Chapter 7

Mycotrophy and Its Significance in Wetland Ecology and Wetland Management

A.G. Khan

School of Science, Food, and Horticulture, College of Science, Technology, and Environment, University of Western Sydney, Locked Bag 1797, Penrith South DC, NSW 1797, Australia

Abstract. Rivers, marshes, creeks, and ponds are ecological habitats for plants adapted to withstand stress arising from waterlogging, anaerobiosis, and high salinity. Universal mycosymbionts like arbuscular mycorrhizal fungi may enhance the ecological adaptations of these plants to such environments. This chapter reviews the general mycorrhizal status of various life forms of aquatic macrophytes growing in such ecological habitats and the relationships of arbuscular mycorrhizae (AM) to redox potential in sediments and its P-status. Future studies will have to provide the data required to evaluate the effectiveness of mycorrhizal inoculation of wetland plants, including rice, in order to assess the significance of AM in wetland ecology and wetland management.

7.1. Introduction

Arbuscular mycorrhizal (AM) fungi, belonging to order Glomales, form symbiotic associations with roots of 80–90% of land plants in natural and agricultural ecosystems (Brundrett, 2002). Plants associated with these fungi benefit in the increased uptake of immobile nutrients like P, Zn, and Cu (Smith, 1980; Smith & Read, 1997; Jamal et al., 2002). In addition, AM mycorrhizal infection also leads to increased tolerance of plants to various soil environmental stresses like draught, waterlogging, and salinity (Khan, 1995). These associations represent a key factor in the below ground network which influences diversity and plant community structure (O'Conner et al., 2002), but we know very little about the enormous AM fungal diversity in soils and their properties and behavior in the soil environment (Khan, 2002a). However, not all plants are mycorrhizal and not all AM fungi benefit host plants under all growth conditions

(Francis & Read, 1995). The presence of AM in aquatic and wetland plants suggests that they are ecologically significant, but their function is not well understood. The aim of this review is to assess the occurrence of arbuscular mycorrhizae (AM) in aquatic plants and their significance in wetland ecology and management.

7.2. Early History of Glomales

Glomales are one of the oldest group of fungi, older than land plants. The first land plants, Bryophytes, appeared in the Mid Ordovician to Early Silurian periods (430−476 million years old). The oldest fossil evidence of Bryophyte-like land plants, 100 million years ago in Early Devonian, had AM-like infections even before roots evolved. Phipps & Taylor (1996) reported morphological structures resembling modern arbuscular mycorrhizal fungi (AMF) in Triassic roots confirming evolution of mycorrhizal fungi by that time. The first land plants are most likely to have evolved from algae (Kenrick & Crane, 1997). No fossil records are available for the rootless freshwater Charophycean algae, which are the probable ancestors of land plants, to show if they were mycorrhizal. Mosses, liverworts, and hornworts often contain AMF structures like hyphae, vesicles, and arbuscules (Turnau et al., 1999; SchuBler, 2000). Fossil evidence of AM in the rhizomes of early vascular plants suggests that the origin of vascular terrestrial plants is likely to have been from their bryophyte-like ancestors (Edwards et al., 1998). Bryophytes represent a radically different way of doing things by evolving desiccation tolerance strategy for adaptation to life on land and, in species number, are the biggest group of green land plants (Proctor, 2000). Sphenophytes, Lycopodophytes and Pteridophytes are among the first land plants with roots which originated in mid-Devonian era, and AM associations are reported in these plants (for references, see Brundrett (2002)). Both living and Triassic fossil cycads had AMF in their roots. Members of Pinaceae have ectomycorrhize. AM associations are ubiquitous in the living angiosperms (Newman & Reddell, 1987; Trappe, 1987), which probably arose in the early Cretaceous (Stewart & Rothwell, 1993; Taylor & Taylor, 1993). The phylogenetic relationships between origin and diversification of AM fungi and coincidence with vascular land plants was investigated by Simon et al. (1993) by sequencing ribosomal DNA genes (SS sequences) as a molecular clock to infer dates, from 12 Glomalean fungal species. The authors estimated the origin of AM-like fungi to be 353−462 million years ago, which is consistent with the hypothesis that AM were instrumental in the colonization of land by ancient plants. This hypothesis is also supported by the observation that AM can now be found worldwide in the angiosperms, gymnosperms as well as ferns, suggesting that its nature is ancestral.

