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Nutrient acquisition and community structure in co-occurring mycotrophic and non-mycotrophic old-field annuals

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Summary

1. Three annual plant species, *Abutilon theophrasti*, *Amaranthus retroflexus* and *Setaria lutescens* were grown together in field plots at two different phosphorus levels and in either fumigated soil, fumigated soil which was subsequently re-inoculated with spores of the mycorrhizal fungus *Glomus intraradices* or untreated soil containing indigenous mycorrhizal fungi.

2. The response of each plant species to the mycorrhizal treatments differed significantly. The results indicated that mycorrhizal fungi reduced the growth of *Amaranthus* (non-mycotrophic) and increased the growth of *Abutilon* (mycotrophic). Mycorrhizal treatment had little effect on the performance of *Setaria* (mycotrophic).

3. Significantly higher concentrations of phosphorus in mature reproductive parts of both mycotrophic species in treatments where mycorrhizal fungi were present suggest that the mycorrhizal symbiosis could significantly affect the quality of seed and may have long-term effects on the structure of plant communities.

Key-words: Abutilon theophrasti, *Amaranthus retroflexus*, phosphorus allocation, *Setaria lutescens*, vesicular–arbuscular mycorrhizas

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Introduction

It is widely accepted that the vesicular-arbuscular mycorrhizal (VAM) symbiosis between plant roots and zygomycetous fungi can improve plant phosphorus nutrition and growth (Harley & Smith 1983). While the evidence for host benefit has been demonstrated in numerous pot experiments, results from field investigations of the ecological significance of VAM are inconclusive (Fitter 1985, 1990).

Although a direct benefit of VAM fungi on plant nutrition has not been adequately demonstrated in the field (McGonigle 1988), studies in recent years demonstrating that interspecific differences in response to VAM infection are large suggest that the mycorrhizal symbiosis may significantly affect plant competition and community structure. Grime *et al.* (1987) observed that floristic diversity was higher in experimental microcosms of co-existing plants in the presence of VAM fungi than in their absence. By reducing VAM fungal colonization using the fungicide iprodione Gange, Brown & Farmer (1990) observed a decrease in the diversity in old-field plant communities. However, neither of these studies related the effects of VAM on community structure to the phosphorus acquisition of the plant species involved and very few investigations have looked at phosphorus allocation of plants of different mycorrhizal status in the field.

Janos (1980, 1985) hypothesized that under conditions of low phosphorus availability the absence of VAM will result in dominance by species of non-mycotrophic or low mycotrophic status. Indeed, phosphorus availability affects the functioning of the VAM symbiosis and may be important in interspecific competition. However, the effect of increased phosphorous nutrition by VAM can be significantly reduced at high root density (Koide 1991; Koide & Li 1991) and therefore mycotrophic plants growing in dense communities may not benefit from being mycorrhizal owing to the lack of available phosphorus to the extra-radical VAM hyphae.

Benefit from the VAM symbiosis may not be important to plant communities in only a single generation or growth season. In experiments carried out in greenhouse conditions mycorrhizas significantly affected the offspring vigour of *Avena fatua* L.

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(Lu & Koide 1991; Koide & Lu 1992) and therefore have the potential to exert a significant influence on future generations of mycotrophic species.

In this investigation we grew three species of old-field annuals together in the field. The species co-exist naturally and they range in their mycotrophic status from being non-mycotrophic to strongly mycotrophic. The three species were grown in the presence and absence of VAM fungi and at low and high levels of phosphorus in order to test whether (1) the mycorrhizal symbiosis affects plant growth, nutrient acquisition and allocation under differing conditions of nutrient availability, and (2) any effects of the VAM symbiosis could alter community structure in this and in subsequent generations.

