Accepted Manuscript

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

Wayan Wangiyana, Peter S. Cornish and E. Charles Morris

Type Research Article

Information Experimental Agriculture , Volume 42 , Issue 4 , October 2006 , pp. 427 – 439

DOI: https://doi.org/10.1017/S0014479706003826

Running title: *AMF dynamics in cropping systems of Lombok*

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

By W. WANGIYANA[1], P. S. CORNISH* *and* E.C. MORRIS

University of Western Sydney (Hawkesbury Campus), Locked Bag 1797,

PENRITH SOUTH DC, NSW 1797, Australia

SUMMARY

Arbuscular mycorrhizal (AM) fungi may have a major role in P nutrition of crops in Lombok, where fertiliser 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 colonisation 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 versus 13.7 mg kg^{-1}). Colonisation was poor in flooded rice (3.1-5.1%), but 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 colonisation in flooded rice appeared to be the result of flooding, not 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 colonised (19-33%) regardless of system. These non-flooded crops appear to replenish depleted AMF propagules.

[1] Current address: Faculty of Agriculture, University of Mataram, Jln. Majapahit 62, Mataram, Lombok, NTB, Indonesia; email: *w_wangiyana@telkom.net*

* Corresponding author: email: *p.cornish@uws.edu.au*

INTRODUCTION

Most soils used to produce rice (*Oryza sativa* L.) in Asia are deficient in phosphorus (P), and P fertiliser is needed for high yields (De Datta *et al.*, 1990). In Lombok, and elsewhere in Indonesia, fertiliser use on rice has fallen since the Indonesian economic crisis in 1998 that led to increased fertiliser prices. Farmers in Lombok (West Nusa Tenggara province) applied an average of 2.1 kg P ha^{-1} in 1999 compared with 4.7 kg ha^{-1} in 1997 (Diperta Tk.I NTB, 1999). With average rice yields of 4 t ha^{-1}, P inputs in fertiliser are well below exports in grain. Although some P fertiliser is used on flooded rice in Lombok, no fertiliser 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 fertiliser.

In the absence of adequate P fertiliser, effective AM symbiosis has the potential to help crops access more soil P (Solaiman and Hirata, 1995; Arihara and Karasawa, 2001) and achieve higher yields. Integrating AM symbiosis 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 colonisation, 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 inoculum during flooded rice and demonstrated the benefits of AMF inoculation for non-rice crops.

Given the evidence that AMF are important in crops where fertiliser-P inputs are limited, that flooded rice may deplete AMF inoculum in soil, and that AMF inoculation improves 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 practiced 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 southeast. Although rice is the preferred crop in irrigated areas, the local government enforces prescribed rotations to avoid a recurrence of pest and disease outbreaks that occurred in 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 colonisation 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 variety 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 in each soil type, four representative sites were surveyed (system replicates). The sites in 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 every sampling time, at random from a diagonal transect across the selected field, the location of each transect being randomly chosen for each sampling time. Each 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).

Insert Tables 1 & 2 about here

Sampling and sample processing

Each of the five field samples was taken from topsoil of 20 cm x 20 cm and up to 15 cm depth to include plant roots and rhizosphere soil. The roots from each field sample were separated from the soil for inspection of AMF colonisation 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 colonisation 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 20g air-dried soil for each site replicate. The data are reported as spore number per gram oven-dried soil (after conversion using moisture content of the air-dried soil samples). The sieves used had opening sizes of 38, 105 and 750 μm, respectively, from bottom to top.

Variables and measurement

The variables measured were AMF colonisation 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 time while the others were 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 colonisation was measured as percentage length of root colonised in each root fragment observed under a compound microscope at 100x magnification, by putting 10-15 stained root fragments in a parallel position on a deck glass. From 25 to 150 root fragments were observed per site replicate depending on the total stained root fragments obtained. The percentage of root colonisation for that sample was obtained by averaging the percentage length of root colonised 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 categorised 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 were different between the two spore fractions obtained. Spores from the sieving-fraction of 105µm were counted on the entire area of the filter papers while those from the sieving-fraction of 38µm 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, calculation was based on Riley (2001).

Based on the pre-analyses, site mean data were transformed into hyperbolic arcsine [Asinh(x+0.5)] for root colonisation, Ln(x) for transparent spore number, and 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 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 versus 6.62, p<0.05), but the difference between the soil types at sampling 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).

Insert Table 3 about here

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).