7.3. Evolution of Roots

Early land plants faced selection pressure to increase surface area of their roots in soil. It has been suggested that roots evolved as habitats for mycorrhizal fungi: thus intracellular air spaces in the cortex of plants are for AM fungal hyphal growth. Large cortical cells in the roots are to accommodate AMF structures like hyphal coils, arbuscules and vesicles. The endodermis layer is for restricting AM fungal growth in vascular tissue of the roots, and the epidermis is for appresoria formation and root penetration by AMF hyphae. Long, slow-growing, long-lived, relatively thick roots are typical of plants with obligate AM associations. Plants with fine root systems exclude AMF and are non-mycorrhizal. Brundrett (2002) gave a detailed account of coevolution of roots and mycorrhizae in land plants, and assessed the recent evidence available from palaeobotanical and morpho-logical studies and the analysis of DNA-based phylogenies. The author also discussed major evolutionary trends and the relative success of plants with different root types.

7.4. Roots of Aquatic Plants

The concept of aquatic plants adopted for this chapter is much wider and includes not only vascular plants living habitually in or on water but also some species living in semi-aquatic and terrestrial habitats subject to seasonal inundation due to flooding and or increase in height of the soil water table, after periods of heavy rain.

Roots and leaves of aquatic plants possess a well-developed system of air lacunae (Armstrong, 1979; Justin & Armstrong, 1987) that allow transport of CO_2 from sediment through root lacunae to leaves and transport O_2 in the opposite direction (Pedersen et al., 1995). Roots of wetland plants can adapt to anaerobic conditions via the development of these air lacunae (Armstrong et al., 1991). Mycorrhiza formation is the most important evolutionary factor determining presence or absence of lacunae in roots.

7.5. Mycotrophy of Aquatic Plants

In the past, less attention was given to the presence of those soil microorganisms, such as AM fungi, that are an integral part of wetland soil regimes and that may play an important role in the establishment and diversity of plants (DeAngelis et al., 1986). However, the phenomenon has received increased attention in the recent years (Cook & Lefor, 1998; Turner & Friese, 1998; Miller & Bever, 1999;

Thormann et al., 1999). The presence or absence of mycorrhizae in the plant species used in wetland restorations might be an important factor in the re-establishment of wetland plant associations.

7.5.1. Mycorrhizal Status

Information regarding the presence of AM in aquatic and wetland habitats is limited and often contradictory. AM in aquatic macrophytes were first recorded by Sondergaard & Laegaard (1977). This observation was subsequently supported by others (for references see review articles by Khan (1995) and Khan & Belik (1995)). Mycorrhizal status of the dominant families of aquatic plants, i.e. Cyperaceae, Juncaceae, and Typhaceae found in most wetlands, varies across habitats due to local environmental conditions. Because AM fungi are obligate aerobes, their occurrence and survival in the anoxic aquatic habitat, characteristic of wetland plants, was postulated to be the reason for non-mycorrhizal status of aquatic plants reported by earlier workers. But recently many reports of their occurrence in wetland habitats have appeared in the literature (Khan, 1993a; Turner & Friese, 1998; Miller & Bever, 1999). The survival of AM fungi in the aquatic plant root and near the plant root in the rhizosphere under anoxic conditions, may be due to the fungus obtaining oxygen directly from the root or as oxygen diffuses from the root into the rhizosphere.