Materials and methods

FIELD SITE AND FUMIGATION

The field site was located at the R. A. Larson Agricultural Research Center at Rock Springs (Centre County, Pennsylvania, USA). The soil is a Hagerstown silt-clay loam (pH 5·8) with a bicarbonate extractable phosphorus concentration of 6 μg g^{-1}. Areas of the field site which were designated as being non-mycorrhizal or which were to be re-inoculated with VAM fungal spores were fumigated by injection with a mixture of chloropicrin and methyl–bromide gas (33:67) on 20 May 1991. The fumigant persisted only for a few days at the field site under the conditions that the fumigant was used. More than 3 weeks were allowed after fumigation to facilitate diffusion of the fumigant out of the soil prior to planting. Other areas of the field were left untreated and therefore retained the indigenous VAM fungal population. The site was subsequently marked into 2 × 2 m plots with 1 m spacing between. On 24 May nitrogen (50 kg N ha^{-1} as NH_4NO_3) was applied to all plots and phosphorus (60 kg P ha^{-1} as super phosphate) was applied to half the plots.

EXPERIMENTAL DESIGN

The experiment was a three-factor design arranged into blocks using a split-plot layout with mycorrhizal treatment as the main plot and phosphorus treatment as a subplot and species as an additional factor. There were four blocks, each block containing four replicate plots of the three mycorrhizal treatments and the two phosphorus treatments (total of 96 plots). The mycorrhizal treatments were fumigated soil (MB), fumigated and re-inoculated soil (MBG) and untreated soil (C), and the two phosphorus applications were no phosphorus application (P_0) and phosphorus application (P_1).

PLANTING AND INOCULATION

Seeds of *Abutilon theophrasti* Medic., *Amaranthus retroflexus* L. and *Setaria lutescens* (Weigle) Hubb (F. & J. Seeds, California, USA) were sown into the plots on 14 June. The decision to use these three species was made because they are all annuals which co-exist in much of eastern USA. Much information already exists regarding the physiology and population biology of *Abutilon* and *Setaria* (Weiland & Bazzaz 1975; Bazzaz 1984; Garbutt & Bazzaz 1987); they exhibit differing responses to mycorrhizal infection (Koide & Li 1991). *Amaranthus* is a non-mycotrophic species. In order to improve the germination rate, prior to planting, seeds of *Abutilon* were treated with concentrated H_2SO_4 (15 min). Half of the fumigated plots were re-inoculated by raking in, to a depth of 6 cm, 681 g of Nutri-link® (an inoculum in the form of mycorrhizal spores on a clay based carrier; NPI, Utah, USA), containing approximately 4×10^5 spores of *Glomus intraradices* Schenk & Smith. This number of spores is higher than levels naturally. *Glomus intraradices* was chosen because it was commercially available in large quantities. Previous tests showed that the carrier had no independent effects on plant performance (L. Staszak & R. T. Koide, unpublished data). Approximately 770, 2560 and 930 seeds of *Abutilon*, *Amaranthus* and *Setaria*, respectively, were sown into each plot. Seed numbers were estimated to result in approximately 30 plants per plot (based on a knowledge of the germination rate and mortality). All plots were raked before planting and the seed was sown uniformly by hand. Other plant species which had not been planted in the plots were weeded by hand.

MEASUREMENT OF VAM INFECTION AND NUTRIENT ANALYSIS

On 21 July, 23 August and 23 September four individuals of each species were removed from one replicate plot of all of the treatment combinations within each block (total of 24 plots). These three dates are subsequently referred to as harvests. At each of these harvests a different replicate set of 24 plots was used so that harvesting was never repeated in a plot. Four random coordinates were assigned to each plot and the nearest individual of each species to that point was removed. The four individuals of a species from one plot were pooled for subsequent analyses. Plant root systems were washed carefully, stained and assessed for mycorrhizal infection using a grid–intersect technique (Koide & Mooney 1987). Stems, leaves and flowering parts were dried and weighed. These samples were subsequently ground, digested in H_2SO_4 at 400 °C, and analysed for phosphorus (Watanabe & Olsen 1965) and nitrogen content (Jensen 1962).

