Is plant performance limited by abundance of arbuscular mycorrhizal fungi? A meta-analysis of studies published between 1988 and 2003

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Summary

• We conducted meta-analyses of 290 published field and glasshouse trials to determine the effects of various agricultural practices on mycorrhizal colonization in nonsterile soils, and the consequence of those effects on yield, biomass, and phosphorus (P) concentration.

• Mycorrhizal colonization was increased most by inoculation (29% increase), followed by shortened fallow (20%) and reduced soil disturbance (7%). The effect of crop rotation depended on whether the crop was mycorrhizal. Increased colonization resulted in a yield increase in the field of 23% across all management practices.

• Biomass at harvest and shoot P concentration in early season were increased by inoculation (57 and 33%, respectively) and shortened fallow (55 and 24%). Reduced disturbance increased shoot P concentration by 27%, but biomass was not significantly affected. Biomass was significantly reduced in 2% of all trials in which there was a significant increase in colonization.

• Irrespective of management practice, an increased mycorrhizal colonization was less likely to increase biomass if either soil P or indigenous inoculum potential was high.

Key words: arbuscular mycorrhizal fungi, biomass, colonization, management practice, meta-analysis, phosphorus, yield.

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Introduction

Arbuscular mycorrhizal fungi (AMF) are components of the great majority of natural and agricultural ecosystems. They colonize roots and form a symbiosis, arbuscular mycorrhiza, involving species of most families of angiosperms and gymnosperms (Smith & Read, 1997). The fungi have the potential to increase the uptake of phosphorus (P) (Hayman & Mosse, 1971; Sanders & Tinker, 1971) and zinc (Zn) (Hamilton *et al.*, 1993; Thompson, 1994) into the host plant. Other possible benefits include improved resistance to certain root pathogens (Borowicz, 2001; Graham, 2001) and to drought (Augé, 2001). Much of our understanding of the functions of this symbiosis is derived from studies in which plants have been grown in sterilized soil with or without addition of AMF inoculum. Comparatively little is known about the symbiosis in nonsterile soil, which can harbor many other kinds of organisms that independently influence both plants (Cohn & Spiegel, 1991; Gerson, 1991; Kapulnik, 1991; Katan, 1991) and AMF (Warnock *et al.*, 1982; Finlay, 1985; McGonigle & Fitter, 1988).

In 1988, McGonigle reviewed 78 published field trials to address the relationship between plant yield and increased colonization resulting from inoculation. He showed that, while plant yield increased by an average of 37% with increased colonization, the evidence for mutualism in the field was weak because there was no strong relationship between the increase in yield and the increase in mycorrhizal colonization. Since then, other review articles that discuss arbuscular mycorrhiza in agriculture have been published (e.g. Bagyaraj & Varma, 1995; Hooker & Black, 1995; Atkinson *et al.*, 2002; Ryan & Graham, 2002; Jeffries *et al.*, 2003). However, the conclusions that were drawn in those reviews regarding the utility of AMF

differ markedly. Different conclusions might have been drawn because the various authors reviewed different sets of studies that emphasized different production systems. This disparity in conclusions suggests that we may not yet have a clear understanding of either the relative importance of various agricultural practices to mycorrhizal colonization or the response of host plants to increased mycorrhizal colonization.

Since 1988, a great many papers on the effects of AMF on plant nutrient uptake and growth have been published, including those showing that tillage practices, fallow durations and crop rotations affect the extent of mycorrhizal colonization (McGonigle & Miller, 1993; Abbott *et al*., 1995; Hamel, 1996). Therefore, it is now possible to compare inoculation with these other agricultural practices in their effects on mycorrhizal colonization. The larger data set also gives us a better opportunity to test whether a quantitative relationship exists between increased mycorrhizal colonization and increased yield.

To do this, we used a meta-analysis approach, as did McGonigle (1988), which involves the numerical analysis of data extracted from trials in previously published articles. Meta-analyses were first developed for the social and medical sciences, but they have been used successfully in ecology to reveal important trends and interactions among factors (Curtis & Wang, 1998; Downing *et al*., 1999; Allison & Goldberg, 2002). One clear advantage of a meta-analysis over qualitative reviews and vote-counting procedures is that it generates means and confidence intervals for standardized variables of interest. By coding trials prior to the statistical analysis, the meta-analyst can evaluate the strength of various factors and their interactions. Moreover, potential problems of bias are easier for the reader to detect in a meta-analysis than in a traditional review because the criteria for the selection of trials and the statistical methods applied to them are explicitly stated.

For our analyses, we selected trials from articles published from 1988 to 2003 to address the following questions.

- What are the effects of soil disturbance, fallow duration, crop rotation and inoculation on per cent mycorrhizal colonization?
- Is an increased mycorrhizal colonization associated with changes in harvestable yield, biomass, and P concentration of the host plant?
- In cases where mycorrhizal colonization is increased, is there a correlation between increased P uptake and increased harvestable yield or biomass?
- What factors affect whether increased mycorrhizal colonization results in benefit to the host plant?

We focused on P but not other nutrients because of the well-researched connection between mycorrhizal fungi and plant P uptake (Smith & Read, 1997) and the importance of this element for crop production.

Materials and Methods

To select trials for the analyses, we searched for articles published from January 1988 to August 2003 on the ISI Web of Science®, which is an expanded web-based Science Citation Index (http://isi4.isiknowledge.com/portal.cgi?DestApp=WOS&Func=Frame). The search combinations entered were 'mycorrhiza* and agriculture', 'mycorrhiza* and tillage', 'mycorrhiza* and fallow', 'mycorrhiza* and cropping system', 'mycorrhiza* and cover crop' and 'mycorrhiza* and inoculation and field'. The use of the '*' character ensured that words such as mycorrhizae, mycorrhizas and mycorrhizal were included. All glasshouse and field studies that reported colonization were included except when either (1) fumigation or other soil sterilizing methods were used, because sterilization of the soil can result in the destruction of more than mycorrhizal fungi (discussed in Smith & Read, 1997), or (2) seedlings were inoculated prior to outplanting, because small differences between mycorrhizal and nonmycorrhizal plants established early, prior to outplanting, could be the sole cause of the mycorrhizal effect observed at the harvest.

As with other meta-analyses (McGonigle, 1988; Curtis & Wang, 1998; Englund *et al*., 1999), several trials were extracted from each article, and this was not considered a violation of independence. For example, separate trials reported in the same article assessing the effect of AMF on different plant species, or on the same plant species in different years, or the effect of different AMF species, were considered no less independent than two tillage trials of maize from the same laboratory but reported in two separate articles. However, whenever different varieties of the same plant species were used in a single study, the values were pooled because of concerns of lack of independence. This procedure yielded 290 separate trials extracted from 71 articles in 32 journals (see Table 1).