Earlier reports regarding the mycorrhizal status of aquatic plants ranged from complete absence to reduced or temporary absence due to anaerobiosis, and recurring under aerated and drier conditions (Shuja et al., 1971). Khan (1974) reported absence of mycorrhizal infection in the roots of aquatic plants collected from diverse aquatic habitats in Pakistan but a re-examination of these hydrophytes by Hussain et al. (1994, 1995) found them to be mycorrhizal. It is possible that the endophyte may be existing in the reported non-mycorrhizal plants in the form of mycelia, not considered by the researchers as AM infection. The presence of arbuscules was used by earlier workers as a definition indicating the presence of AM fungi in plant roots (Malloh & Malloh, 1981), but the presence of vesicles alone in root cortex is now regarded as sufficient evidence for the presence of AM fungi (Thormann et al., 1999).

However, the presence of non-AM fungi like *Rhizoctonia* producing vesicle-like structures in plant roots may sometimes leads to misidentification (Dhillion, 1994). For example in addition to the AM fungal structures, Thormann et al. (1999) also reported the occurrence of a diverse assemblage of sterile dark-pigmented or hyaline, septate or non-septate, with or without clamp connections, fungal hyphae and swollen hyphal structures resembling vesicles of AM fungi: those structures occurred in and on the roots of plant species growing in peatlands

along a bog-fen-marsh gradient in Southern Boreal Alberta, Canada. These fungi have also been found in great abundance in highly stressed ecosystems like peatlands (Thormann et al., 1999) and high altitude ecosystems (Malloh & Malloh, 1994; Treu et al., 1996). Turnau et al. (1999) suggested creating a new category of mycorrhizae to encompass these fungi. The role of these root endophytes and their ecological significance, if any, is unclear and needs further investigation (Jumpponen & Trappe, 1998).

AM infections were found in the young roots of trees growing on creek and river banks, in stationary or slowly flowing fresh water or brackish waters in swamps, creeks, drains and channels, and in seepage areas of New South Wales, Australia (Khan, 1991, 1993a, 1993b, 1993c). By contrast, the free-floating roots of these trees growing in water on the banks of the water bodies were non-mycorrhizal. Split root-system studies with rooted cuttings of Weeping Willow (*Salix babylonica*) confirmed that the free-floating roots became mycorrhizal when subjected to rooting sediments (Khan, 1991). The variations found in literature regarding mycorrhizal status are common in wet and waterlogged habitats, where conditions fluctuate on a seasonal or annual basis so as to favor or hinder mycorrhiza formation. Stevens & Peterson (1996) found higher AM colonization of roots of *Lythrum salicaria* growing in wetter areas in the field, and the reverse pattern in greenhouse experiments. Typically non-mycorrhizal plant species may become colonized under certain environmental conditions. Louise (1990) found that the number of mycorrhizal species increased from 0 to 87.5% as zones were sampled further from the sea. These and other examples suggest that soil saturation may be a limiting factor to colonization of wetland plant species that are typically non-mycorrhizal. However, the mechanism underlying these observations is still unclear and requires further research into the prevalence and role of AM in aquatic habitats.

Miller et al. (1999) studied the root hair morphology of 23 species of *Carex* (Cyperaceae), which are generally considered non-mycorrhizal, occurring in upland and wetland habitats, and found that certain species were typically mycorrhizal, other species were usually non-mycorrhizal and the mycorrhizal status of a third group of species depended upon the environment. The authors found lowest infection in the third group of *Carex* spp. in soils with high moisture and low pH, conditions typical of many wetland habitats.

Generally, AM infections noted in moist to wet habitats were found to be lacking arbuscules. A relationship between the characteristic AM infection pattern and soil moisture gradient was found in a study of a *Casuarina cunninghamiana* transect on a creek embankment (Khan, 1992), 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 vesicles and arbuscules were absent in flooded creek bed where