MEASUREMENTS OF COMMUNITY STRUCTURE

Wire rings covering an area of 100 cm^2 were placed in 48 plots representing two replicates of each of the treatments in each block. The position of the ring was the same in each of the 48 plots, the edge of the ring being positioned at exactly 20 cm from two edges of the plot. This facilitated refinding the rings. On 10 July all the plants in each of the rings were tagged and counted. This was repeated on 31 July when the number of individuals of each species which were in flower was also recorded. On 28 August 24 of these rings were visited representing one replicate of each treatment in each block. These three dates are subsequently referred to as censuses. All the previous measurements were made and in addition the leaf and flowering part numbers were recorded for each individual. The number of flowers, or seed capsules, were counted on *Abutilon*. However, the number of flowers was more difficult to record for the other two species as they both form numerous small florets. As a consequence the number of flowering spikes on *Amaranthus* and *Setaria* was recorded. From these censuses calculations were made for plant density, percentage of total density attributed to each species, mortality (calculated between censuses 1–2 and 2–3) and the percentage mortality for a given species out of the total number of plants of that species.

In order to measure the percentage cover by each species a frame with seven vertical pins reaching to the ground was placed in two replicate plots of each treatment combination in each of the four blocks (total of 48 plots) on 12 August and 3 September. In each plot the total number of times that each plant species touched any part of the pins was recorded. Where a pin did not touch any vegetation this was recorded as bare ground. The proportion of the number of touches on one plant species to the total number of touches on all species and bare ground was used to calculate the percentage cover occupied by each species in each plot.

Measurement of seasonal productivity was carried out at one harvest on 9 September in 24 of the plots, representing one replicate plot of each of the treatments in each block. The above-ground vegetation was cut at ground level using a hedge trimmer, placed in bags and dried for 4 days in fan-assisted ovens at 60 °C. The material was subsequently sorted into each species and weighed.

STATISTICAL ANALYSIS

Each of the variables was analysed as a split-plot model using multifactor analysis of variance (STSC 1987) with block, mycorrhizal treatment, phosphorus treatment and species as factors. The block × mycorrhizal treatment interaction was used as the error term for mycorrhizal treatment. Separate ANOVA were performed on the data from each harvest or census and not across dates. All proportional values for mycorrhizal infection, density, mortality, cover and productivity were analysed after making an arcsin square root transformation (Zar 1984). Mean contrasts were carried out using the least significant difference (LSD) based on the experiment-wise error.

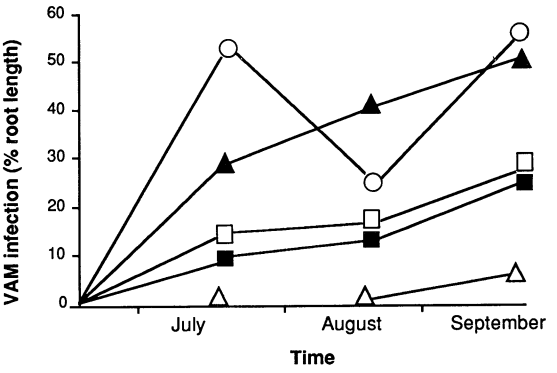

Fig. 1. Mean per cent root length infected by mycorrhizal fungi in *Abutilon* and *Setaria* at harvests 1, 2 and 3 (between June and September 1991). (▲) *Abutilon* and (■) *Setaria* in untreated soil (C); (○) *Abutilon* and (□) *Setaria* in fumigated soil, re-inoculated with spores of VAM fungi (MBG); (△) *Abutilon* in fumigated soil (MB). Values for *Setaria* in the MB treatment are not shown because no infection was observed in this treatment at any time. Values are averaged across P treatments and all values within one harvest are significantly different from each other ($P \leq 0{\cdot}05$) according to the LSD test.

Results

MYCORRHIZAL INFECTION

The mycotrophic species *Abutilon* and *Setaria* had become infected by mycorrhizal fungi by mid-July (Fig. 1) in both the C and MBG treatments. Mycorrhizal infection was only detected in the MB treatment by mid-September in *Abutilon* roots. However, this value (mean ± SE per cent of root length infected = 5·4 ± 1·2) was significantly lower than the level of mycorrhizal infection in any other species in any treatment. Phosphorus treatment did not have a significant effect on the level of VAM infection at any harvest. Mycorrhizal infection was not detected in *Amaranthus* at any time during the investigation.

