

D. Adjoud · C. Plenchette · R. Halli-Hargas  
F. Lapeyrie

## Response of 11 eucalyptus species to inoculation with three arbuscular mycorrhizal fungi

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**Abstract** Numerous publications have reported growth stimulation of *Eucalyptus* following ectomycorrhizal inoculation in nursery or field conditions. Although *Eucalyptus* species can also form arbuscular mycorrhiza, their dependency on this type of mycorrhiza is still debatable. This paper presents information on the effect of inoculation of arbuscular mycorrhizal fungi on eucalypt growth. Twenty weeks after mycorrhizal inoculation, *Eucalyptus* seedlings' stem dry weight could be increased up to 49% compared to non-inoculated control plants. Intensity of root colonization by a given fungus depended on the host species, but it was not related to a plant growth response. Leaf phosphorus concentration of non-inoculated *Eucalyptus* seedlings varied greatly between species. Increases in leaf phosphorus concentration following mycorrhizal infection were not necessarily associated with plant growth stimulation. The most mycorrhiza-dependent *Eucalyptus* species tended to be those having the highest leaf phosphorus concentration in the absence of a fungal symbiont. These mycorrhiza-dependent *Eucalyptus* species seem to have greater phosphorus requirements and consequently to rely more on the symbiotic association.

**Key words** *Eucalyptus* · Arbuscular mycorrhiza · Phosphorus · Endomycorrhizal dependency

D. Adjoud · R. Halli-Hargas  
Unité de Recherche en Biologie et Agro-Foresterie,  
Université de Tizi-Ouzou, Tizi-Ouzou 15000, Algeria

C. Plenchette  
INRA, Station d'Agronomie, 17 Rue Sully, BV 1540,  
F-21034 Dijon Cedex, France

F. Lapeyrie (✉)  
INRA, Centre de Nancy, Laboratoire de Microbiologie  
Forestière, F-54280 Champenoux, France  
Fax +33-83 39 40 69; e-mail: lapeyrie@nancy.inra.fr

### Introduction

Many attempts have been made to improve eucalypt plantation productivity through fertilization, breeding programs or controlled mycorrhizal inoculation. The genus *Eucalyptus* forms both arbuscular mycorrhizas and ectomycorrhizas on the same root system or even on the same root (Chilvers et al. 1987; Boudarga et al. 1990). The anatomy, ecology and physiology of *Eucalyptus* ectomycorrhizas have been extensively studied. However, studies on *Eucalyptus* arbuscular mycorrhizas are fairly recent, with the first controlled synthesis by Malajczuk et al. in 1981 and the first ultrastructural study by Boudarga and Dexheimer in 1988.

Whilst there have been some reports of growth stimulation of *Eucalyptus* species inoculated with ectomycorrhizal fungi in nurseries and in plantations (Garbaye et al. 1988; Grove et al. 1991), *Eucalyptus* growth responses to inoculation with arbuscular mycorrhizal fungi remains controversial. Lapeyrie and Chilvers (1985) suggested that arbuscular mycorrhizas of *E. dumosa* contributed largely to tolerance of calcareous soil and stimulated growth, because they were the dominant type of mycorrhiza on roots of 2-month-old plants. Schoeneberger (1984) found that *Gigaspora margarita* was able to stimulate the growth of 4-month-old *E. regnans*. In contrast, none of 30 arbuscular mycorrhizal isolates tested was able to stimulate growth of eight different *Eucalyptus* species up to 3 months after inoculation (Gomez et al. 1987). More recently, arbuscular mycorrhizal inoculation was found to have no effect on *E. grandis* growth, and even to have a depressive effect on plant growth when inoculum was added to ectomycorrhizal plants (Amorim and Muchovej, cited by Lapeyrie et al. 1992; Muchovej and Amorim 1990).

This study presents data on the response of 11 *Eucalyptus* species to arbuscular mycorrhizal inoculation. Mycorrhizal dependency of these species was determined and related to specific phosphorus requirement. Mycorrhizal dependency of the eucalypt species was

defined as “the degree to which a plant is dependent on the mycorrhizal conditions to produce its maximum growth or yield at a given level of soil fertility” (Gerde-mann 1975).