Insert Table 4 about here

AMF variables: colonisation, 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 colonisation 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 colonisation and transparent spore number, whilst the interaction between soil type and time was significant only for transparent spore number. The farming system by sampling time interaction was significant only for AMF colonisation. There was no significant three-way interaction for the AMF variables measured. Thus, levels of AMF colonisation 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 soil*time and system*time interactions, in which colonisation and transparent spores showed the opposite responses.

The percentage of roots colonised in vertisol soil was higher than in regosol soil in all farming systems, with the difference in mean colonisation (22.3% *versus* 9.5%, or transformed values of 3.11 and 2.44 in Table 5) being statistically significant (p<0.05).

Colonisation was highest in all systems at sampling time 1, i.e. during the dry, non-rice season (Table 5). The subsequent decline in colonisation 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 colonisation between farming systems, the most notable effect was the interaction ($p<0.05$) between system and sampling time. The decline in colonisation 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 colonisation at sampling time 1, it suffered the least reduction in colonisation over time.

Insert Table 5 and about here

Mean transparent spore numbers were significantly higher in vertisol soil compared with regosol soil (19.3 *versus* 15.4 spores g^{-1} soil, or the transformed values of 2.91 *versus* 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}).

Insert Table 6 about here

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}).

From the trend in transparent spore numbers averaged over systems (Figure 1), the lowest transparent spore numbers were 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 big reduction in transparent spores in the transition from the pre-rice crop to the beginning of the subsequent rice crop.

Insert Figure 1 near here

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

Insert Table 7 about here

DISCUSSION

Across 32 sites sampled in this study, soil P (Bray-1) concentrations ranged from 3-18 mg kg^{-1}. Regosol soils on average had higher P concentrations than vertisols (13.7mg kg^{-1} *vs* 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 fertiliser 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 colonisation and transparent spore numbers amongst the 32 sites was between soil types. Both colonisation and transparent spore numbers 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 colonisation is reduced by higher plant-available P concentration (e.g. de Miranda and Harris, 1994). Soil P concentration was related negatively to colonisation 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 colonisation and available P, respectively.

The differences in colonisation 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 colonisation in a clay vertisol soil compared with silty sand.

Apart from the effect of soil type, colonisation 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 soil is not flooded and only non-rice crops or weeds were growing, sites in the upland system had the lowest colonisation (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 colonisation on this soil type and lower the average colonisation of plants growing in the two soils. Low colonisation 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* Crantz) and legumes, and those sites with cassava had the highest spore number during sampling 1. Many reports show that crop species affect colonisation 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 colonisation, with less than 5% of roots being colonised. Both the upland and particularly the dryland farming systems had substantially greater colonisation at both sampling times. The poor colonisation 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 colonised in the upland system. Ilag *et al.* (1987) suggested that lower numbers of infective AMF propagules in rice-rice rotations compared with rice-corn-mungbean rotations in the Philippines was due to prolonged inundation during the wet season rice. Although upland rice was more extensively colonised than rice in either of the flooded systems, colonisation 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 colonisation 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 colonisation in flooded rice, the field survey could not conclusively differentiate between the effect of flooding on colonisation 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 colonised at about 22% 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 colonisation. In another experiment, inoculation with *Glomus* sp. resulted in about 5% colonisation in continuously flooded pots *versus* about 34% colonisation in non-flooded pots at 60 days after seeding (Solaiman and Hirata, 1995). Thus it seems almost certain that the poor colonisation 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 oxygenise 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 2 (the early stage of rice crop) and sampling 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 colonisation to seedlings in upland rice.

Despite the poor colonisation 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 colonised. 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 colonised. 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 colonise. These non-rice crops then have the potential to rebuild inoculum levels.

P-fertiliser 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 colonised in this study, they were only observed late in their development. The high levels of colonisation 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 colonisation, 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-fertiliser 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 on Lombok (e.g. 2.5 mg kg^{-1} in twice-rice systems on vertisol soil), and with consistently poor colonisation of flooded rice by AMF, there is a strong possibility that rice is also deficient in P.

CONCLUSIONS

Colonisation 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-colonised soon after transplanting under flooded conditions, but subsequent colonisation and transparent spore numbers are reduced by prolonged flooding. The effect of flooding on transparent spore numbers, which provides the inoculum for later crops, appeared to be greater in cropping systems which include two rice crops per year compared with one. Non-rice crops in the rotation were well colonised, 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 colonisation 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 fertiliser. Research is also needed to determine the minimum inoculum level after flooded rice that is required to give sufficient colonisation 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-fertiliser has been used on soils with low P.

Acknowledgments. We thank Mr. Abdul Hamid Kule, Sigit and Rohman for consistent help in the laboratory, the University of Mataram for study-leave permission, AusAID for a PhD scholarship at UWS, and others who assisted field sampling and laboratory activities.