PLANT DENSITY, MORTALITY AND COVER

At each of the three censuses the density of *Amaranthus* was significantly higher ($P \leq 0{\cdot}001$) than the densities of the other two species. The total density of plants was significantly higher in the MBG treatment than in either MB or C treatments at each census (Fig. 2, data presented for census 2 only) irrespective of species. At census 2 the density of *Amaranthus* was significantly higher ($P \leq 0{\cdot}05$) in the P_1 treatment (mean density 170 ± 24 plants m^{-2}) than in the P_0

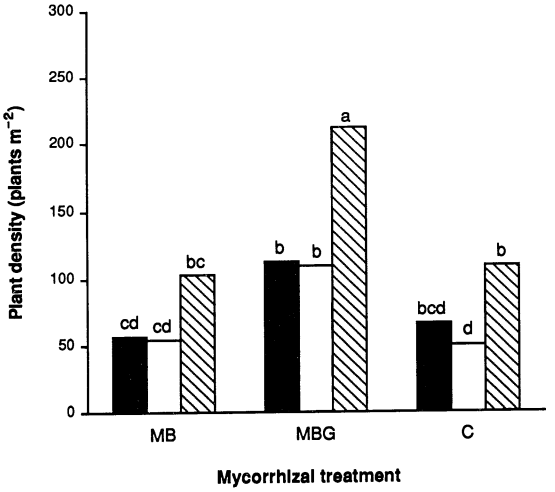

Fig. 2. Mean densities of *Abutilon* (■), *Setaria* (□) and *Amaranthus* (▨) in plots with different mycorrhizal treatments at census 2 (31 July): (C) untreated soil, (MB) fumigated soil and (MBG) fumigated soil, re-inoculated with VAM fungal spores. Different letters above bars indicate a significant difference ($P \leq 0{\cdot}001$) according to LSD test.

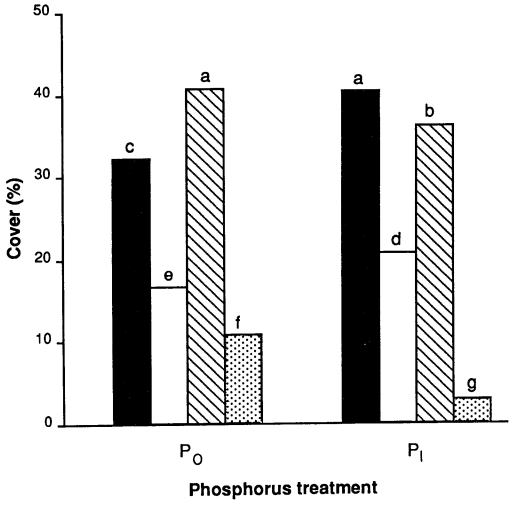

Fig. 3. Mean percentage cover for *Abutilon* (■), *Setaria* (□), *Amaranthus* (▨) and bare ground (⊠) with either no phosphorus treatment (P_0) or with phosphorus treatment (P_1) on 3 September 1991. Different letters above bars indicate a significant difference ($P \leq 0{\cdot}005$) according to the LSD test.

treatment (mean density 113 ± 19 plants m^{-2}) or either of the other two species. Similar patterns were observed at censuses 1 and 3. The same effects were also obtained if the ANOVA was performed on the proportion of density of each species contributing to the total density in the plot (data not presented). Percentage cover of all species differed according to phosphorus treatment during early September (Fig. 3). Cover by *Amaranthus* was higher in plots which received no phosphorus application than in those which received phosphorus. In contrast, the cover of *Abutilon* and *Setaria* was significantly higher in plots where phosphorus had been applied.