roots were associated with coenocytic intercellular hyphae containing abundant lipid droplets (Shuja et al., 1971; Khan, 1993a,b). These observations are consistent with those of Rickerl et al. (1994) and Stevens & Peterson (1996) who also reported high mycorrhization at the drier end of a moisture gradient. Miller (2000) also found lower AMF colonization in wetter sites for two wetland grasses. Thormann et al. (1999) reported no mycorrhizae in 11 species of herbaceous plants including sedges growing in three Alberta fens, but found AMF structures like arbuscules in a few roots and vesicles in many roots of woody fen plants. The authors attributed decreased arbuscular and increased vesicular frequency in the roots of mycorrhizal wetland plants, from early spring to summer and fall, to reported seasonality of VA-mycorrhizal formation in many plant species and ecosystems (Brundrett, 1991). Brown & Bledsoe (1996) and Sharma et al. (1998) have not documented arbuscules in the roots of aquatic plants they studied. Stenlund & Charvat (1994) reported that root colonization in aquatic plants is limited to only hyphae and vesicles. Miller & Sharitz (2000) found that flooding decreased the proportion of roots infected by AM fungi in wetland grasses, and that there was a direct relationship between flooding and mycorrhizal colonization. However, the fungi remained viable under flooded conditions in the roots of the wetland grasses, as shown by staining the roots with Nitroblue Tetrazolium (NBT)-succinate stain, suggesting that once mycorrhizal colonization has taken place, the fungus–root associations may endure prolonged exposure to flooding, depending upon the persistence of functioning and oxygenic roots (Miller, 2000).

Cornwell et al. (2001) studied mycorrhizal status of monocots and dicots growing in a ground-water-fed, low-P New York fen and found monocots generally non-mycorrhizal despite the fact that their roots showed a significantly higher percentage of air-filled root porosity. The authors also reported nine out of 10 dicot fen plant species to be mycorrhizal.

7.5.2. *Plant Life Forms and Mycorrhizae*

Mycorrhizae have been reported in ferns and angiosperms growing as emergent, free-floating or submerged (permanently or periodically) plants in aquatic environments (for references see review by Khan & Belik (1995)). Beck-Nielson & Madson (2001) have reported the presence of AM in five out of 25 emergent as well as submerged macrophyte spp. growing in streams. Typical infections with internal and external mycelia, and characteristic vesicles and arbuscules were found in submerged leaves of *Salvinia cucullate* (Bagyaraj et al., 1979). Belik & Khan (1992) reported well-established AM infection, mainly vesicles, in 38% of the root segments of *Ruppia polycarpa*, a submerged and surface-flowering plant

growing in shallow waters at Prospective Reservoir, Sydney, Australia. A survey of 17 aquatic macrophytes in the Sydney area representing submerged, emergent, floating, and free-floating growth forms by Belik & Khan (1993a), showed that 35% of plants, including free-floating *Elatine gratilioides*, were mycorrhizal (Table 1). These findings established that AM fungi can infect permanently submerged plants under natural conditions.

It has been known for a long time that desiccation-tolerant liverworts and hornworts, which are the product of some 450 million years of evolution since their origin (Edwards et al., 1998), form AM-like infections (Stahl, 1949). These earlier observations are supported by many recent researchers (Rabatin, 1980; Duckett & Read, 1991; Turnau et al., 1999). SchuBler (2000) synthesized AM-like infections using Glomalean fungi (*Glomus claroideum*) and a bryophyte *Anthroceros punctatus* (L.) for the first time. These observations provide further support to the hypothesis that symbiotic association with AMF was a primary event during the evolution of land plants and that mycotrophy is the essential condition in land plants.