Trials were coded based on the management practice that altered mycorrhizal colonization, including reduced soil disturbance (RD, 62 trials), shortened fallow (SF, 66 trials), inoculation (Inoc, 103 trials), or crop rotation. Crop rotation trials were separated into those comparing mycorrhizal with nonmycorrhizal species in the rotation (M/NM, 34 trials) and those comparing mycorrhizal rotational systems with mycorrhizal continuous cropping systems [CR(M), 25 trials]. The different management practices were further coded based on whether the study was conducted in the field (189 trials) or in the glasshouse (101 trials) and on the basis of whether the experimental plant was a member of the Poaceae or not. The latter coding was used because grasses, which often possess finer root systems than dicotyledonous species, may generally be less mycotrophic than other species (Baylis, 1972; Tawaraya, 2003). The great majority of trials were conducted on annual plants. Trials were also coded to reflect the P availability of the soil, as this factor is well known to affect plant response to colonization (references cited in Allison & Goldberg, 2002). A total of six different methods were used to determine P availability in the selected articles and, unfortunately, there is no reliable way to compare the results from one method to another. It was therefore impossible to compare large numbers of trials, and only a

Table 1 References for articles and details of their experiments

Source	Management practice	No. of trials	Site	Plant type	Growth	P uptake	P treatment
Al-Karaki (2002a)	Inoc	1	F	NG	*	*	*
Al-Karaki (2002b)	Inoc	1	F	NG	*	*	*
Allen *et al*. (2001)	SF	2	F	NG/G	*	*	*
Bagayoko *et al*. (2000)	CR(M)	9	F	NG/G			
Behl *et al*. (2003)	Inoc	1	F	G			
Bell *et al*. (2003)	Inoc	2	P	NG			*
Boswell *et al*. (1998)	SF	2	F	G	* (1)	* (1)	
Brandon *et al*. (1997)	Inoc	1	P	NG	*		*
Chandrashekara *et al*. (1995)	Inoc	1	F	NG	*	*	*
Douds *et al*. (1995)[1]	RD	4	P	G			
El-Ghandour *et al*. (1996)	Inoc	2	F	NG	*	*	
Ellis *et al*. (1992)	CR(M)	4	F	NG/G			
Entry *et al*. (1996)	RD	1	F	G	*	*	
Espindola *et al*. (1998)[2]	SF	5	F	NG		*	
Fagbola *et al*. (1998a)	Inoc	2	F	NG	*	*	
Fagbola *et al*. (1998b)	Inoc	2	F	NG	*		
Feldmann *et al*. (1995)	Inoc	2	F	NG/G	*		*
Fracchia *et al*. (2000)	Inoc	2	P	NG	*		
Galvez *et al*. (2001)	RD	4	F	G	*	*	
Gaur & Adholeya (2000a)	Inoc	6	F	NG	*	*	
Gaur & Adholeya (2000b)	Inoc	6	F	NG	*	*	
Gaur & Adholeya (2002)	Inoc	5	F	NG/G	*	*	
Gavito & Miller (1998)	RD & M/NM	2	F	G			
Gemma & Koske (1997)	Inoc	1	F	G			
Goss & Varennes (2002)	RD	1	P	NG	*		
Gupta *et al*. (2002)	Inoc	1	F	NG	*	*	
Hamel *et al*. (1996)[3]	RD	6	F	G	*	*	*
Hamilton *et al*. (1993)	SF	5	F	NG	* (2)	* (2)	
Höflich *et al*. (1999)	RD	7	F	G			
Hulugalle *et al*. (1998)	SF	2	F	NG	*		
Johnson (1998)[1]	Inoc	1	F/P	G	*	*	*
Kabir & Koide (2002)	SF	3	F	G	*	*	*
Kabir & Koide (2000)	SF	2	F	G	*	*	
Kabir *et al*. (1997, 1998)	RD	6	F	G	*	*	
Kabir *et al*. (1999)	RD & SF	7	P	G	*	*	
Karasawa *et al*. (2001)[1]	M/NM	17	P	G	*		
Khaliq & Sanders (2000)	Inoc	1	F	G	*	*	*
Khaliq & Sanders (1998)	Inoc	1	P	G	*	*	
Khaliq & Sanders (1997)	Inoc	1	P	G	*	*	*
Khare *et al*. (1998)	SF	3	F	G	*	*	
Mamatha *et al*. (2002)	Inoc	2	F	NG	*	* (1)	*
McGonigle *et al*. (1990)	RD	3	F	G	*	*	*
McGonigle & Miller (1996)	RD	2	F	G	*	*	*
McGonigle & Miller (1993)	RD	4	F	G	*	*	
McGonigle *et al*. (1999)	RD	7	F	NG/G	*	*	
Mohammad *et al*. (1998)	Inoc	1	F	G	*	*	*
Mozafar *et al*. (2000)	RD	2	F	G	*	*	
Naik *et al*. (1995)	Inoc	3	F	NG	*	*	*
Nakamoto *et al*. (2001)	RD	1	F	G	*		
Noyd *et al*. (1996)[1]	Inoc	1	F	G	*		*
Oliveira & Sanders (1999)	SF & RD	3	F	NG	*		
Omar (1998)	Inoc	2	P/F	G	*	*	*
Ortas (2003)	Inoc	3	P	G	*	*	*
Pattison & McGee (1997)	SF & RD	13	P	NG	*	* (9)	
Prados-Ligero *et al*. (2002)	Inoc	1	F	NG	*		
Requena *et al*. (1996)	Inoc	3	P	NG	*		
Rubio *et al*. (2003)	Inoc	2	P	G	*	*	*
Rutto *et al*. (2003)[1]	SF	6	P	NG			
Ryan & Angus (2003)	SF & RD	6	F	NG/G	*	*	*
Ryan *et al*. (2002)[2]	M/NM & SF	27	F	G	*	*	

Table 1 *continued*

Source	Management practice	No. of trials	Site	Plant type	Growth	P uptake	P treatment
Sanginga *et al*. (1999)[1]	M/NM	12	P	NG			
Sari *et al*. (2002)	Inoc	2	F	NG	*	*	*
Secilia & Bagyaraj (1994)	Inoc	3	F	G	*	*	*
Singh & Tilak (1991)	SF & Inoc	5	F	G	*	*	*
Stamford *et al*. (1997)	Inoc	1	P	NG	*	*	*
Tarafdar & Rao (1997)	Inoc	6	F	NG	*	* (3)	
Thompson (1994)[4]	Inoc	1	P	NG	*		*
Vivekanandan & Fixen (1991)	SF & RD	6	F	G	*	*	*
Wu *et al*. (2002)	Inoc	27	F/P	NG	*	* (6)	
Xavier & Germida (1997)	Inoc	2	P	NG/G	*	*	*
Zak *et al*. (1998)	SF	1	F	NG			

Management practices included inoculation (Inoc), shortened fallow (SF), reduced soil disturbance (RD), crop rotation using mycorrhizal vs nonmycorrhizal plants (M/NM), and continuous cropping vs crop rotational systems where all crops were mycorrhizal [CR(M)]. The site was either the field (F) or the glasshouse (P for pots). The plant type was either Poaceae (G for grass) or nongrass (NG). An asterisk indicates, for growth, that either yield or biomass was recorded; for phosphorus (P) uptake, that shoot P concentration was determined; and, for P treatment, that the experiment included a P treatment. The value in parentheses indicates the number of trials where the measurements were taken if they were not recorded for all trials.

[1]Mycorrhizal colonization was evaluated in the glasshouse as a bioassay, but biomass was measured in the field. For effects on mycorrhizal colonization, they were considered as pot trials. For Johnson (1998), the shoot P concentration was measured on glasshouse grown plants and was considered a pot trial for that variable.

[2]Growth was reported but so clearly affected by other factors [nitrogen from cover crops in Espindola *et al*. (1998), and root pathogens in some trials in Ryan *et al*. (2002)] that they were not included in yield, biomass and P concentration analyses.

[3]Growth, P uptake and P treatment were measured but values could not be extracted as raw data were not given. All the data were plotted solely as a result of a principle components analysis.

[4]P application to the same field in a separate experiment showed a P limitation.

subsample of trials that used the Olsen method (Olsen *et al*., 1954) were included in analyses involving soil P availability. In one-fifth of the trials, either available soil P or the method used to determine available P was not reported, or P availability was measured only prior to P fertilization.

A meta-analysis is performed on some measure of the effect of the treatment relative to the control from each trial. This so-called 'effect size' standardizes the response and allows for comparisons between studies. In our analyses, we placed in the control group the management practices that are known from previous studies to reduce per cent mycorrhizal colonization. These included longer fallow, soil disturbance, and crop rotation with nonmycorrhizal species. This coding was consistently applied even if, for example, soil disturbance actually increased colonization. Thus, shortened fallow, reduced soil disturbance and avoidance of nonmycorrhizal crops were placed in the +AMF group. In the Inoc trials the control group consisted of the treatment to which no additional mycorrhizal fungi had been added and the +AMF group consisted of the inoculated treatment. In the CR(M) trials, we consistently considered the continuous cropping of one mycorrhizal species as the control group and rotations of mycorrhizal species as the +AMF treatment.