Mortality of *Amaranthus* was significantly higher than that of *Abutilon* between censuses 1 and 2 and was higher than that of both *Abutilon* and *Setaria* between censuses 2 and 3 (Table 1). Averaged across all species, significantly more plants had died by census 2 in the MBG + P_0 treatment than in the MBG + P_1 treatment (Fig. 4) and this was indicated by a highly significant phosphorus × mycorrhizal treatment interaction [$F_{2,117}$ ($P \leq 0{\cdot}01$) = 5·1]. This effect was not a result of higher mortality in *Amaranthus* as there was no significant species × mycorrhizal treatment interaction. In addition, the significant phosphorus × mycorrhizal treatment interaction term [$F_{2,117}$ ($P \leq 0{\cdot}05$) = 3·4] and lack of a significant species effect for the percentage mortality of each species strongly indicated that this trend was irrespective of species. However, by the final census the mortality (expressed as a percentage of total plant density) was significantly higher ($P \leq 0{\cdot}05$) in the P_1 treatment (10·6%) than in the P_0 treatment (4·8%), irrespective of mycorrhizal treatment or species.

Table 1. Mean ± SE mortality of each plant species (plants m^{-2}) between censuses 1 and 2 (10–31 July) and 2 and 3 (31 July–28 August)

	Censuses 1–2	Censuses 2–3
Abutilon	$2{\cdot}5 \pm 1{\cdot}0^{b}$	$7{\cdot}5 \pm 2{\cdot}2^{b}$
Setaria	$6{\cdot}3 \pm 1{\cdot}7^{ab}$	$10{\cdot}4 \pm 2{\cdot}4^{b}$
Amaranthus	$9{\cdot}2 \pm 2{\cdot}2^{a}$	$28{\cdot}9 \pm 6{\cdot}5^{a}$

Values followed by different letters within one interval between two censuses are significantly different ($P \leq 0{\cdot}05$) according to the LSD test.

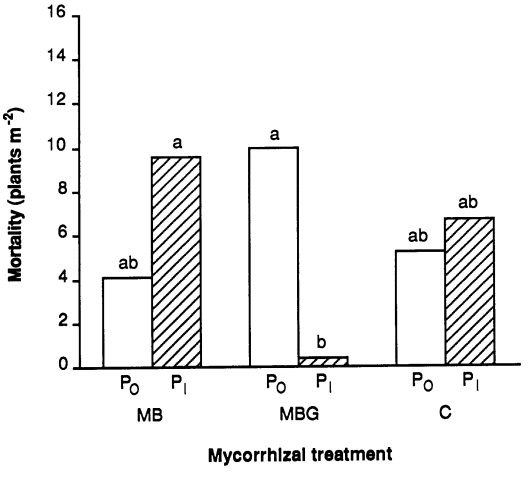

Fig. 4. Mean mortality of all species in plots with different mycorrhizal and phosphorus treatments between censuses 1 and 2 (10–31 July): (□) with no phosphorus application; (▨) with phosphorus application: (C) untreated soil, (MB) fumigated soil, (MBG) fumigated soil, re-inoculated with VAM fungi. Different letters above bars indicate a significant difference ($P \leq 0{\cdot}001$) according to the LSD test.

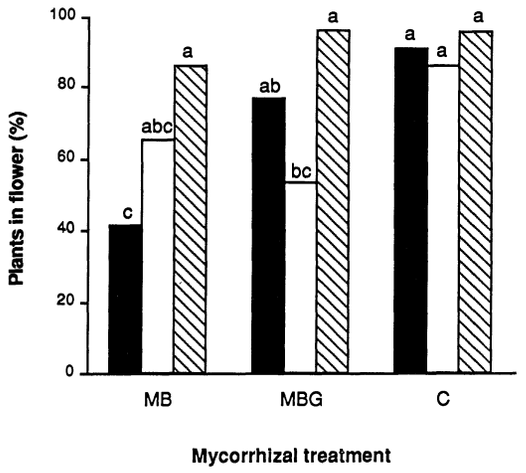

Fig. 5. Mean percentage of the total numbers of *Abutilon* (■), *Setaria* (□) and *Amaranthus* (▨) plants flowering at census 3 (28 August): (MB) fumigated soil, (MBG) fumigated soil, re-inoculated with VAM fungi, (C) untreated soil. Different letters above bars indicate a significant difference ($P \leq 0{\cdot}05$) according to the LSD test.