## Materials and methods

### Host plants and fungi

Eleven *Eucalyptus* species were used: *E. dives* Schauer, *E. delegatensis* R. T. Bak., *E. globulus* Labill., *E. viminalis* Labill., *E. largiflorens* F. Muell., *E. gomphocephala* D. C., *E. dumosa* A. Cunn. ex Schau., *E. viridis* R. T. Bak., *E. bosistoana* F. Muell., *E. urophylla* S. T. Blake and *E. macarthurii* Deane et Maiden. Seeds were germinated in plastic pots over a peat moss-vermiculite mixture (50/50).

Three arbuscular mycorrhizal fungi were used: *Glomus intraradices* Schenck and Smith (isolate CP103/CP), *G. mosseae* (Nicolson and Gerdemann) Gerdemann and Trappe (isolate CP101/VF) and *G. caledonium* (Nicolson and Gerdemann) Trappe and Gerdemann (isolate CP105/VF). These strains were propagated in a greenhouse, on leeks maintained in plastic pots containing 1500 cm<sup>3</sup> Terragreen, a calcined clay (Plenchette and Perrin 1992), and watered with 10 ml per week of Long Ashton nutrient solution (Hewitt 1966), the composition of which is as follows (mg l<sup>-1</sup>): N, 166; P, 41; K, 156; Ca, 159; Mg, 36; S, 48; Mn, 0.55; Cu, 0.064; Zn, 0.065; B, 0.54; Cl, 3.5; Mo, 0.048; Fe, 2.8.

### Experimental protocol

The experiment was carried out in plastic pots containing 1300 cm<sup>3</sup> Terragreen. A 5-week-old *Eucalyptus* seedling was transplanted into each pot. The fungal inoculum consisting of colonized leek roots (1 g of fresh leek roots per plant) plus spores (about 20 spores per plant), was introduced into the planting hole. Before inoculation, colonized leek roots were surface disinfected for 5 min in a chloramine T (2%) mercryl (10%) solution. The spores were collected from the potting substrate of the leeks by wet sieving (125 µm) and decanting (Gerdemann 1955). The non-inoculated seedlings received boiled leek roots (20 min at 100°C) and filtered spore washings (<10 µm).

Pots (10 replicates for each treatment) were kept in a greenhouse with a supplement of artificial light (280 µmol s<sup>-1</sup> m<sup>-2</sup>) (16-h day; 28°C day, 15°C night). Control and inoculated seedlings of each *Eucalyptus* species were fully randomized in a block design

and redistributed randomly once a week. Blocks were randomly redistributed in the glasshouse every 15 days. The seedlings were watered as necessary, avoiding excessive drainage and were fertilized once a week with 10 ml of Long Ashton nutrient solution. By the end of the experiment, each pot had received 8.2 mg of phosphorus.

### Harvesting and measurements

Twenty weeks after inoculation, plant height was recorded and seedlings harvested. The roots were cleared in 10% KOH and stained with acid fuchsin to assess mycorrhizal infection (Phillips and Hayman 1970) using the “gridline intersect” method (Giovannetti and Mosse 1980). Shoots were oven-dried over 18 h. Stem dry weights were recorded, and leaf phosphorus contents were determined colorimetrically (Charlot 1966). Data were analyzed statistically using Duncan’s test ( $P < 0.05$ ) when significant ANOVA results were found (SAS Institute 1987), and mycorrhizal dependency (MS) was calculated according to Plenchette et al. (1983):

$$MD = \frac{\text{mycorrhizal plant stem dry weight} - \text{non-mycorrhizal plant stem dry weight}}{\text{mycorrhizal plant stem dry weight}} \times 100$$

## Results and discussion

### Root colonization

Each *Eucalyptus* species studied was infected by at least one fungal strain (Table 1). The extent of root infection, when successful, varied from 1% of total root length to 80% (*E. urophylla*/*G. intraradices*). Root colonization by a given fungus varied greatly depending on the host species and this might be related to specific interactions between the mycorrhizal fungus and host species. However, variation in the ecological specificity of the eucalypt species cannot be ruled out, as only one experimental condition has been tested. In this experiment, *E. dumosa* and *E. viridis* formed only limited mycorrhizal infection.

