

## Occurrence and importance of mycorrhizae in aquatic trees of New South Wales, Australia

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**Abstract.** Vesicular arbuscular mycorrhizal (VAM) infection was found in KOH-cleared and lactophenol-blue-stained roots of *Salix babylonica*, *Melaleuca quinquenervia* and *Casuarina cunninghamiana*. These are all trees growing on creeks and river banks, in stationary or slowly flowing fresh or brackish waters in swamps, creeks, drains and channels, and in seepage areas of New South Wales, Australia. Larger and older roots lacked VAM infection in the inner cortex, probably due to suberisation of cells, and the endophyte was restricted to the epidermal layers. Spores and sporocarps of the VAM fungi *Glomus fasciculatus*, *G. mosseae*, *Sclerocystis rubiformis*, *Gigaspora margarita* and an unidentified *Scutellospora* sp. were wet sieved and decanted from aquatic sediments and soils. The presence of similar VAM fungal spores in the aquatic sediments and terrestrial soil suggests that they probably enter the aquatic sediments through run off from the land ecosystem. All three plants formed vesicular arbuscular (VA) mycorrhizae almost exclusively in the marshy, periodically inundated soils, but the same plant species formed endo-/ectomycorrhizae when growing in soil with higher redox potentials ( $E_h$ ). *Salix* and *Melaleuca* tree roots possessed both VAMycorrhizae and ectomycorrhizae. VAM roots of *Casuarina* were equipped with both N-fixing Frankia nodules and proteoid roots. VAM endophytes did not invade nodular cortical tissues, suggesting the presence of an exclusion mechanism which needs further study. The highest VAM infection was found in nodulated specimens. Free-floating roots growing in water close to the banks were non-mycorrhizal but were mycorrhizal in the bottom-rooting state. VAM spore number and mycorrhizal infection seem to be associated with redox-potential, i.e. lower at sites such as swamps, water or sediments with lower  $E_h$  values than in terrestrial soils with higher  $E_h$  values. A relationship between soil moisture gradient and VAM infection pattern became apparent from the study of a *C. cunninghamiana* transect on a creek embankment, i.e. typical vesicles and arbuscules were found in roots from drier soils, there was a lack of arbuscules in relatively wet soils but large lipid-filled intracellular vesicles were present, and typical vesicles and

arbuscules were absent in flooded creek beds where roots were associated with coenocytic intercellular hyphae with abundant lipid droplets. The importance of VA mycorrhiza, ectomycorrhizae, N-fixing root nodules and proteoid roots at the land-water interface is discussed with reference to the use of these trees as pioneering species for stabilising river and stream banks, reducing erosion, windbreaking, and as a long-term and inexpensive means of achieving biological control of aquatic weeds by shading waterways.

**Key words:** Vesicular arbuscular mycorrhizae (VAM) – Aquatic VAM – *Salix babylonica* – *Melaleuca quinquenervia* – *Casuarina cunninghamiana*

### Introduction

There is increasing interest in vesicular arbuscular mycorrhizal (VAM) fungi due to their well-documented role in improving plant growth under limiting soil conditions. However, information about the mycorrhizal status of river, pond, creek, and marsh plants is scanty and inconsistent.

Earlier reports on the mycorrhizal status of aquatic plants varied from complete absence to reduced or temporary absence during anaerobiosis until aerated and drier conditions returned (Maeda 1954; Mejsstrik 1965, 1976; Wojciechowska 1960; Shuja et al. 1971; Khan 1974; Filer 1975; Trinick 1977; Reid and Bowen 1979; Sieverding 1979; Malloch et al. 1980; Pirozynski 1980; Chaubal et al. 1982; Currah and Van Dyke 1986). Aquatic VAMs were first reported in 0.3 to 0.8-m deep aquatic plants (Sondergaard and Laegaard 1977), and VAM tolerance of submerged conditions was shown to be related to well-developed aerenchyma in the host by Keeley (1980). Recently, other researches have reported vesicular arbuscular (VA) mycorrhizae in aquatic plants and VAM spores in sediments (Bagyaraj et al. 1979; Clayton and Bagyaraj 1984; Rosema et al. 1986; Ragupathy et al. 1990; Sengupta and Chaudhuri 1990). These

recent findings suggest that VAM fungi can be of benefit to plants subjected to water saturation. However, the conclusions are sometimes based on single observations on a small part of a root system. Furthermore, the incidence of mycorrhizal colonisation may vary with season, soil type, soil moisture availability, habitat, composition of plant community and plant species. For example, Khan (1974) found no VA mycorrhizae in 16 hydrophytes growing in communities dominated by intrinsically non-mycorrhizal plants, although VAM spores were present in their rhizospheres. These spores probably entered the aquatic sediments in run off from nearby land ecosystems. Many aquatic plants recorded as non-mycorrhizal are now found to be mycorrhizal in other habitats.