LEAF AND FLOWER PRODUCTION

Positive responses by all species to the application of phosphorus was observed in the leaf and flower or flowering spike number (Table 2). However, a significant mycorrhizal treatment × species interaction occurred on the percentage of plants flowering at census 3 [$F_{4,45}$ ($P \leq 0{\cdot}05$) = 3·1]. A significantly higher percentage of *Abutilon* plants flowered in plots containing VAM fungi (treatments MBG and C) than in fumigated plots (treatment MB). The same effect was not observed on the flowering of *Setaria* and no effect was observed on the flowering of *Amaranthus* (Fig. 5).

BIOMASS, NITROGEN AND PHOSPHORUS

There were no significant mycorrhizal treatment effects on the biomass or phosphorus and nitrogen contents and concentrations at harvest 1 (21 July). Significant species × mycorrhizal treatment effects on the biomass of leaves and nitrogen and phosphorus contents of flowering heads occurred at harvest 2. However, in each of these cases the biomass, nitrogen and phosphorus were higher in *Amaranthus* in the fumigated soil (treatments MB and MBG) than in the untreated soil (treatment C). There were no significant species × mycorrhizal treatment effects on the nitrogen and phosphorus concentrations of any of these species at harvest 2. Productivity was only measured in early September, when productivity of *Amaranthus* was higher in fumigated plots, irrespective of the presence of mycorrhizal fungi (data not presented).

Significant species × mycorrhizal treatment interactions also occurred for the biomass, nitrogen and phosphorus contents of the stems, leaves and mature seed heads at harvest 3. The biomass of *Abutilon* was significantly higher in plants from plots containing indigenous VAM fungi (treatment C) than in fumigated soil (treatments MB and MBG). Phosphorus contents of *Abutilon* were significantly higher in plots containing VAM fungi (treatments C and MBG) than in the absence of VAM fungi (treatment MB). In contrast, the biomass and phosphorus contents of *Amaranthus* were lower in plots containing VAM fungi than in fumigated soil (Fig. 6a,b). No mycorrhizal treatment effect was observed for the biomass, nitrogen or phosphorus contents of *Setaria*. The absence of a significant mycorrhizal treatment effect on plant nitrogen and phosphorus concentrations in the stems and leaves of any of the species indicated that elevated contents of these elements were size dependent. However, phosphorus concentrations in the flowering heads were significantly different between species and mycorrhizal treatments [mycorrhizal treatment × species interaction, $F_{4,45}$ ($P \leq 0{\cdot}05$) = 3·5]. These concentrations were higher in the mycotrophic plants (*Abutilon* and *Setaria*) in plots containing VAM fungi (treatments MBG and C) than in the fumigated soil (treatment MB) (Fig. 6c).

Discussion

EFFECTS OF THE VAM SYMBIOSIS ON PLANT GROWTH, NUTRIENT ACQUISITION AND ALLOCATION

By the end of the growth season (late September) mycorrhizal *Abutilon* plants were larger in terms of weight and as a consequence also had higher nitrogen and phosphorus contents. However, this was not so for *Setaria*, the other mycotrophic species. Different soil treatments had little effect on the growth of this species. During July and August *Amaranthus* (non-mycotrophic) grew well in the fumigated soil treatments, irrespective of inoculation with VAM fungi. The decrease in the accumulation of biomass, nitrogen and phosphorus in this species between late August and late September was concurrent with the positive effects of VAM fungi on the growth of *Abutilon*. This suggests that the mycorrhizal symbiosis may modify the competition between some mycotrophic and non-mycotrophic species. Although

Table 2. Mean ± SE leaf, flower or flowering spike number at census 3 (28 August) at low phosphorus (P_0) and high phosphorus (P_1) levels

	Leaf no.		Flower (or spike) no.	
	P_0	P_1	P_0	P_1
Abutilon	5·7±0·6	6·7±0·4	4·8±1·2	5·9±1·2
Setaria	7·0±0·8	9·6±2·1	1·0±0·1	1·7±0·3
Amaranthus	6·7±0·6	11·1±1·8	5·5±0·9	8·5±0·9