**Table 1** Mycorrhizal root length (% of total root length) of 11 *Eucalyptus* species, 20 weeks after inoculation with three *Glomus* species (mean of six replicates ± confidence interval,  $P = 0.05$ ; – missing observation)

Eucalyptus species	<i>Glomus</i> species		
	<i>G. intraradices</i>	<i>G. mosseae</i>	<i>G. caledonium</i>
<i>E. dives</i>	10 ± 1	14 ± 1	7 ± 2
<i>E. viridis</i>	0	11 ± 1	—
<i>E. bosistoana</i>	6 ± 3	17 ± 2	—
<i>E. dumosa</i>	4 ± 1	1 ± 0.5	—
<i>E. delegatensis</i>	36 ± 1	28 ± 2	24 ± 2
<i>E. largiflorens</i>	54 ± 3	7 ± 2	2 ± 1
<i>E. urophylla</i>	80 ± 5	12 ± 1	—
<i>E. gomphocephala</i>	54 ± 3	—	0
<i>E. macarthurii</i>	38 ± 2	31 ± 2	—
<i>E. viminalis</i>	15 ± 2	16 ± 3	0
<i>E. globulus</i>	47 ± 3	58 ± 5	0

## Seedling growth

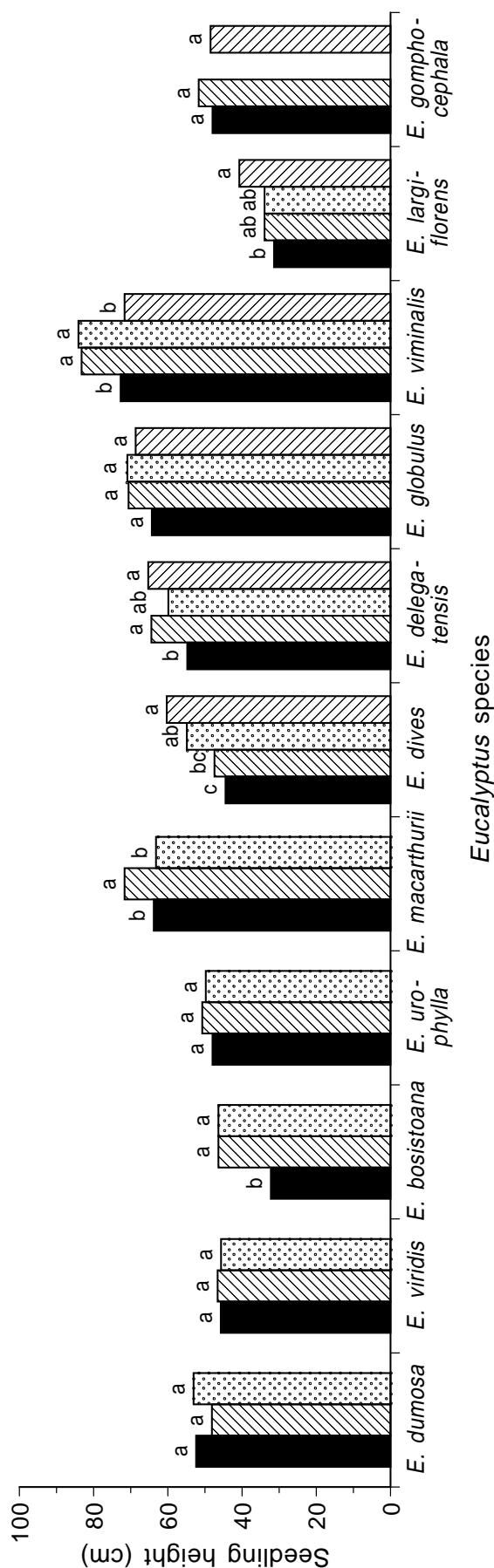
Twenty weeks after mycorrhizal inoculation, most species tested showed a significant growth stimulation compared to control plants (Figs. 1, 2). The increase in plant height reached 44% (*E. bosistoana*/*G. mosseae*) while stem dry weight was increased by up to 49% (*E. dives*/*G. caledonium*).