This present paper reports the occurrence of mycorrhizae in three aquatic trees of New South Wales, *Salix babylonica* (weeping willow, Salicaceae), *Casuarina cunninghamiana* (River She oak, Casuarinaceae) and *Melaleuca quinquenervia* (paperbark, Myrtaceae).

## Materials and methods

### Sampling sites

Roots, sediments and soil samples from trees growing on the banks of rivers, creeks and lakes, in shallow water along creeks, in shallow swamps, and sometimes in brackish waters and ephemeral pools in periodically inundated floodwater creek beds were collected from various locations in New South Wales, Australia over a period of 2 years. The *C. cunninghamiana* transect on a creek embankment at the University of Western Sydney Macarthur, Campbelltown Campus was studied over a period of 1 year by collecting samples from the creek bed in April/May 1991 (dry season), August 1991 (the creek bed was swampy after heavy rainfall in June), November 1991 (when the creek bed was dry) March/April 1992 (after a wet season when the creek bed was flooded for over 4 months).

### Root collection and examination

Root samples were obtained from five different sites around each tree from the upper 0–20 cm of the soil/sediment profile. Free-floating distal roots away from the main roots of trees growing on the banks of water bodies were also collected. Smaller roots attached to larger tree roots were removed, washed in a sieve and cut into 1- to 2-cm pieces. Transverse sections of fresh roots collected from various sources were examined microscopically for aerenchyma. Root pieces were cleared in 10% (w/v) KOH at 90°C for about 1 h, bleached for 30 min in alkaline H<sub>2</sub>O<sub>2</sub> solution at room temperature, acidified for 2–3 min with 1% HCl, stained with 0.5% trypan blue in lactophenol for 10–15 min at 90°C (after Phillips and Hayman 1970) and examined under an inverted microscope for mycorrhizal infection. The percentage of VAM infection was estimated by examining 100 random root segments per sample mounted on slides in groups of 10 using a grid-intersect method (Giovannetti and Mosse 1980). Dual mycorrhizae were included in the estimation of both VA mycorrhizae and ectomycorrhizae (ECM).

### VAM spore extraction

Sediments and soils (100-g subsamples from a mixture of 5 × 100 g samples from each site) were wet sieved and decanted (Gerdemann

and Nicolson 1963) to recover VAM spores and sporocarps. Relative spore numbers and VAM infection in *C. cunninghamiana* roots growing in a transect on the creek embankment were monitored over a period of 1 years. Several taxonomic keys were used for the identification of VAM fungi (Morton 1988; Schenck and Perez 1988; Morton and Benny 1990). No attempt was made to identify ECM fungi.

### Redox potential

Redox potentials ( $E_h$ ) of soil, water and sediments were measured using an oxidation-reduction potential value tester (Hana Instruments).