For each trial, we recorded per cent mycorrhizal colonization, harvestable yield, shoot biomass [except for Fagbola *et al*. (1998b) and Khaliq & Sanders (1997), where a combined value of shoot and root biomass was reported] and plant P concentration (where available) of plants from control and +AMF treatments. Only trials that used per cent as the unit of colonization were included in the analysis for the effect of management practice on mycorrhizal colonization. If measurements were taken over time, we recorded colonization from the first harvest, except in some Inoc trials where differences became apparent at the second harvest and were consistently different at later stages. For inclusion in the analyses, per cent mycorrhizal colonization had to have been estimated either from the gridline intersect method or by the proportion of randomly selected root pieces containing AMF (Giovannetti & Mosse, 1980). The latter method may overestimate root colonization (Giovannetti & Mosse, 1980), but we did not consider this to be a significant source of error as we always employed values relative to controls in our analysis rather than absolute values. In fact, when we eliminated the 32 trials that used the root segment method for assessing colonization, there was no significant effect on the result (data not shown).

For analysis of yield, biomass and P concentration, all trials in which mycorrhizal colonization was significantly increased were included, irrespective of the method of estimating colonization. The latest available value reported for biomass was recorded because it best represents the cumulative effect of the treatment. For tissue P concentration we recorded the earliest value reported, as early differences are likely to be important for harvestable yield and biomass production (Grant *et al*., 2001). Later values were recorded if earlier values were measured very early during the course of plant growth such that they were

considered to be more reflective of seed P concentration than the result of subsequent P uptake. If a trial had a P treatment (< 25% of all trials), we recorded the response to additional P. No direct comparisons were made between systems with different inputs, such as high-input vs low-input agroecosystems, or where colonization levels were altered as a result of P fertilizer. In some cases values were visually extracted from published figures.

For our first question regarding the effect of management practice on mycorrhizal colonization, the effect size was simply the difference in colonization between the controls and +AMF treatment:

$$\Delta AM = AM_{+AMF} - AM_{control}$$

(AM, mycorrhizal colonization.) This effect size was considered biologically significant because it reflects the change in fungal activity. If the root length were the same in the two treatments, a disturbance that reduced colonization from 75 to 50% would therefore be considered the same as a disturbance that reduced colonization from 50 to 25%.

To determine the effect of an increased colonization on harvestable yield, biomass or plant P concentration, only trials in which mycorrhizal colonization was increased significantly were selected for analysis. If no means separation was conducted in the original trial, two standard errors of the mean were used to establish a significant difference between treatments. If significance in mycorrhizal colonization could not be clearly established, the trial was excluded from further analysis.

We chose the mycorrhizal response ratio (MR) as the effect size to express the effects of increased colonization on harvestable yield, biomass and P concentration. For example, the effect size for harvestable yield was calculated as:

$$MR_{yield} = Yield_{+AMF}/Yield_{control}$$

By choosing this ratio rather than the difference to represent the mycorrhizal response, a doubling of, say, biomass would be considered the same whether the ratio was 2 : 1 or 8 : 4.

Effect sizes are often weighted in meta-analyses so that trials with better estimates of means (smaller variances) carry more weight than trials with larger variances. This weighting may be important statistically as it accounts for heterogeneities of variance between trials (Gurevitch & Hedges, 1999). Unfortunately, few trials reported measures of variance. Allison & Goldberg (2002) were faced with the same dilemma and weighted effect size based on sample size because this variable has been shown to be inversely proportional to the variance within a trial (Gurevitch & Hedges, 1999). We chose to do the same, but we distinguished between field trials and glasshouse trials and conducted the weighting within each group separately. The few studies that did not report the number of replicates were removed from further analysis. Such studies, however, were included in the correlation plots.

All correlations were conducted in Minitab Release 11 (Minitab Inc., State College, PA, USA), and were transformed when necessary to fulfil the requirements for the statistical analyses. However, all *r*-values given are based on nontransformed data as there is no assumption regarding the distribution for this calculation.

The effect size to express a change in mycorrhizal colonization, ΔAM, was analyzed using a three-factor analyses of variance (ANOVA) as a mixed model in SAS (SAS Institute Inc., Cary, NC, USA). The three factors were management practice [Inoc, RD, SF, M/NM or CR(M)], plant type (grass or nongrass) and site (field or glasshouse). The effect sizes expressing a change in yield, biomass, and shoot P concentration as a result of a significant increase in mycorrhizal colonization, MR_{yield}, $MR_{biomass}$ and MR_{Pconc}, could not be analyzed in three-factor ANOVAs because of confounding main effects that became apparent in this reduced data set. For example, a majority of RD and SF trials that reported on yield, biomass, or shoot P concentration were conducted on grasses, whereas Inoc trials were conducted mostly on nongrasses. In these situations, we conducted single-factor ANOVAs within groups, such as field-grown grasses. Data were transformed to fulfil the requirements of normality and homogeneity of variance when necessary for ΔAM and were always natural log (ln) transformed for MR, as lnMR possesses well-known statistical properties (Hedges *et al.*, 1999). If a treatment combination (management practice × plant type × site) consisted of two or fewer trials, it was excluded from the analysis because the data were not considered robust enough to adequately represent the treatment combination. The 95% confidence interval (CI) around the estimated least significant mean was calculated using the formula:

$$CI = \text{mean} \pm t_{df,\alpha/2} \times SE$$

($t_{df,\alpha/2}$, critical *t*-value; SE, standard error.) For ln MR, the confidence intervals were calculated before back-transforming the values, which resulted in slightly asymmetrical confidence intervals. When the confidence intervals included the MR = 1 reference line, we considered there to be no significant effect of the treatment on the measured variable. Also, treatments were considered significantly different from each other whenever their respective confidence intervals did not overlap.

To ensure that effects on biomass and harvestable yield were the result of increased mycorrhizal colonization and not caused by an indirect effect of management practice, we analyzed $MR_{biomass}$ and MR_{yield} in all the trials where mycorrhizal colonization was *not* increased significantly. In order to obtain a data set of reasonable size for this analysis, we used both $MR_{biomass}$ and MR_{yield} data in a combined data set (MR_{growth}). Where both biomass and harvestable yield were reported in the same trial, we selected $MR_{biomass}$ for the analysis because we hypothesized that biomass is more responsive to an increase in mycorrhizal colonization than harvestable yield. To explore if this was a reasonable assumption, the relationship between

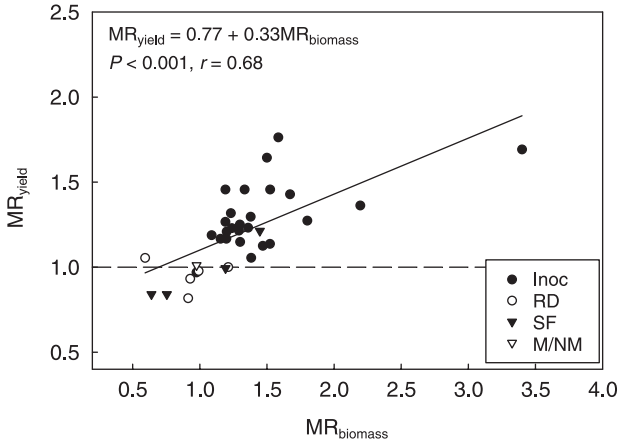

Fig. 1 Correlation between mycorrhizal response ratio (MR) for biomass ($MR_{biomass}$) and yield (MR_{yield}) for field trials with both plant types separated into management practices including inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM). Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in yield between control plants and plants with significantly higher mycorrhizal colonization.

changes in yield (MR_{yield}) and biomass ($MR_{biomass}$) was plotted for a separate data set of field trials in which mycorrhizal colonization was significantly increased. As shown by the slope of the line in Fig. 1, for every unit of change in biomass, yield changed 0.33 times, suggesting that biomass was more responsive than yield in association with a change in mycorrhizal colonization. Thus, by choosing $MR_{biomass}$ for the analysis of growth responses where mycorrhizal colonization was *not* increased, we believe that we increased the probability of detecting an effect not attributable to increased mycorrhizal colonization.