Plant growth stimulation was not related to the extent of root colonization ( $r=0.17$ ). Indeed, *E. urophylla*, *E. gomphocephala* and *E. globulus* did not show any significant growth stimulation despite high root colonization (80% of root length for *E. urophylla*/*G. intraradices*, 54% for *E. gomphocephala*/*G. intraradices* and 58% for *E. globulus*/*G. mosseae*). Conversely, only 7% of *E. dives* root length was infected by *G. caledonium*, but its stem dry weight was increased by 49%. The same trend – absence of correlation between mycorrhizal infection and plant growth responses – has been observed with various arbuscular mycorrhizal associations (Lambert et al. 1980; Powell 1980; Saif 1987).

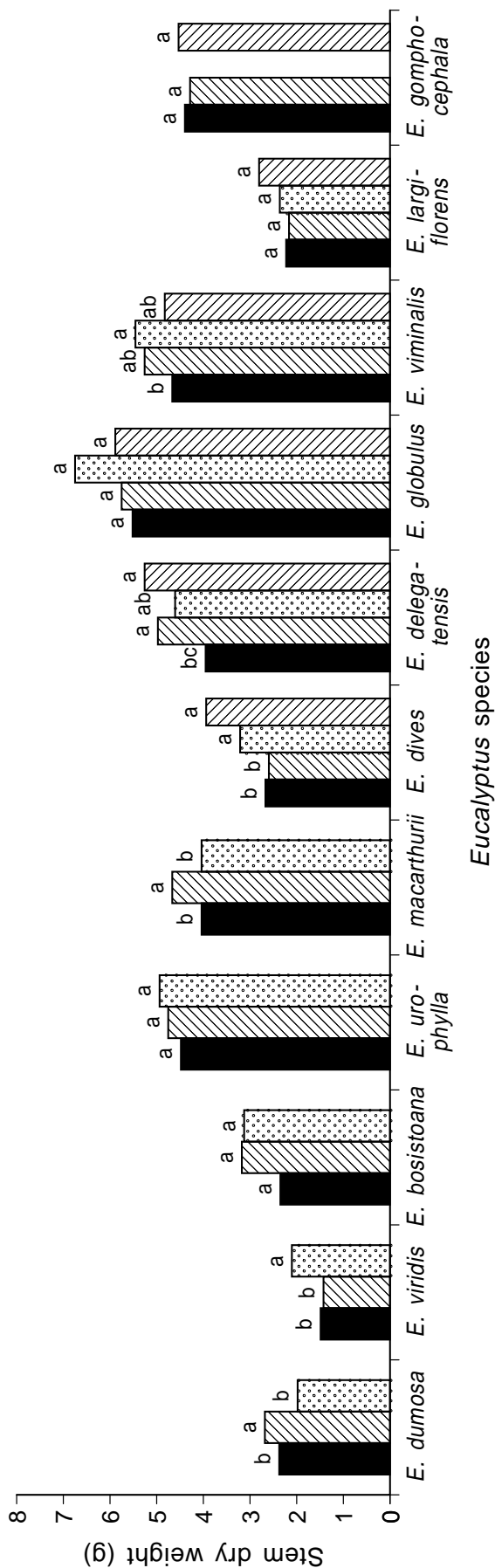
## Leaf phosphorus concentration

Leaf phosphorus concentration of 20-week-old non-inoculated *Eucalyptus* seedlings varied greatly according to species (Table 2). Such interspecific variability has been reported previously (Barrow 1977; Mulligan 1988), as has intraspecific variability (Mulligan and Sands 1988). Here, leaf phosphorus concentration ranged from 810  $\mu\text{g g}^{-1}$  dry weight (*E. globulus*) to 2765  $\mu\text{g g}^{-1}$  dry weight (*E. dives*). These values are in the range of those published by Dell and Robinson (1993), when *Eucalyptus* seedlings were raised in adequate phosphorus nutrition conditions.