## Results

### VAM infections

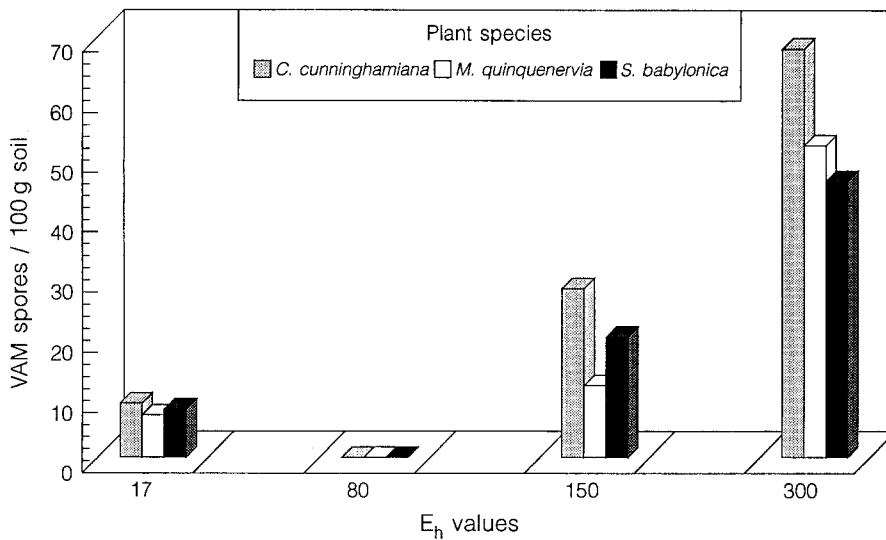
All three tree species almost exclusively possessed VAM infections, especially in young roots (Fig. 1). VA mycorrhizae were abundant in soil, moderate in swamps, absent in free-floating roots in water and rare in sediments (Fig. 1). Roots of *C. cunninghamiana*, growing in the flooded creek bed contained intercellular coenocytic hyphae but lacked vesicles and arbuscules (Table 1). However, characteristics of VAM infection, i.e. vesicles, arbuscules and intracellular hyphal coils were observed in the cleared and stained root segments of the same plant when the creek bed was dry (Table 1). No vesicles were observed in the roots infected with *Gigaspora margarita*. VAM infection in larger and older roots was restricted to outer epidermal cells, perhaps due to suberisation. Lateral roots generally had higher VAM infection than main roots. The highest VAM infection was found in *C. cunninghamiana* roots which were studded with N-fixing *Frankia* nodules (Fig. 1). No VAM infection of nodular tissue was observed. *C. cunninghamiana* also possessed clusters of proteoid roots which were very hairy and devoid of VAM infection.

Abundant lipid droplets were present in the mycelium extending along the surface and intercellularly in the roots of *C. cunninghamiana* growing in the swampy creek bed and infected with VAM endophytes. Small lipid droplets appeared to have accumulated in developing spores on the external hyphae as well as in intracellular vesicles in the root cortex of River She oak until most of the structure was filled with one large lipid globule. No arbuscules were observed in these heavily vesiculated roots.

### VAM endophytes

VAM spores were recovered from wet sieved and decanted soil/sediment samples from all three trees studied (Table 2). Spores were abundant in terrestrial soil samples, moderate in swamps, rare or absent in water and moderate to rare in sediments (Table 2).

Five VAM species from the family Glomaceae, *Glomus mosseae* (Nicol & Gerd.) Gerdemann & Trappe.



**Fig. 1.** Effect of redox potential ( $E_h$ ) on percentage vesicular arbuscular mycorrhizal (VAM) infection in three aquatic trees of New South Wales, Australia. Values are means of two samples from each site

**Table 1.** Relationship between vesicular-arbuscular mycorrhizal (VAM) infection characteristics and soil-moisture gradient pattern in a *Casuarina cunninghamiana* transect on a creek embankment. Values in parentheses represent average monthly rainfall<sup>a</sup> in the 3 months previous to collection

Sampling period	Creek bed	$E_h$ values	Vesicles	Arbuscles	Coenocytic hyphae
April/May 1991 (54 mm)	Dry	> 300 ± 47	+	+	+
August 1991 (131 mm)	Swamping	150 ± 12	+	-	+
November 1991 (13 mm)	Dry	> 300	+	+	+
March/April 1992 (176 mm)	Flooded	17 ± 11	-	-	+

<sup>a</sup> Provided by the Bureau of Meteorology

**Table 2.** Survey of VAM spore population in the rhizospheres of the three aquatic trees of New South Wales, Australia. -, Absent; ×, rare; × ×, moderate; × × ×, abundant