7.5.3. *Relationships to Redox Potential*

The reduced mycorrhizal infection reported in aquatic plants by various researchers may be due to the low availability of oxygen (Russell, 1977; Rabatin, 1980; Saif, 1981) to the roots under flooded conditions (Saif, 1983). Tanner & Clayton (1985) demonstrated that decreased redox potential was associated with significantly reduced AM infection. The redox potential in sediments of Danish streams with non-mycorrhizal specimens ranged from 54 to 280 mV and in sediments with mycorrhizal spp. from 250 to 530 mV, indicating that the redox potential of sediments might play a role in the development of AM associations. Belik & Khan (1993a) and Khan (1993a) found a correlation between mycorrhizal infection and redox potential. Mycorrhizae were absent or less frequent in roots of aquatic trees growing in reduced environment of waterlogged soils with low Eh values (Eh < 150 mV) than in well-oxidized terrestrial soils with higher Eh values (Eh > 300 mV). Khan (1992) reported AM infections in the roots of *Casuarina cunninghamiana* growing in a transect on a creek embankment in the marshy and periodically inundated soils, but the same plant spp. formed ectomycorrhizae as well as AM associations when growing in well drained and aerated soils with higher Eh values. Surface roots of aquatic plants, growing in swampy areas of Sydney with higher redox potentials, were found to be heavily mycorrhizal as compared to their counterparts in deep sediments with lower Eh values (Belik & Khan, 1993a).

Table 1: Mycorrhizal status of aquaphytes studied in Pakistan (1974 and 1995).

Hosts	Life form	% AM	AMF	References
Cyprus eleusinoides Kunth	An	0.0	Nil	Khan (1974)
Cyprus diformis L.	An	0.0	Nil	Khan (1974)
Eichornia crassipes (Mart.) Schlecht	F	0.0	Nil	Khan (1974)
Hydrilla verticillata (L.f) L.C. Rich	S	0.0	Nil	Khan (1974)
Juncus bufonius L.	An	0.0	Nil	Khan (1974)
Lemna polyrhiza L.	F	0.0	Nil	Khan (1974)
Nelumbium speciosum Wild.	F	0.0	Nil	Khan (1974)
Nymphaea lotus L.	F	0.0	Nil	Khan (1974)
Nasturtium officinale R.Br.	An	0.2	Nil	Khan (1974)
Populus euroamericana	An	EM/AM	H,V	Shuja et al. (1971)
Potamogeton crispus L.	S	100	H,V,A	Khan (1974)
Potamogeton indicus Roxb.	An	0.0	Nil	Khan (1974)
Phragmites karka (Ritz.) Trin. Ex Steu	An	0.0	Nil	Khan (1974)
Ranunculus aquatilis L.	An	0.0	Nil	Khan (1974)
Sagittaria guayanesis H. B. and Khan	An	0.0	Nil	Khan (1974)
Trapa bispinosa Roxb.	An	0.0	Nil	Khan (1974)
Typha angustifolia Bory and Chaub.	An	0.0	Nil	Khan (1974)
Vallisneria spiralis L.	An	0.0	Nil	Khan (1974)
Agrostis sp.	An	40.5	H,V,A	Hussain et al. (1994, 1995)
Conyzanthus sp.	W	100	H,V,A	Hussain et al. (1994, 1995)

Echornia crassipes L.	S,F	92	H,V,A	Hussain et al. (1994, 1995)
Hydrilla verticillata (L.F.) L.C. Rich	S	95.5	H,V,A	Hussain et al. (1994, 1995)
Lemna gibba L.	F	19.8	H,V,A	Hussain et al. (1994, 1995)
Myriophyllum spicatum L.	S	98.5	H,V,A	Hussain et al. (1994, 1995)
Mentha longifollia (L.) Huds.	W	100	H,A,V	Hussain et al. (1994, 1995)
Potamogeton nodosus Poir	S	100	H,A,V	Hussain et al. (1994, 1995)
Phragmites karka (Reitz.) Trin. ex Ste.	An	50	H,A,V	Hussain et al. (1994, 1995)
Setaria spp.	W	100	H,A,V	Hussain et al. (1994, 1995)
Scripus spp.	Am	100	H,V	Hussain et al. (1994, 1995)
Scirpus maritimus L.	Am,W	49.5	H	Hussain et al. (1994, 1995)
Vallisneria spiralis L.	S	100	H	Hussain et al. (1994, 1995)
Veronica beccabunga L.	W	100	H,A,V	Hussain et al. (1994, 1995)

Am = amphibious; S = submerged; F = free floating; An = anchored; W = wetland; H = hyphal; A = arbuscular; V = vesicular; EM = Ectomycorrhiza; AM = Arbuscular mycorrhiza. Highlighted plant species were found to be non-mycorrhizal in 1974 but mycorrhizal in 1995.