Following mycorrhizal inoculation of *E. dives*, *E. bosistoana*, *E. viminalis*, *E. largiflorens* and *E. delegatensis* with one or two fungal strains, leaf phosphorus concentration was significantly increased, by up to 41% (*E. dives* inoculated with *G. mosseae*) (Fig. 3). Such phosphorus accumulation in *Eucalyptus* seedlings has previously been reported together with growth stimulation following ectomycorrhizal inoculation (Heinrich and Patrick 1986; Heinrich et al. 1988; Bougher et al. 1990). However, increases in leaf phosphorus concentration and intensity of arbuscular mycorrhizal infection were not correlated ( $r=0.15$ ); for example, only 14% of *E. dives* root length was infected by *G. mosseae*, while leaf phosphorus concentration increased by 41%. Some eucalypt species studied here (*E. viridis*, *E. dumosa*, *E. urophylla*, *E. gomphocephala*, *E. macarthurii*, *E. globu-*



**Fig. 1** Influence of inoculation by arbuscular mycorrhizal fungi (*Glomus intraradices*, *G. mosseae*, *G. caledonium*, non-inoculated control) on growth (height) of 11 *Eucalyptus* species harvested after 20 weeks. For a given *Eucalyptus* species, columns labelled with the same letter do not differ significantly (Duncan's multiple range test,  $P < 0.05$ )



lus) did not accumulate significantly more phosphorus in leaves per unit mass as a result of endomycorrhizal inoculation (Fig. 3).

Increases in leaf phosphorus concentration were not always associated with plant growth stimulation (height and/or stem dry weight). Four different responses were observed: increase in leaf phosphorus concentration associated with growth stimulation (*E. dives*/*G. mosseae*; *E. delegatensis*/*G. intraradices*; *E. viminalis*/*G. intraradices*; *E. bosistoana*/*G. mosseae*; *E. largiflorens*/*G. caledonium*), increase in leaf phosphorus concentration without a growth stimulation (*E. delegatensis*/*G. mosseae*; *E. largiflorens*/*G. intraradices*), no increase in leaf phosphorus concentration, but stimulated growth (*E. dives*/*G. caledonium*; *E. delegatensis*/*G. caledonium*; *E. viminalis*/*G. mosseae*; *E. bosistoana*/*G. intraradices*; *E. macarthurii*/*G. intraradices*; *E. dumosa*/*G. intraradices*; *E. viridis*/*G. mosseae*), and, in the remaining cases, no increase in either leaf phosphorus concentration or growth. Such observations suggest that under the present experimental conditions phosphorus is not limiting growth of all *Eucalyptus* species investigated. Moreover, for a given *Eucalyptus* species (e.g. *E. delegatensis*), growth stimulations (Figs. 1, 2), occurring either together with phosphorus nutrition improvement (e.g. *E. delegatensis*/*G. intraradices*) or not (e.g. *E. delegatensis*/*G. caledonium*) (Fig. 3), are not significantly different from each other, confirming that phosphorus is not the only growth-limiting factor. Most *Eucalyptus* species responded differently to mycorrhizal infection depending on the fungal strain inoculated (growth stimulated or not, with or without leaf phosphorus concentration increase), confirming, as expected, that the functioning of the symbiotic association is under both seedling and fungal control.