VAM fungus	Plant species	Sampling site			
		1 Soil	2 Swamp	3 Water	4 Sediments (<0.5 m deep)
<i>Glomus mosseae</i>	<i>Casuarina cunninghamiana</i>	× × ×	× ×	-	× × ×
	<i>Malaleuca quinquenervia</i>	× × ×	× ×	×	×
	<i>Salix babylonica</i>	× × ×	×	-	× ×
<i>Glomus fasciculatus</i>	<i>C. cunninghamiana</i>	× ×	× ×	×	× ×
	<i>M. quinquenervia</i>	× ×	×	×	-
	<i>S. babylonica</i>	× ×	× ×	×	-
<i>Sclerocystis rubiformis</i>	<i>C. cunninghamiana</i>	×	×	-	-
	<i>M. quinquenervia</i>	×	-	×	×
	<i>S. babylonica</i>	×	×	-	×
<i>Gigaspora margarita</i>	<i>C. cunninghamiana</i>	× × ×	× × ×	-	× ×
	<i>M. quinquenervia</i>	× ×	×	-	-
	<i>S. babylonica</i>	× ×	×	×	×
<i>Scutellospora</i> sp.	<i>C. cunninghamiana</i>	× ×	-	×	× ×
	<i>M. quinquenervia</i>	-	-	-	-
	<i>S. babylonica</i>	-	-	-	-

comb. nov., *G. fasciculatus* (Thaxter sensus Gerd.) Gerdemann & Trappe comb. nov., *Sclerocystis rubiformis* Gerdemann & Trappe sp. nov., and the family Gigasporaceae, *Gigaspora margarita* Becker and Hall and *Scu-*

*tellospora* spp., (Morton and Benny 1990), were recovered in this study. Soil water content seemed to be the determinant of VAM fungi, e.g. *G. mosseae* was abundant in soils, *G. fasciculatus* was moderate in swamps,

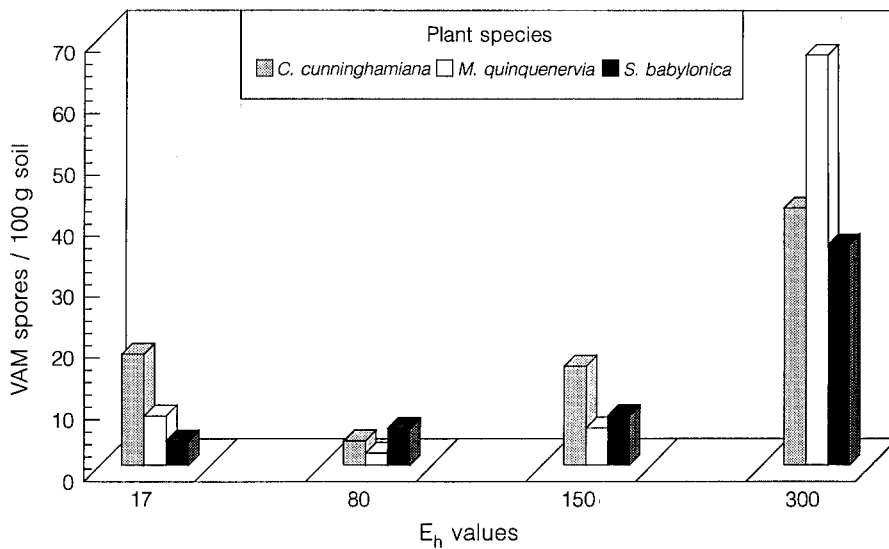


Fig. 2. Effect of redox potential ( $E_h$ ) on VAM spore population in the rhizospheres of three aquatic trees of New South Wales, Australia. Values are means of two samples from each site

*S. rubiformis* was rare in soils and rare or absent in swamps and water, *G. margarita* was abundant in swamps and moderate in sediments, and *Scutellospora* spp. was moderate in sediments (Table 2).

#### ECM infections

The roots of all three species possessed ECM when growing in drained and aerated soils but not in swamps, water or sediments. ECM fungi did not penetrate the hypodermis of *Casuarina* sp., although typical well-developed mantles and Hartig networks were present in *Melaleuca* sp. and *Salix* sp.

#### Dual/triple infections

ECM and VAM fungi simultaneously colonised roots in some samples. *M. quinquenervia* had both ECM and VAM fungi growing on the same root and even on the same root segment. Fungal connections between nodulated *C. cunninghamiana* and non-nodulated *M. quinquenervia* were observed after careful examination of the root systems of trees growing on the bank of Georges River in Sydney, suggesting a possible inter-plant nutrient transfer.