REFERENCES

Arihara, J. & Karasawa, T. (2001). Phosphorus nutrition in cropping systems through arbuscular mycorrhizal management. **In:** *Plant Nutrient Acquisition: New Perspectives*, 319-337 (Eds N. Ae, J. Arihara, K. Okada and A. Srinivasan). Tokyo, Japan: Springer-Verlag.

Brandon, D.M. & Mikkelsen, D.S. (1979). Phosphorus transformation in alternately flooded California soils: I. Cause of plant phosphorus deficiency in rice rotation crops and correctional methods. *Soil Sci. Soc. Am. J.* 43:989-994.

Brundrett, M., Bougher, N., Dell, B., Grove, T. & Malajczuk, N. (1996). *Working with Mycorrhizas in Forestry and Agriculture*. ACIAR Monograph 32. Canberra, Australia:ACIAR.

de Datta, S.K., Biswas, T.K. & Charoenchamratcheep, C. (1990). Phosphorus requirements and management for lowland rice. **In:** *Phosphorus Requirements for Sustainable Agriculture in Asia and Oceania*, 307-323. Los Banos, Philippines:IRRI.

de Miranda, J.C.C. & Harris, P.J. (1994). Effects of soil phosphorus on spore germination and hyphal growth of arbuscular mycorrhizal fungi. *New Phytologist* 128: 103-108.

Diperta Tk.I NTB (1999). "Laporan Tahunan 1999". Mataram:Dinas Pertanian Tanaman Pangan Propinsi Nusa Tanggara Barat.

Fowler, J., Cohen, L. & Jarvis, P. (1998). *Practical Statistics for Field Biology.* 2nd Edition. Chichester, England: John Wiley & Sons.

Hinsinger, P. (2001). Bioavailability of soil inorganic P in the rhizosphere as affected by root-induced chemical changes: a review. *Plant and Soil* 237:173-195.

Ilag, L.L., Rosales, A.M., Elazegui, F.A. & Mew, T.W. (1987). Changes in the population of infective endomycorrhizal fungi in a rice-based cropping system. *Plant and Soil* 103:67-73.

Land, S. & Schonbeck, F. (1991). Influence of different soil types on abundance and seasonal dynamics of vesicular-arbuscular mycorrhizal fungi in arable soils of North Germany. *Micorrhiza* 1:39-44.

Miyasaka, S.C. & Habte, M. (2001). Plant mechanisms and mycorrhizal symbioses to increase phosphorus uptake efficiency. *Commununications in Soil Science and Plant Analysis* 32:1101-1147.

Olsen, S.R. & Sommers, L.E. (1982). Phosphorus. **In**: *Methods of Soil Analysis. Part 2. Chemical and Microbiological Properties*, 403-430 (Eds A.L. Page *et al.*). Second edition. Madison, Wisconsin, USA: American Society of Agronomy, Inc.

Riley, J. (2001). Presentation of statistical analyses. *Expl. Agric.*, 37: 115-123.

Solaiman, M.Z. & Hirata, H. (1995). Effects of indigenous arbuscular mycorrhizal fungi in paddy fields on rice growth and N, P, K nutrition under different water regimes. *Soil Science and Plant Nutrition* 41: 505-514.

Solaiman, M.Z. & Hirata, H. (1997). Effect of arbuscular mycorrhizal fungi inoculation of rice seedlings at the nursery stage upon performance in the paddy field and greenhouse. *Plant and Soil* 191: 1-12.

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, 5wk	Peanut, 2wk	Peanut, maturity
2	Dryland	Cassava, 4wk	Cassava, vegetative	Cassava, maturity
3	Dryland	Cassava, 3wk	Cassava, vegetative	Weeds
4	Dryland	Cassava, 8wk	Cassava, maturity	Weeds
5	Upland rice	Weeds, rice ratoon, cassava	Rice, upland, 2wk	Rice, upland, maturity
6	Upland rice	Weeds, rice ratoon, pigeon-pea	Rice, upland, 2wk	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 1wk 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, 4wk	Rice, flooded, 4 WAT	Rice, just harvested
14	Twice-rice	Tomato (1wk), 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