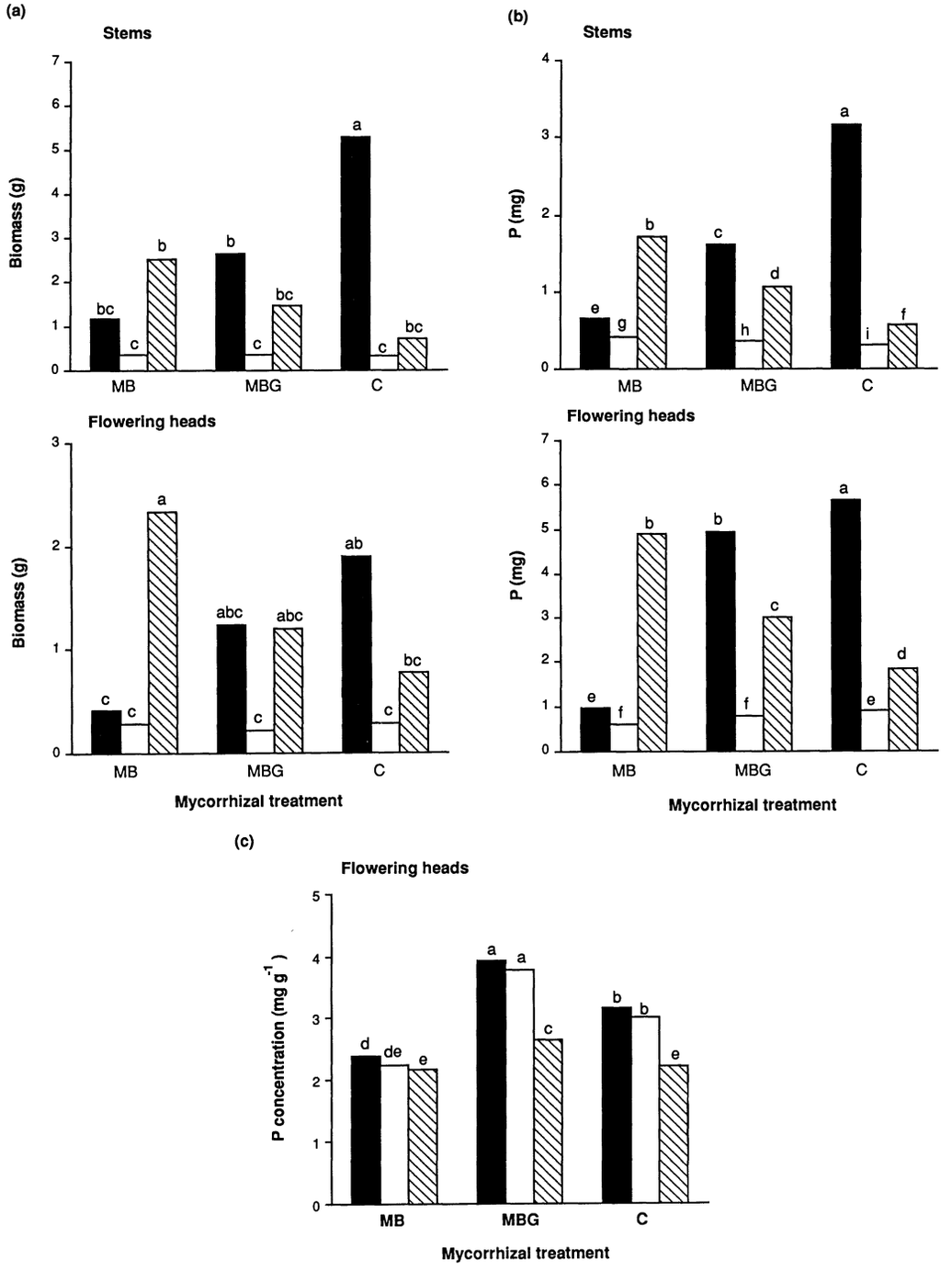

Fig. 6. Mean values for (a) biomass, (b) phosphorus content and (c) phosphorus concentration in the stems and flowering heads of *Abutilon* (■), *Setaria* (□) and *Amaranthus* (▨) at harvest 3 (23 September). (MB) fumigated soil, (MBG) fumigated soil, re-inoculated with VAM fungi, (C) untreated soil. Letters above bars indicate a significant difference ($P \leq 0{\cdot}05$) according to the LSD test.