To determine whether the results could be affected by a random selection of a subset of trials, we conducted each of the analyses with a restricted data set in which only one trial per treatment combination per article was used. We arbitrarily chose the first trial in each treatment combination for the analyses. The results from this reduced data set were surprisingly similar to those from the entire data set; in none of the analyses did our interpretations change significantly. We therefore report only the results from the entire data set.

Results

What are the effects of soil disturbance, fallow duration, crop rotation and inoculation on mycorrhizal colonization?

The three-factor ANOVA showed a highly significant effect of management practice on change in mycorrhizal colonization (ΔAM; Table 2). Plant type (grass vs nongrass) nearly significantly ($P = 0.07$) influenced ΔAM. Nongrasses had a higher ΔAM than grasses. The significant management practice × site interaction (Table 2) was a result of a greater ΔAM in the glasshouse for all management practices except for inoculations (Inoc) in which case ΔAM was higher in the field. There were no other significant two-way or three-way interactions.

Table 2 Analysis of variance of the effects of management practice (see the Materials and Methods section), plant type (grass or nongrass), and site (glasshouse or field) on change in mycorrhizal colonization (ΔAM)

Source	d.f.	*F*-value	*P*-value
Management practice (MP)	4	14.71	< 0.0001
Plant type (grass vs nongrass)	1	3.59	0.07
Site (field vs glasshouse)	1	1.35	0.23
MP × plant type	3	2.23	0.08
MP × site	4	3.19	0.02
Plant type × site	1	1.57	0.24
MP × plant type × site	1	1.41	0.20
Error	264		

d.f., degrees of freedom.

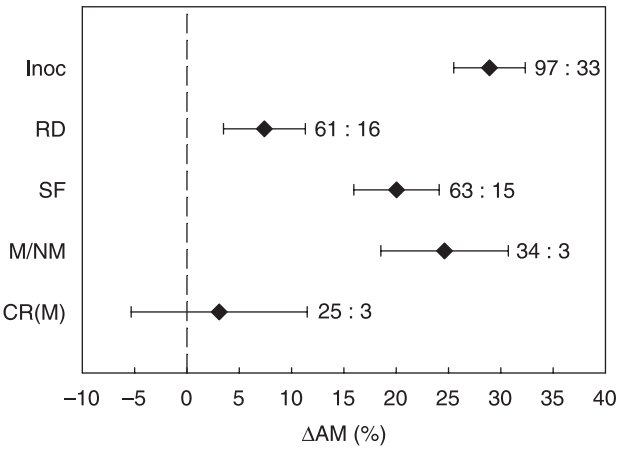

Fig. 2 Means and 95% confidence intervals of effects of inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), avoidance of nonmycorrhizal plants in crop rotations (M/NM), or mycorrhizal rotational systems vs mycorrhizal continuous cropping systems [CR(M)] on change in mycorrhizal colonization (ΔAM), irrespective of site (glasshouse or field) and plant type (grass or nongrass). The reference line of zero indicates that there is no effect of the management practice on per cent mycorrhizal colonization. The numbers after each mean and confidence interval refer to the number of trials and articles, respectively, that were included in the calculation.

The confidence intervals of ΔAM for all management practices except CR(M) did not include zero, indicating with 95% confidence that inoculation, reduced soil disturbance (RD), shortened fallow (SF) and rotation with a mycorrhizal crop instead of a nonmycorrhizal crop (M/NM) all increased mycorrhizal colonization in nonsterile soils (Fig. 2). Inoc, SF, and M/NM altered mycorrhizal colonization more than did RD or crop rotations with mycorrhizal plants CR(M). The values in the M/NM and the CR(M) trials, however, were based on

only three articles. Because it is possible that ΔAM was highest in the Inoc trials only because the researchers chose to inoculate when there was a low indigenous AMF inoculum potential, we compared mycorrhizal colonization among the control groups. We found that mycorrhizal colonization in the Inoc trial controls (19.8 ± 3.3, mean ± 95% CI) was not significantly different from that in the controls in the SF (23.2 ± 3.9), RD (23.1 ± 3.8) or M/NM (23.6 ± 5.6) trials.

Is an increased mycorrhizal colonization associated with changes in harvestable yield, biomass, and P concentration of the host plant?

The three-factor ANOVA as performed on ΔAM could not be performed on yield. Only one glasshouse trial reported on yield and therefore, according to the criteria we set, it was excluded from the analysis. In addition, plant type was confounded by management practice. A majority of Inoc trials that reported on yield were conducted on nongrasses, whereas SF and RD trials were conducted mostly on grasses. Therefore, we were only able to calculate average yield increases as a consequence of a significant increase in mycorrhizal colonization. The overall yield increase in the field, irrespective of plant type and management practice, was 23% ± 8% (mean ± 95% CI). For the field Inoc trials (consisting of two grass trials and 34 trials with nongrasses), the average yield increase was 34% ± 9%. For RD trials (consisting of 11 grass trials and one trial with a nongrass), there was a slight, but nonsignificant, yield reduction of 3% ± 15%, and for the SF trials (consisting of six grass trials and one trial with a nongrass), the average yield increase was 27% ± 21%. These values for each of the management practices cannot be compared amongst themselves because they are confounded by plant type, as mentioned above.

As with yield, the three-factor ANOVA could not be performed on biomass because of confounding effects. The RD and SF trials that reported on biomass were conducted solely on grasses in the field. The original data set contained other treatment combinations under those management practices, but because of their low frequency (two or fewer trials) they were removed from the data set prior to the analysis. Therefore, we performed a single-factor ANOVA to test the effect of management practices on field-grown grasses. Nongrasses were included in the Inoc trials because a separate analysis showed that $MR_{biomass}$ did not differ between grasses and nongrasses in this management practice ($P = 0.90$, $F = 0.02$, $df_{error} = 38$). The ANOVA showed that management practice significantly affected $MR_{biomass}$ ($P < 0.001$, $F = 6.43$, $df_{error} = 62$), such that $MR_{biomass}$ was increased more by Inoc and SF than by RD (Fig. 3). The M/NM trials were all extracted from a single article (Ryan *et al.*, 2002). The Inoc trials contained enough glasshouse studies to allow us to test for the effect of site (glasshouse vs field) on $MR_{biomass}$. Here biomass increased significantly more ($P = 0.006$, $F = 8.10$, $df_{error} = 70$) in glasshouse trials (95% CI 84–304%) than in field trials (95% CI 35–83%). This difference, however, was not related to a higher ΔAM in glasshouse trials because this showed the opposite trend, as mentioned above.