#### Mycorrhizal dependency

For a given fungus, mycorrhizal dependency (MD) values varied depending on the host species (Table 3). Such variation between species or even between cultivars has been frequently noticed (Menge et al. 1978; Azcon and Ocampo 1981; Plenchette et al. 1983; Pope et al. 1983; Hetrick et al. 1988). MD values obtained in this study with *Eucalyptus*, which did not exceed 34% (*E. dives*/*G. caledonium*), appear moderate or low when compared with values reported for highly dependent plant species (Plenchette et al. 1983; Saif 1987). Nevertheless, comparisons must be made cautiously, as the experimental conditions were not identical. Considering Baylis' hypothesis (1975), such a low

**Fig. 2** Influence of inoculation by arbuscular mycorrhizal fungi (*Glomus intraradices*, *G. mosseae*, *G. caledonium*, non-inoculated control) on growth (stem dry weight) of 11 *Eucalyptus* species harvested after 20 weeks. For a given *Eucalyptus* species, columns labelled with the same letter do not differ significantly (Duncan's multiple range test,  $P < 0.05$ )

**Table 2** Leaf phosphorus concentration of 11 *Eucalyptus* species harvested after 20 weeks. Means followed by the same letters do not differ significantly (Duncan's multiple range test,  $P < 0.05$ )

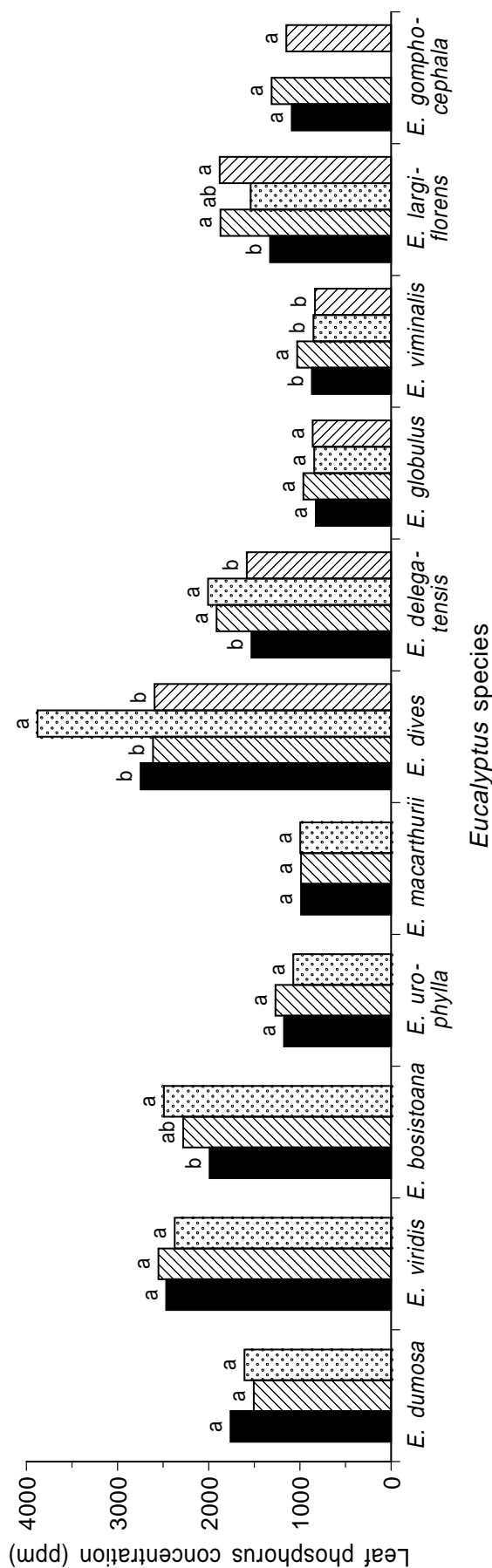
Species	Leaf phosphorus (ppm)
<i>E. dives</i>	2765 a
<i>E. viridis</i>	2501 ab
<i>E. bosistoana</i>	2010 bc
<i>E. dumosa</i>	1783 cd
<i>E. delegatensis</i>	1533 cde
<i>E. largiflorens</i>	1339 def
<i>E. urophylla</i>	1177 def
<i>E. gomphocephala</i>	1075 ef
<i>E. macarthurii</i>	981 ef
<i>E. viminalis</i>	870 f
<i>E. globulus</i>	810 f

arbuscular mycorrhizal dependency of *Eucalyptus* could be expected, as most species have a highly branched root architecture, with numerous fine roots and long root hairs (Baylis 1972, 1975; St John 1980; Hetrick et al. 1988; Manjunath and Habte 1991). Nevertheless, this might not be the only explanation. Indeed, according to Rajapakse and Miller (1988) only 27% of intraspecific MD variation was explained by cowpea root morphology, and other plant models which do not conform to Baylis' hypothesis have been reported (Schultz et al. 1979; Saif 1987).