#### Mycorrhizal infection and redox potential

Mycorrhizae were absent or less frequent in roots growing in swamps, water or sediments with low  $E_h$  values than in terrestrial soils with higher  $E_h$  values (Fig. 1). Mycorrhizae were absent in the free-floating distal roots of *M. quinquenervia*, which were also devoid of air passages. The roots of plants growing in shallow waters of swamps ( $E_h = 150$ ) were endomycorrhizal though not as heavily as their counterparts in the soil ( $E_h > 300$ ) (Fig. 1). VAM spore numbers, like VAM infection, also appeared to be positively correlated to redox potential values (Fig. 2).

#### Discussion

The occurrence of characteristic VAM and ECM infections in the three aquatic species reported here suggests that the roots of these trees provide an endophyte habitat similar to that of terrestrial plant roots. The presence of dual mycorrhizal associations in aquatic trees in the present study confirms their existence in their counterparts in terrestrial habitats (Lodge 1989). However, Khan (1974) reported that roots of *C. cunninghamiana* growing on sandy soils in Pakistan lacked VAM infections although VAM spores were present in the rhizosphere. This may be due to the soil type (Land and Schönbeck 1991). Dual infection has been known for some time (Dominik 1958) but now appears to be more common than was previously recognised. The implications of this phenomena for ecosystems, as stated by Harley (1989), are "great and yet unconsidered". The coexistence of the two types of symbionts within a single root found in the present study indicates a lack of antagonism once they have established themselves within the root system. Lodge (1989), however, reported that infection of *Populus* and *Salix* by VAM fungi was lowest where infection by ECM fungi was high, suggesting competition or antagonism. Pot experiments by Rose (1980) with *Alnus rubra* suggested that colonisation by ECM fungi established a physical barrier to VAM fungal penetration. McGee (1986) also observed VAM and ECM infections in roots of *Melaleuca uncinata*, and dual infections have been reported in other members of the Myrtaceae, such as *Eucalytus* and *Leptospermum*, which are major forest species in Australia (Sward 1978; Khan 1981; Malajczuk et al. 1981; Lapeyrie and Chilvers 1985; Chilvers et al. 1987). Willows and poplar trees are also known to possess both VA mycorrhizae and ECM (Dominik 1958; Shuja et al. 1971; Vozzo and HacsKaylo 1974; Lodge 1989), as do terrestrial *Casuarina* and *Allocasuarina* spp. (Diem et al. 1981; McGee 1986; Ba et al. 1987; Bougher et al. 1990).

The present study indicates that mycorrhizal infection is related to redox potential. Less infection occurs

in reducing environments such as swamps, water or sediments with lower  $E_h$  than oxidising terrestrial soils with higher  $E_h$  values. Redox potential is known to affect the exchange of nutrients such as N and P at the sediment-water interface (Mortimer 1941), and mycorrhizal formation is reduced in sediments by higher availability of P (Smith 1980). The absence of mycorrhizal infection in free-floating distal roots of *M. quinquenervia* as against its presence in the rooting state in sediments is consistent with observations in *Populus euroamaricana* (Shuja et al. 1971) and *Eichhornia crassipes* (Ragupathy et al. 1990). This lack of VA mycorrhizae may be due to the low availability of oxygen to distal roots under flooded conditions (Russell 1977). Water-logged soil is presumed to inhibit mycorrhizal formation as a result of low levels of dissolved oxygen. Mosse et al. (1981) reported inhibition of VAM spore germination under reducing conditions, and Reid and Bowen (1979) reported a lower number of VAM entry points on root epidermis in wet soils. Saif (1981, 1983) found a corresponding increase in VAM development as the partial pressure of oxygen in the soil increased from 0 to 21%. The occurrence of VAMycorrhizae on trees growing in shallow waters in swamps in the present study indicates the availability of enough dissolved oxygen to allow mycorrhizal infection. Redox potentials were higher in swamps than in water (Table 1). In marked contrast, some researchers found no significant correlation between soil moisture and the degree of VAM infection (Dickman et al. 1984; Cerlignone et al. 1988) or between soil moisture and VAM spore counts (Neeraj et al. 1991).