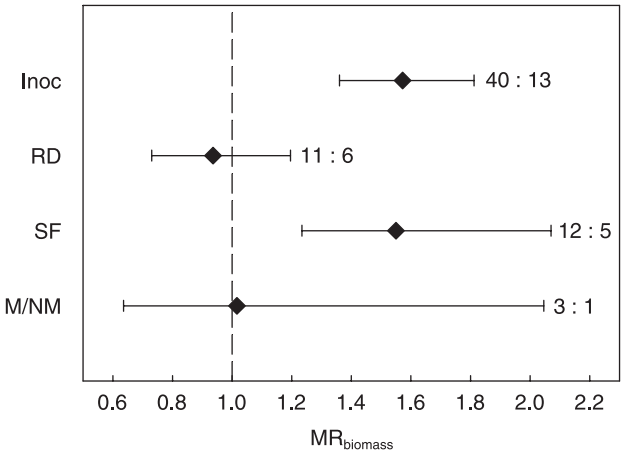

Fig. 3 Means and 95% confidence intervals of effect of inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM) on mycorrhizal response ratio for biomass ($MR_{biomass}$). The analysis was conducted on field-grown grasses only, except for the Inoc treatment, which also included field-grown nongrasses. Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in biomass between control plants and plants with significantly higher mycorrhizal colonization. The numbers after each mean and confidence interval refer to the number of trials and articles, respectively, that were included in the calculation.

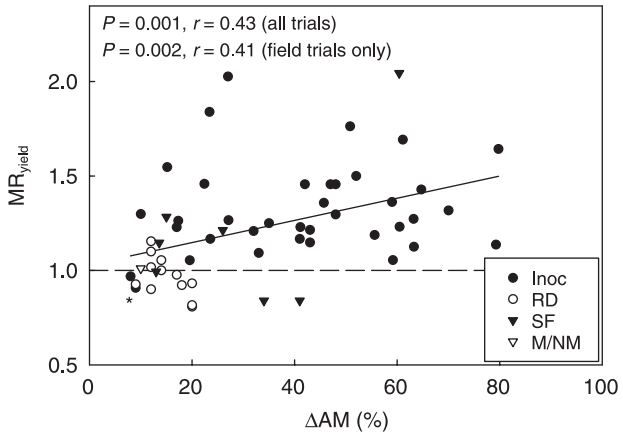

Fig. 4 Correlation between change in mycorrhizal colonization (ΔAM) and mycorrhizal response ratio for yield (MR_{yield}) for field and glasshouse trials and both plant types separated into management practices including inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM). Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in yield between control plants and plants with significantly higher mycorrhizal colonization. The single glasshouse trial is indicated by an asterisk.

There was a significant positive relationship between ΔAM and MR_{yield} for all trials ($P = 0.001$, $r = 0.43$, $n = 56$; Fig. 4)

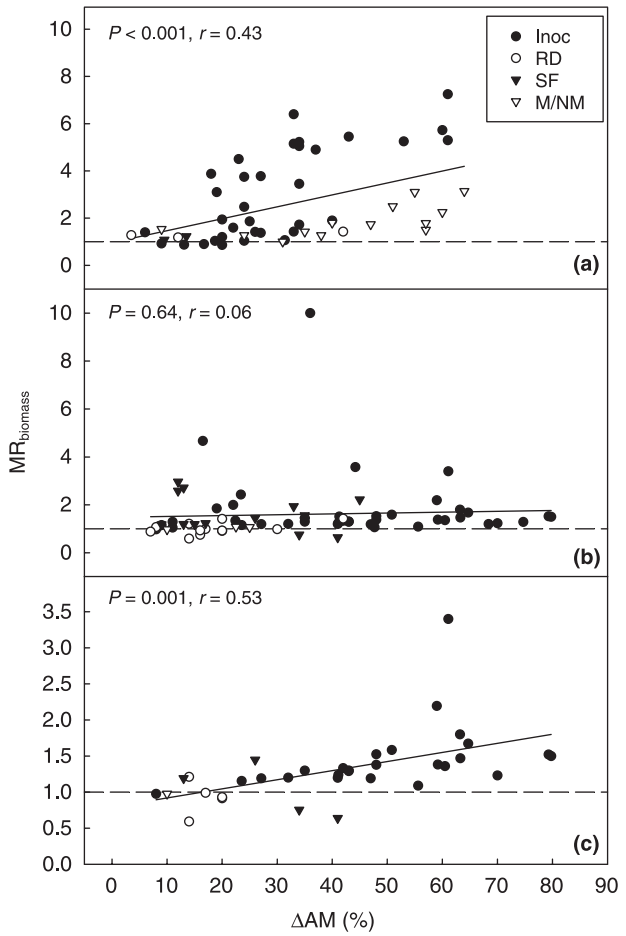

Fig. 5 Correlation between change in mycorrhizal colonization (ΔAM) and mycorrhizal response ratio for biomass ($MR_{biomass}$) for glasshouse trials (a), field trials (b), and field trials that also reported on yield (c) with both plant types separated into management practices including inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM). Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in biomass between control plants and plants with significantly higher mycorrhizal colonization. The outlier in (b) is from Wu *et al*. (2002), where the inherent inoculum potential was very low and the control plants were severely P limited. Please note the difference in scale in (c).

and for field trials only ($P = 0.002$, $r = 0.41$, $n = 55$; Fig. 4). For the relationship between ΔAM and $MR_{biomass}$, however, there was a significant positive relationship with glasshouse-grown plants ($P < 0.001$, $r = 0.43$, $n = 52$; Fig. 5a), but not with field-grown plants ($P = 0.64$, $r = 0.06$, $n = 68$; Fig. 5b). Because one would normally expect a good correspondence between vegetative growth and yield (Rathcke & Lacey, 1985; Bazzaz *et al*., 1987), we decided to plot a subset of the trials in Fig. 5b for which yield has also been reported. Within this subset of data, there was indeed a significant correlation between ΔAM and $MR_{biomass}$ ($P = 0.001$, $r = 0.53$, $n = 35$; Fig. 5c). A sensitivity analysis of the data in Fig. 5b showed that the non-significant result was driven by five data points, all of which had greater biomass responses at lower ΔAM compared with the other trials. Three of the five trials were SF trials with ΔAM < 20 and $MR_{biomass} > 2$. These trials are from Vivekanandan & Fixen (1991) where biomass data from very early in the season (36 days after planting) were reported. Two out of the five trials were Inoc trials with $MR_{biomass} > 4$, which had been conducted in degraded soils with very low inherent inoculation potentials. When these five trials were removed from Fig. 5b, the relationship between ΔAM and $MR_{biomass}$ became significant ($P = 0.006$, $r = 0.35$, $n = 63$). Irrespective of the relationship between ΔAM and $MR_{biomass}$, the majority of the trials in Figs 4 and 5 were above the reference lines (MR_{yield} and $MR_{biomass} = 1$), which is to say that, in most cases in which mycorrhizal colonization increased, yield or biomass also increased.

In trials where mycorrhizal colonization was not significantly increased, the effect of management practice on MR_{growth} (a combined set of results including those of MR_{yield} and $MR_{biomass}$) was not significant ($P = 0.58$, $F = 0.66$, $df_{error} = 39$). In this analysis, the mean MR_{growth} values for the SF, RD, M/NM and Inoc trials were not significantly different from unity [1.00 ($n = 12$), 0.94 ($n = 13$), 1.02 ($n = 9$) and 1.15 ($n = 9$), respectively]. This suggests that the increase in biomass or harvestable yield seen in the +AMF treatment in the SF and Inoc trials was not caused by the management practice independent of an increase in mycorrhizal colonization.

As with yield and biomass, the three-factor ANOVA could not be performed on shoot P concentrations because of confounding effects. Because glasshouse trials that reported plant P concentration were Inoc trials only, glasshouse trials were removed and only field trials were analyzed. Also, the M/NM, RD and SF field trials included only grasses, but nongrasses were included from the Inoc trials because a previous analysis had shown that nongrasses and grasses did not differ significantly from each other ($P = 0.95$, $F < 0.01$, $df_{error} = 23$). This single-factor ANOVA showed that management practices differed significantly from each other ($P = 0.028$, $F = 3.32$, $df_{error} = 47$). M/NM showed no significant increase in MR_{Pconc}, whereas SF, RD and Inoc trials all resulted in significant, positive values (Fig. 6). In the Inoc, RD and SF trials, the confidence intervals did not include unity, indicating that a significant increase in mycorrhizal colonization was associated with a significant increase in P concentration. All the M/NM trials were extracted from a single article (Ryan *et al*., 2002). There was a significant positive relationship between ΔAM and MR_{Pconc} for all trials ($P = 0.004$, $r = 0.35$, $n = 62$) and for field trials only ($P = 0.002$, $r = 0.42$, $n = 54$), but there was a considerable amount of scatter in the plot (Fig. 7).