VAM fungi had little effect on the growth of *Setaria* the concentrations of phosphorus in the flowering heads of mycorrhizal *Abutilon* and *Setaria* were higher than in non-mycorrhizal individuals of the same species and in *Amaranthus* (Fig. 6c). This VAM effect on P concentration was not apparent at the end of August although by this time seeds had begun to form in both species. By the time maturation of the seeds had taken place (late September) the higher P concentrations were observed in the seed heads.

It is difficult to propose a mechanism for the allocation of P to the seed heads of the mycorrhizal plants. Soil P levels were not recorded during this study and therefore predictions cannot be made on whether the additional P had been taken up from the soil between late August and late September or whether re-allocation of existing P in the plant had occurred.

The plant responses to P application observed in this investigation were also difficult to interpret.

Some measurements, e.g. percentage cover, leaf and flower and flowering spike number, indicate that the mycotrophic species responded to P application. However, the lack of a similar trend in the data recorded on plant biomass, P and N content in this investigation, makes it impossible to explain the effect of the mycorrhizal symbiosis on plant community structure with respect to environments of differing phosphorus levels.

DOES THE VAM SYMBIOSIS AFFECT COMMUNITY STRUCTURE?

In many cases significant mycorrhizal effects on indicators of community structure differed according to plant species (indicated by a significant mycorrhizal treatment × species interaction term in the ANOVA). Therefore the responses of the three plant species to the mycorrhizal symbiosis were different, with a beneficial effect of the VAM fungi on the performance of *Abutilon* (mycotrophic) and a negative effect on *Amaranthus* (non-mycotrophic). The communities in the MBG *vs* C treatments differed in plant density, biomass, and P and N contents. This could be due to competition between soil microflora, VAM fungi and roots for the same nutrient sources. In a recent investigation the functioning of the mycorrhizal symbiosis has been altered by reducing levels of soil micro-organisms (Schreiner & Koide 1993). Reduction of VAM effectiveness could also be attributed to high levels of grazing by soil microfauna (Fitter & Sanders 1992) or differing efficacy between *Glomus intraradices* and the indigenous fungal population.

While the positive effect of VAM on most of the parameters of plant growth was reduced when other components of the soil biota had not been eliminated by fumigation it is possible that the increased P concentration in the mature flowering heads of the mycotrophic species could have longer-term effects on community structure. Seeds from mycorrhizal mother plants contain higher P concentrations (Lu & Koide 1991). In addition, seeds from mycorrhizal mother *Abutilon* plants when grown in the absence of P exhibit faster leaf expansion rates than those which come from non-mycorrhizal mothers (Lewis & Koide 1990). Similar data are not currently available for seeds of *Setaria* but increased P concentrations in the mature seed heads of mycorrhizal individuals of this species suggest that this trend may be consistent. It is possible that *Abutilon* and *Setaria* seeds produced by mycorrhizal plants have a greater competitive advantage, in low P conditions, over those from non-mycorrhizal parentage, although whether this would be the case in the field has not been tested. This is the first report that mycorrhizal fungi can affect the phosphorus concentration of the seeds of mycotrophic plants while in coexistence with other plant species (one being non-mycotrophic). Perhaps when predicting longer-term effects on community structure the viability of the seed should also be considered. *Abutilon* has an extremely tough seed coat which allows the seed to remain viable for up to 50 years and also allows gradual germination to occur over this time period (Lueschen & Anderson 1980; Egley & Chandler 1983; Kremer & Spencer 1989). However, in order to model the outcome of changes in seed quality on future community structure more information is required regarding the offspring performance in situations where mycorrhizal fungi are either present or absent and on whether differences also occur in other seed properties such as ability and time taken to germinate and survival after germination (Venable 1989).

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