. These studies should measure responses to both AMF inoculation and P fertilizer. Research is also needed to determine the minimum inoculum level after flooded rice that is required to give sufficient colonization during the non-rice season, as well as to determine what crops are best to increase AMF populations after flooded rice.

With respect to rice, further studies are needed to determine if AMF inoculation of flooded rice in the field can improve nutrient uptake and yield when inadequate P-fertilizer has been used on soils with low P.

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