In cases where mycorrhizal colonization is increased, is there a correlation between increased P uptake and increased harvestable yield or biomass?

There was a significant positive correlation between MR_{Pconc} and MR_{growth} for all trials ($P = 0.005$, $r = 0.32$, $n = 61$; Fig. 8)

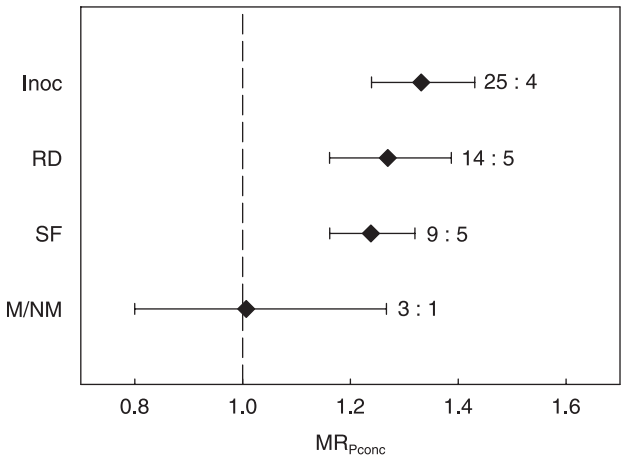

Fig. 6 Means and 95% confidence intervals of effects of inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM) on mycorrhizal response ratio for phosphorus (P) concentration (MR_{Pconc}). The analysis was conducted on field-grown grasses only, except for the Inoc treatment, which also included field-grown nongrasses. Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in P concentration between control plants and plants with significantly higher mycorrhizal colonization. The numbers after each mean and confidence interval refer to the number of trials and articles, respectively, that were included in the calculation.

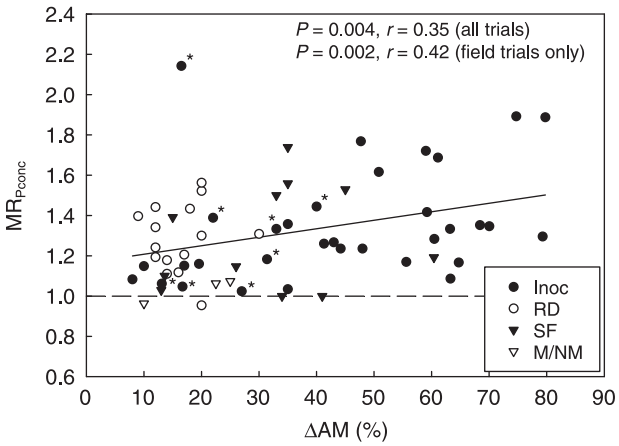

Fig. 7 Correlation between change in mycorrhizal colonization (ΔAM) and mycorrhizal response ratio for phosphorus (P) concentration (MR_{Pconc}) for field and glasshouse trials and both plant types separated into management practices including inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM). Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in P concentration between control plants and plants with significantly higher mycorrhizal colonization. The outlier is from Johnson (1998), where the inherent inoculum potential was very low and the control plants were severely P limited. The glasshouse trials are indicated by asterisks.

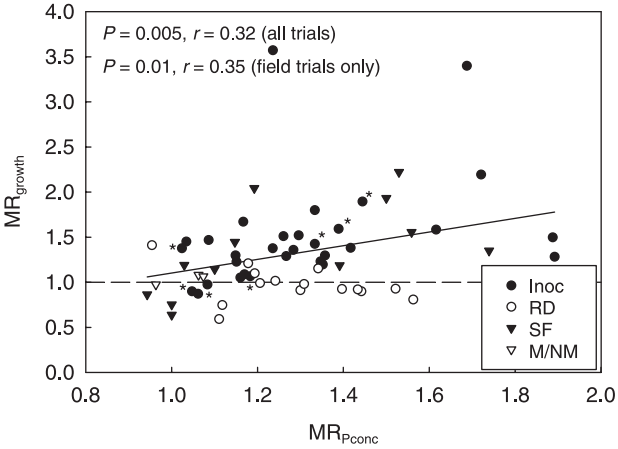

Fig. 8 Correlation between mycorrhizal response ratio for phosphorus (P) concentration (MR_{Pconc}) and that for growth (MR_{growth}) separated into management practices including inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM). Mycorrhizal colonization was significantly increased in all trials included in this analysis. The reference line of unity indicates that there is no difference in growth between control plants and plants with significantly higher mycorrhizal colonization. The glasshouse trials are indicated by asterisks.

and for field trials only ($P = 0.01$, $r = 0.35$, $n = 54$; Fig. 8), suggesting that early differences in P concentration were associated with differences in biomass or harvestable yield. However, it appeared that, for RD trials alone, higher MR_{Pconc} was not associated with higher MR_{growth}.

What factors affect whether increased colonization results in benefit to the host plant?

In light of the common notion that AMF are less beneficial under conditions of high available soil P, we explored the relationship between Olsen P and MR_{growth} (Fig. 9). It appeared that lower available soil P allowed a greater potential growth response (ranging up to approximately 3.5 for available soil P concentrations of ≤ 10 μg g^{-1}) as a result of an increased mycorrhizal colonization than higher available soil P, which supported a much smaller range of MR_{growth} (less than 1.5 beyond 30 μg g^{-1}). However, as indicated by the scatter in MR_{growth} at lower available soil P, there are other, unaccounted factors that determine the size of the growth response. We chose not to model the relationship but instead to simply illustrate the great variability among studies without implying any particular mathematical relationship. Because ΔAM showed the same trend as MR_{growth} and was reduced at higher Olsen P (data not shown), it is possible that the effect of Olsen P on MR_{growth} was mediated by ΔAM.

The relationships between $AM_{control}$ and $MR_{biomass}$ for glasshouse trials (Fig. 10a) and for field studies (Fig. 10b) were similar to the relationship between Olsen P and MR_{growth}. The potential growth response was large at low inoculum potentials ($MR_{biomass}$ up to 10.0 below 10%) but much smaller with higher

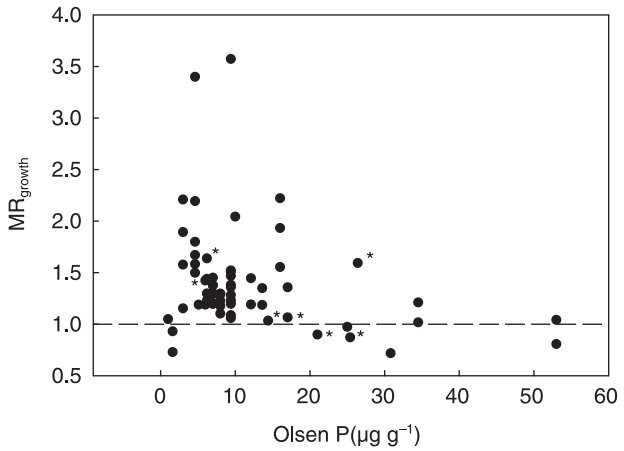

Fig. 9 Correlation between Olsen phosphorus (P) concentration and mycorrhizal response ratio for growth (MR_{growth}). The reference line of unity indicates that there is no difference in growth between control plants and plants with significantly higher mycorrhizal colonization. The glasshouse trials are indicated by asterisks.