Note: 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, 8wk	Soybean, 3wk	Soybean, just harvested
18	Dryland	Peanut/chilli, 5wk	Soybean, 3wk	Peanut, 1wk
19	Dryland	Weeds, fallow	Soybean, 3wk	Soybean, just harvested
20	Dryland	Cassava, 12wk	Soybean/Peanut, 3wk	ex-Soybean, weeds
21	Upland rice	Weeds, fallow	Upland rice, 3wk	Upland rice, just harvested
22	Upland rice	Sweet-potato, weeds	Upland rice, 3wk	Upland rice, just harvested
23	Upland rice	Weeds, fallow	Upland rice, 3wk	Upland rice, just harvested
24	Upland rice	Weeds, fallow	Upland rice, 3wk	Upland rice, just harvested
25	Once-rice	Rice-ratoon, Cowpea 2wk	Rice, flooded, 4 WAT	Rice, maturity
26	Once-rice	Peanut, 8wk	Rice, flooded, 4 WAT	Rice, just harvested
27	Once-rice	Soybean, 8wk	Rice, flooded, 4 WAT	Rice, maturity
28	Once-rice	Soybean, 7wk	Rice, flooded, 3 WAT	Rice, maturity
29	Twice-rice	Soybean, 10wk	Rice, flooded, 4 WAT	Rice, just harvested
30	Twice-rice	Soybean, 10wk	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

Note: WAT = weeks after transplanting.

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

Soil type	Farming systems				Mean [1)]
	Dryland	Upland rice	Once-rice	Twice-rice	
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)

[1)] 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 back-transformed data (in bold).

Soil type	Farming systems								Mean[1)]	
	Dryland		Upland rice		Once-rice		Twice-rice			
	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)	

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

Table 5. Root colonisation with AMF in each combination of soil type and farming system, and sampling time and farming system, in Lombok[1)]. Values are means (± s.e.) of transformed data for colonisation (%) (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**

[1)] 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 ($p<0.05$).

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

Soil or Sampling time (T)	Farming system				Mean
	Dryland	Upland rice	Once-rice	Twice-rice	
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**

[1)] 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 ($p\geq0.05$).

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[1)].

		Farming systems				Mean
		Dryland	Upland rice	Once-rice	Twice-rice	
Soil type[1)]	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)

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

List of Figures

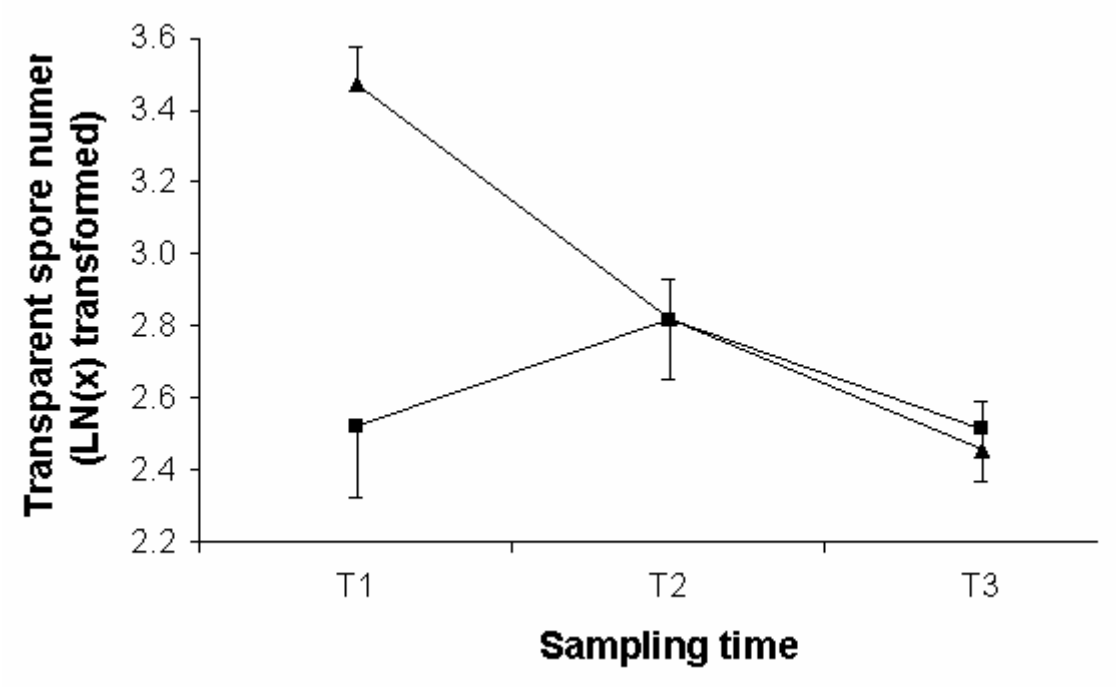
Transparent spore numer
(LN(x) transformed)
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
T1
T2
T3
Sampling time

Figure 1.