A relationship between the characteristics of VAM infection and soil-moisture gradient was found in the study of the *C. cunninghamiana* transect on the creek embankment (Table 1). Typical vesicles and arbuscules occurred in roots from drier soils, and there were no arbuscules but many large, lipid-filled, intracellular vesicles in roots from relatively wetter soils. In flooded creek beds there was a complete absence of typical vesicles and arbuscules but the presence of coenocytic intercellular hyphae with abundant lipid droplets in the roots. These observations confirm the conclusions of Filer and Broadfoot (1968) that once mycorrhizal formation has taken place, VAMycorrhizae may endure prolonged exposure to flooding. As was also observed by Filer (1975), flooding temporarily reduced VAM infection to coenocytic, intercellular mycelium, and after the flood water receded, characteristic VAM associations returned. Stenlund and Charvat (1990) reported the presence of VAMycorrhizae with abundant vesicles but no arbuscules in floating mats of *Typha* sp. Roots of *Myrica gale* from peat and sphagnum bogs were colonised by a fungal endophyte which produced many small vesicles in the cortex and sparse inter- and intracellular hyphae (Rose 1980). Extensive vesicle formation may have been due to improved host nutrition or the production of growth-promoting hormones (Barea et al. 1975; Barea 1986). The development of vesicles and absence of arbuscules in swampy conditions in roots of *Casuarina* sp. in the present study indicate a greater availability of carbohydrates to the fungal endophyte,

probably due to N-dependent increase in photosynthesis. In a study of VAM associations across a soil moisture-nutrient gradient, Anderson et al. (1984) reported a lack of vesicles and arbuscules but the presence of coenocytic VAM hyphae in plants growing in the wettest habitats. No VAM infections were found in submerged aquatic plant samples collected from shallower areas of Lake Taupo, New Zealand, although hyphae of similar appearance were occasionally observed (Clayton and Bagyaraj 1984). Liberta et al. (1983) speculated that VAM fungi in wet habitats act as almost benign parasites when the soil is saturated for extended periods of time. However, when sites become seasonally dry, functional associations may redevelop. Anderson et al. (1986) examined VA mycorrhizal development in a typical wet habitat prairie cordgrass and suggested that under their experimental conditions the VA mycorrhizal colonisation was a nearly ineffective mutualism. The abundance and size of lipid bodies seen in *G. mosseae* mycelium and vesicles in *Casuarina* sp. roots in the present study agrees with observations by Cooper and Losel (1978). Higher contents of lipid in the intramatrical hyphae and vesicles suggest a hormonal change in VAM which may help VAM fungi to maintain their viability under waterlogged conditions. VAM colonisation under these reducing habitats may be an ineffective mutualism or even benign parasitism. As Allen et al. (1989) postulated, VAMycorrhizae are highly elastic and they respond to environmental pressures that we do not yet understand.

The absence of Hartig net in *Casuarina* sp. in the present study is in agreement with observations by others (Ba et al. 1987; Bougher et al. 1990). Lundeberg (1960) reported deep intracellular mycorrhizal infection without a Hartig net in *Pinus sylvestris* roots growing in nutrient solution. Wojciechowska (1960) recorded ECM without mantles in spruce growing in stagnant water. The absence or rare occurrence of ECM in roots growing in water and sediments in the present study is consistent with observations by others (Filer 1975; Shuja et al. 1971; Lorio et al. 1972; Maronek et al. 1980; Lodge 1989). However, Stenstorm and Unestam (1987) noted that when ectomycorrhizal pine seedlings grown without flooding for 3 weeks were subsequently flooded for up to 18 h on 4 days per week, already established ECM was not eliminated.

VAM spore number in this study, like the percentage of VAM infection, also seemed to be related to redox potential i.e. higher numbers at sites with higher  $E_h$  values. Mosse and Bowen (1968) suggested that low spore counts in the sand-dune soils of the east coast of Australia were in response to high soil moisture. Soil moisture activity may be an important determinant of the species spectrum of VAM fungi, as suggested by Read and Boyd (1986). The occurrence of *Gigaspora* and *Scutellospora* spores in aquatic sediments associated with aquatic trees in this study agrees with the observations of Sward et al. (1978), who reported spores of *G. margarita* from wetter areas of heathland soils in south-eastern Australia. Saif et al. (1975) noted that *Gigaspora* sp. was prevalent only in sandy soils which remained at