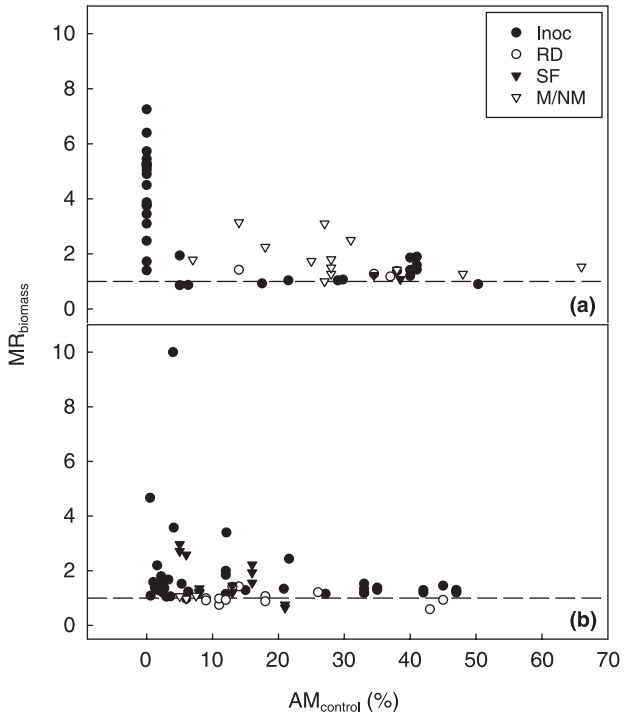

Fig. 10 Correlation between mycorrhizal colonization of control plants ($AM_{control}$) and mycorrhizal response ratio for biomass ($MR_{biomass}$) for glasshouse trials (a) and field trials (b), with both plant types separated into management practices including inoculation (Inoc), reduced soil disturbance (RD), shortened fallow (SF), or avoidance of nonmycorrhizal plants in crop rotations (M/NM). The reference line of unity indicates that there is no difference in biomass between control plants and plants with significantly higher mycorrhizal colonization.

inherent inoculum potentials (less than 2.5 beyond 30%). However, as indicated by the great scatter in $MR_{biomass}$ at lower values of $AM_{control}$, inherent inoculum potential alone was not a particularly reliable predictor of the response to a significant increase in mycorrhizal colonization. As with the relationship between Olsen P and MR_{growth}, we chose not to model this relationship so as not to imply any particular mathematical relationship.

Discussion

The meta-analysis approach allowed us to quantify the effects of various management practices on mycorrhizal colonization, yield, biomass, and shoot P concentration. Whereas inoculations (Inoc) and shorter fallow (SF) significantly increased mycorrhizal colonization, yield, biomass, and shoot P concentration, reduced disturbance (RD) was less effective in increasing mycorrhizal colonization and had no significant effect on yield or biomass in spite of higher shoot P concentrations (Figs 2, 3 and 6). Avoiding nonmycorrhizal plants in crop rotations (M/NM) had a large, positive effect on subsequent mycorrhizal colonization, whereas, compared with continuous cropping, crop rotations with mycorrhizal plants [CR(M)] had no significant effect. The effect of crop rotations on yield, biomass and plant P concentration could not be explored adequately because of the low number of trials in these two management practices. Results from these meta-analyses are useful if the objective is either to choose a management practice that maximizes the benefits of an increased mycorrhizal colonization or to learn about the consequences of a practised management regime on mycorrhizal colonization. We discuss the effect of management practice in more detail below.

As a result of our coding we could explore the effect of site (glasshouse vs field) and plant type (grass vs nongrass) on growth in response to an increased mycorrhizal colonization within inoculation trials. Plants grown in the glasshouse showed significantly greater responses to an increased mycorrhizal colonization than field-grown plants, but this was not attributable to a higher ΔAM in the glasshouse. Instead, it is possible that stresses that could reduce the biomass response, such as drought, pest infestation, predation, and competition with other plants, are more common under field conditions. This result is consistent with the prevailing belief that caution must be taken when extrapolating results from glasshouse trials to field situations. Contrary to expectations, grasses and nongrasses did not respond differently to an increased mycorrhizal colonization within inoculation trials. This is interesting given the common belief that grasses are generally less responsive, and further studies may be needed in this area to clarify this relationship.

The large increase in mycorrhizal colonization from inoculations, shorter fallow, and avoidance of nonmycorrhizal plants (Fig. 2) indicated that low inoculum potential often limits mycorrhizal colonization. Furthermore, it also showed that

this limitation could be alleviated by either adding more fungi through inoculations or maintaining or increasing the abundance of indigenous AMF through shorter fallows or cultivation of mycorrhizal plants. While inoculation was the management practice that led to the largest increase in colonization, it is not always the most practical or economical. However, in certain systems, such as land reclamation or high-value plant production, this practice might be feasible. Shorter fallow, however, is a comparatively easy and cheap management practice to use in the field. It also combats soil erosion, which would be an added benefit. However, growing cover crops to replace the bare fallow might be difficult in certain regions of the world where water is limiting. In such cases, perhaps a more viable solution would be to keep the inoculum potential as high as possible by avoiding nonmycorrhizal plants in crop rotation. Reducing the level of disturbance through minimal tillage and no-tillage practices had less effect on mycorrhizal colonization. Two factors can help explain this. First, disturbance is thought to affect mostly hyphae (Evans & Miller, 1988, 1990), whereas spores and colonized root pieces may still be infective. Secondly, when disturbance occurred, it was closely followed by planting in the majority of trials, so hyphal fragments would likely have remained viable long enough to colonize subsequently grown plants (Kabir *et al.*, 1999). Using crop rotations rather than continuously growing the same crop had the least effect on mycorrhizal colonization. This is not surprising because all plants in this management practice were mycorrhizal. However, crop rotation could be an important agronomical practice as it has been shown to prevent build-up of less beneficial AMF (Johnson *et al.*, 1992) and to reduce pest incidence (Bagayoko *et al.*, 2000).

Inoculations and shorter fallows both significantly increased yield and biomass (Fig. 3). It is interesting to note that the average yield increase for field inoculation trials in our data set was 34%, which is very close to the 37% recorded by McGonigle (1988) using a completely different data set. Perhaps the most surprising finding of this meta-analysis, however, was the plant response to reduced disturbance. This is a management practice that has been promoted by agronomists to reduce erosion and by mycorrhiza researchers to increase AMF inoculum potentials. In spite of higher plant P concentrations, there was no increase in growth with this management practice, suggesting that plant growth was limited by factors other than P. Considering the linear, positive relationship between ΔAM and $MR_{biomass}$ (Fig. 5), it is possible that changes in mycorrhizal colonization by this particular management practice were insufficient to promote biomass. However, growth reductions have been reported before in no-till systems, and have been attributed to increased soil compaction, reduced temperature during planting, poor drainage in certain soils (Lal, 1989), or build-up of plant growth inhibiting soil microorganisms (Simpfendorfer *et al.*, 2002). Thus, it is possible that other factors associated with no-till constrained possible benefits from increased mycorrhizal colonization.

As did McGonigle (1988), we found a significant but weak relationship between a change in mycorrhizal colonization (ΔAM) and a change in yield (MR_{yield}; Fig. 4). Therefore, while an increase in mycorrhizal colonization appears to be associated with an increase in yield, the scatter in the plot suggests that increase in mycorrhizal colonization cannot be the sole predictor of increase in yield. Based on this weak relationship, McGonigle (1988) concluded that the evidence for mutualism in the field was poor. However, even the lack of a significant, positive relationship would not indicate that there was no mutualism. For example, even though Figs 4 and 5b show a weak relationship, or no significant relationship at all between the two variables, a significant increase in mycorrhizal colonization in inoculation and shorter fallow trials resulted in mean MR_{yield} and $MR_{biomass}$ values that were significantly greater than 1 (Fig. 3).