The *Eucalyptus* species most dependent on arbuscular mycorrhizal infection tended to be having the highest leaf phosphorus concentration in the absence of a fungal symbiont (*E. dives*, *E. viridis*, *E. bosistoana*), while the less dependent ones were among those having the lowest leaf phosphorus concentration (*E. globulus*, *E. urophylla*, *E. gomphocephala*) (Fig. 4). The mycorrhiza-dependent *Eucalyptus* species seem to have greater phosphorus requirements and consequently to rely more on the symbiotic association to satisfy these requirements. To date we have been unable to find any published report of such a relationship among mycorrhizal plant species.

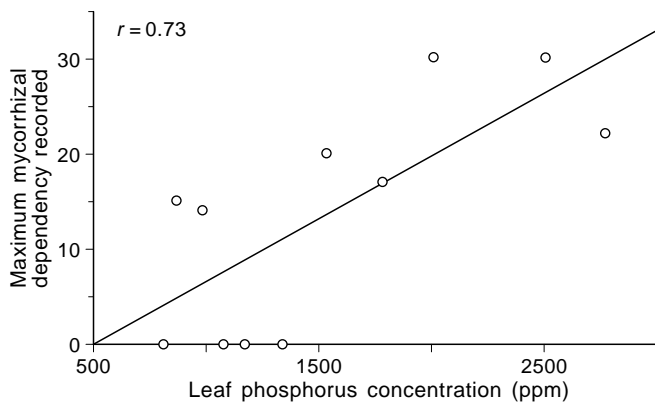
In situ, *Eucalyptus* roots are infected together by both arbuscular mycorrhizal and ectomycorrhizal fungi. Comparisons of the arbuscular mycorrhizal and ectomycorrhizal dependency of each species under different ecological conditions would help us to understand how both types of mycorrhizal fungi interact within the same root system.

**Fig. 3** Influence of inoculation by arbuscular mycorrhizal fungi (▨ *Glomus intraradices*, ▤ *G. mosseae*, ▩ *G. caledonium*, ■ non-inoculated control) on leaf phosphorus concentration (ppm) of eleven *Eucalyptus* species harvested after 20 weeks. For a given *Eucalyptus* species, columns labelled with the same letter do not differ significantly (Duncan's multiple range test,  $P < 0.05$ )



**Table 3** Mycorrhizal dependency values (Plenchette et al. 1983) calculated from stem dry weights of 20-week-old seedlings of 11 *Eucalyptus* species, inoculated or not with three different arbuscular mycorrhizal fungi (– missing observation)

<i>Eucalyptus</i> species	<i>Glomus</i> species		
	<i>G. intraradices</i>	<i>G. mosseae</i>	<i>G. caledonium</i>
<i>E. dives</i>	0	18	34
<i>E. viridis</i>	0	30	—
<i>E. bosistoana</i>	27	26	—
<i>E. dumosa</i>	14	0	—
<i>E. delegatensis</i>	20	0	26
<i>E. largiflorens</i>	0	0	0
<i>E. urophylla</i>	0	0	—
<i>E. gomphocephala</i>	0	—	0
<i>E. macarthurii</i>	14	0	—
<i>E. viminalis</i>	0	15	0
<i>E. globulus</i>	0	0	0



**Fig. 4** Relationship between leaf phosphorus concentration of 11 *Eucalyptus* species (assessed on 20-week-old non-inoculated seedlings) and their maximum mycorrhizal dependency value determined following infection by either *G. intraradices* or *G. mosseae* ( $r = 0.73$ ; software: Cricket Graph 1.3.1.F)

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