around 50%–60% water holding capacity. The mycorrhizal association tests conducted by Anderson et al. (1984) also indicated that *G. margarita* is able to tolerate the wet sites and cause infections of plants occurring on wet soils. Tanner and Clayton (1985) reported a high VAM infection ( $53 \pm 6\%$ ) of roots of submerged aquatic *Ranunculus* sp. using *G. margarita* inoculum. Mathew and Johari (1988) also found that *G. margarita* was the most effective endophyte using the nutrient film technique. Sengupta and Chaudhuri (1990) recorded *G. margarita* spores in rhizospheres of salt marsh plants of the Ganges River delta in India. *G. margarita* was found only in the marine sand dunes of the Pacific Northwest of the USA (Rose 1980). These observations suggest that environmental factors such as soil moisture and soil type influence the taxonomic distribution of VAM fungi. Some VAM species such as *G. margarita* may be ecologically adapted to aquatic sites similar to the ECM fungi *Hymenogaster alnicola* and *Lactarius obscuratus* (Trappe 1977). Accurate determination of factors governing the efficiency of *G. margarita* is required before we can realistically select superior VAM isolates for field inoculation.

The occurrence of hairy proteoid roots devoid of mycorrhizal infection in *C. cunninghamiana* is consistent with observations by Diem and Dommergues (1990). Proteoid roots are known to greatly enhance uptake of P and probably other nutrients by the plant (Malajczuk and Bowen 1974). They thus appear to have an activity similar to that of the VAM and ECM symbionts in nutrient absorption. Proteoid roots have high internal P levels which may prevent VAM colonisation (Khan 1975). Although no mycorrhizal infection of *C. cunninghamiana* nodules was observed in the present study, Cervantes and Rodriguez-Barrueco (1992) reported the occurrence of VAM hyphae in the outer cortex of *C. equisetifolia* infected by *Glomus* sp. However, such hyphae are never found in the zone of the nodule containing the bacterioids. An exclusion mechanism such as anaerobiosis in the internal nodular tissue and/or high internal P levels similar to proteoid roots may exist in nodules. The higher percentage of VAM infection in nodulated than in non-nodulated aquatic plants in this study is in agreement with previous observations by the author (Khan 1978, 1987).

The occurrence of VAM and ECM fungal endophytes concurrently in roots of two non-nodulated and one nodulated trees in the aquatic community in the present study indicates possible nutrient exchange between the N-fixing and nonfixing plants. VAM infection is known to improve symbiotic N-fixation primarily by increasing the nutritional status of the host plant (Kucey and Bonetti 1988) and also by enhancing the activity of nitrogenase at low P levels (Russo 1989). VAM hyphae can translocate and assimilate ammonia (Barea et al. 1987), a fact of great ecological and physiological significance. Shuja (personal communication) observed  $^{15}\text{N}$  transfer from donor to receiver plant, not through the soil but through VAM hyphae. This mycorrhizal inter-plant transfer of nutrients may become significant at the community and ecosystem level, especially when soil is

N and P deficient. N-fixing nodulated species often make a significant contribution to the N economy of ecosystems (Dommergues et al. 1984).

Rivers, marshes, creeks and ponds are ecological habitats for plants adapted to withstand waterlogging and high salinity. Symbionts such as VA mycorrhizae, ECM and N-fixing bacteria in their root zones may enhance the ecological adaptation of these plants to such environments. Reddell et al. (1986) reported that low P supply and the absence of *Frankia* were two of the factors responsible for the absence of nodulation in *Casuarina* in some field soils of Australia. Although the mechanism by which P supply regulates nodulation in *Casuarina* requires definitive studies, VA mycorrhizae and ECM can be manipulated to improve P uptake, thus indirectly increasing nodulation. The successful establishment of pioneering species such as *C. cunninghamiana*, which have fast initial growth rates, is probably dependent on N fixation. Such tripartite or tetrapartite associations in these plant species suggest a selective advantage for these plants in such habitats and that they may be largely responsible for the successful colonisation of aquatic sites in New South Wales. These plant species can be manipulated as pioneering species in order to (a) stabilise river and stream banks and reduce soil erosion after removal of natural vegetation, through improved root growth and binding of soil particles; (b) achieve long-term and inexpensive means of biological control of aquatic weeds by the shading of water ways; (c) promote ecosystem stability. The effects of various indigenous and introduced mycorrhizal species on the growth of aquatic plants need further investigation in order to find ecologically adapted endophyte(s) for inoculating suitable marsh plants used in rural waste-water treatment.

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