A strong relationship between variables generates some predictive ability. Our low *r*-values in Figs 4, 5 and 7 indicate that, while an increase in mycorrhizal colonization is likely to generate positive responses in yield, biomass and P concentration, the size of the response cannot be accurately predicted from ΔAM. Perhaps one should be surprised not by the lack of strong relationships, but rather that significant relationships were found at all, given the range of conditions of the trials that were compared in these meta-analyses. For example, management practices, site, inherent inoculum potential and available soil P concentrations are all expected to affect the response to increased mycorrhizal colonization. None of these factors was controlled for in the correlation plots. In addition, other factors that were not included in the meta-analysis, such as interactions between plant and fungal species (Klironomos, 2003), climate, and duration of the study, may also influence the response to increased mycorrhizal colonization. Furthermore, if the yield or biomass response to an increased mycorrhizal colonization is nonlinear, i.e. the same change in colonization has a different response depending on the indigenous (control) inoculum potential, then a ratio would have been preferable to express a change in colonization levels. However, as this nonlinearity might very well differ between plant species and conditions, we decided that a more conservative approach was to use ΔAM. The fact that we do see significant positive relationships in spite of all other, uncontrolled variables suggests that AMF is one important variable to consider in plant production systems.

A significant increase in mycorrhizal colonization led to a significant decrease in biomass in 2% of all trials (glasshouse and field). Statistically significant and insignificant biomass reductions ($Mr_{biomass} < 1$) were found in 13% of all trials and averaged 14% ± 6% (mean ± 95% CI). These trials consisted mostly of reduced disturbance trials (eight RD, two SF, five Inoc, and one M/NM) (Fig. 5a and b), where no-till practices could have introduced other growth limitations unrelated to AMF, as discussed above. Furthermore, the two shorter fallow trials below the reference line in Fig. 5b were from Ryan *et al.*

(2002), where problems of pathogenic fungi were reported in other trials in the same article. Available soil P was higher than 20 μg g^{-1} (Olsen) in 11 out of the 16 trials and P fertilizers were applied in eight trials, which would have produced conditions where AMF would be unlikely to be beneficial. This is supported by Fig. 9, which indicates that increased mycorrhizal colonization had the smallest consequences in soils of high available soil P. However, the great scatter at lower values in both Figs 9 and 10 indicates that lower available soil P concentrations or inoculum potentials would not necessarily generate large, positive growth responses, but could indicate conditions where large growth responses could potentially occur. In Fig. 5, quite a few trials showed more than a doubling in biomass ($Mr_{biomass}$ > 2) as a result of an increased mycorrhizal colonization. Many were inoculation trials, where mycorrhizal colonization of control plants was below 5% and where available soil P was below 5 μg g^{-1}. Those conditions were clearly more likely to produce positive growth responses from increased mycorrhizal colonization. The soils for these studies were often collected from sites where the inoculum potential was very low, such as eroded or reclaimed soils, or subsoil. One could easily argue that a positive plant response to AMF is most likely to be expressed under those conditions. Because eroded, reclaimed or subsoil trials fulfilled our requirement of using nonsterile soils, we did not exclude them from our analyses.

Compared to the biomass response, the effect on shoot P concentration was more uniform among inoculations, reduced disturbance and shorter fallow trials (Fig. 6) and also considerably smaller for inoculations and shorter fallow trials. The smaller values of MR_{Pconc} compared to $MR_{biomass}$ were most likely a result of dilution of P in the +AMF treatment as a result of the growth response. The consistent increase in P concentration with increased mycorrhizal colonization shown with these three management practices (inoculations, reduced disturbance and shorter fallow) is somewhat contradictory to the work by Fitter (1985, 1986) in natural systems, where a role for AMF in P uptake was not universal. Perhaps this difference is a reflection of the different stresses plants experience in natural and primarily agricultural systems. In agricultural systems, stresses from competition and predation tend to be minimized because of weeding and pesticide applications, which could very well enhance the P effect of AMF. In addition, mycorrhizal researchers sometimes create a situation where P limits plant growth by minimizing all other nutritional stresses. Increases in available soil P in no-till compared to conventionally tilled systems have been reported before (Lal *et al.*, 1994) and may not be related to an increased mycorrhizal colonization. However, Evans & Miller (1988) observed that the advantage of no-till was lost following radiation and application of benomyl, suggesting that a biological factor was involved. Unfortunately, there were too few reduced disturbance trials where mycorrhizal colonization was not increased and P uptake was reported in our data set for a statistical analysis. In any case, the consistent increase in P uptake as a result of the three management practices (inoculation, reduced disturbance and shorter fallow) is potentially very important in light of the frequent P limitations for plant growth in many parts of the world. Even in high-input systems, more efficient use of applied P will become necessary because of pollution concerns and the depletion of the world's high-grade P ore deposits (Cathcart, 1980). Therefore, AMF could become an increasingly important factor to consider in food production systems.

We showed that early effects on shoot P concentration were associated with later effects on plant growth (Fig. 8). Because greater mycorrhizal colonization corresponded to an increased plant P uptake, the relationship in Fig. 8 suggests that the greater biomass in the +AMF treatments in the shorter fallow and inoculation trials was a result of enhanced P uptake. However, correlation does not indicate causation, and it is possible that there were other factors involved that we did not identify. Indeed, there is a considerable amount of scatter in Fig. 8. For the majority of reduced disturbance trials, MR_{growth} was smaller than MR_{Pconc}. This indicates that P concentration increased in the shoots and that growth was limited by factors other than P, as discussed previously. In cases where MR_{growth} was larger than MR_{Pconc}, the increased growth in the +AMF treatment diluted P, possibly because of an alleviation of a P limitation. The two outliers in this category in Fig. 8 are from Gaur & Adholeya (2000a, 2002). In these trials, ΔAM was greater than 70% and Olsen P was lower than 10 μg g^{-1}, making the experimental conditions ideal for detecting an effect of an increased mycorrhizal colonization.

We have summarized 15 years of work with AMF in nonsterile soils. By no means do we claim to have included every study published during that time period as we were limited by the database that we searched. Moreover, one could easily argue that the effects seen here are overestimates of the expected effects because researchers often design mycorrhiza experiments only when they suspect mycorrhizal fungi to limit productivity. Also, the literature is likely to be biased in favor of positive results. However, using the meta-analysis approach, we were able to provide quantitative measures of the effect of AMF on plant performance over a wide range of conditions.

Recommendations

In order to facilitate better comparisons among trials for future meta-analyses, authors should provide some measure of the variance for the estimated means. Moreover, use of the same analytical method to assess available soil P would allow comparisons. One method that is not affected by soil pH or P source is the iron oxide-impregnated filter strip method (Bramley & Roe, 1993), where the filter strip mimics a plant root. Root colonization should optimally be expressed as both per cent of root length colonized and absolute root length colonized, because treatment effects on root growth could lead to contradictory results, as apparent in Rubio *et al.* (2003) or Anderson *et al.* (1987). Mycorrhizal colonization and plant P concentration

should be determined early in the growing season, as early differences can disappear over time, as shown in Gavito & Miller (1998) and Singh & Tilak (1991). Some researchers have chosen to separate overall mycorrhizal colonization into categories of arbuscular, vesicular and hyphal colonization, which may be useful as this separation can estimate symbiotic activity (e.g. Johnson, 1993). However, it is possible that even though mycorrhizal colonization is the easiest measurement, it is not the best measure of either fungal abundance or function. Kabir *et al.* (1997), for example, showed significant differences in hyphal densities over the whole season, whereas differences in root colonization disappeared. In addition, disturbances such as tillage can severely reduce the external mycelium, and thus function, while having no effect on root colonization.

Finally, if effects relating to P are of interest, a P treatment ought to be included. Unless there is a record of previous P limitation, or if other benefits from the mycorrhizal symbiosis are investigated, there should be no *a priori* reason to expect benefits of an increased mycorrhizal colonization.

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