7.5.4. Relationship to Root Hairs

Baylis (1969) found that plants with few roots may become obligatory mycorrhizal in P-deficient soils. Root hair abundance and length were found to be negatively correlated with mycorrhizal dependence or benefit (Baylis, 1975; Schwelger et al., 1995). Belik & Khan (1992, 1993a,b) reported roots of submerged *Ruppia polycarpa* equipped with root hairs and heavily mycorrhizal. On the contrary, the roots of aquaphytic plants *Aster sabulatus* and *Elatine gratilioides* were devoid of root hairs and had a high AM colonization (Belik & Khan, 1993a,b) (Table 2), thus exhibiting the root hair–AM infection relationship. However, roots of *Ottelia ovalifolia* and *Pseudoraphis spenesceus* deviated from this relationship as they lacked root hairs but were non-mycorrhizal, and those of *Ludwigia peploides*, *Scripus validus*, *Triglochin procera*, *Typha orientalis* and *Schoenupluctus validus* had root hairs and no AM colonization (Belik & Khan, 1993b) (Table 2). Beck-Nielson & Madson (2001) found that submerged macrophytes collected from lakes and streams that were infected all lacked root hairs.

Miller et al. (1999) identified a unique root hair morphology with bulbous base, which was found to be associated with the non-mycorrhizal conditions of *Carex* species growing in waterlogged soils. The interspecific variations in the mycorrhizal status of *Carex* species was apparently connected with the morphology of the root hairs and the non-mycorrhizal condition, i.e. species with characteristic bulbous-based root hairs were non-mycorrhizal. Root hairs represent an adaptation to non-mycotrophy.

Clearly, however, the evidence presented above and in other recent publications indicates that the relationship between the mycorrhizal status of aquatic plants and root hairs must be re-evaluated.

7.5.5. Relationship to P-Status (Oligotrophic vs. Eutrophic Status)

The relationship between soil P concentrations and AM colonization has been reported to be negative in P-rich soils and positive in P-deficient soils (Khan, 1975). Under conditions of high P supply, plants accumulate and maintain high internal P concentrations, which reduces or inhibits AM infection (Smith & Read, 1997). A negative effect of elevated P levels on AM root colonization has been demonstrated for wetland macrophytes like *Lythrum salicaria* (White & Charvat, 1999), *Solidago patula* (Cornwell et al., 2001), and *Typha angustifolia* (Tang et al., 2001). The interpretation of AM infection and P uptake for wetland plants is, however, complicated by dual sources of available P (soil and water) and frequent wet and dry cycles. The lack of AM colonization in wetland plants may have been

Table 2: Presence ($+$) or absence ($-$) of root hairs, aerenchyma and AM associations of aquaphytes of Sydney region.

Hosts	Life form	Aerenchyma + or −	Hairs + or −	% AM	AMF
Ruppia polycarpa[a]	**S**	**+**	**+**	**71**	**H,V,A**
Ottelia ovalifolia[b]	**S**	**+**	**−**	**0**	**Nil**
Triglochin procera[c]	S	+	+	0	Nil
Typha orientalis[c]	An	+	+	0	Nil
Ludwigia peploides[c]	An	+	+	0	Nil
Pseudoraphis spenescens[b]	**An**	**+**	**−**	**0**	**Nil**
Schoenupluctus validus[c]	An	+	+	0	Nil
Pasicaria decipiens	An	+	−	0	Nil
Scirpus validus[c]	An	+	+	0	Nil
Elatine gratiliodes[b]	**F**	**+**	**−**	**30**	**H,V**
Paspalum paspaloides	An	+	+	48	H,V
Phragmites australis	An	+	+	55	H,A,V
Aster sabulatus[a]	**An**	**+**	**−**	**62**	**H,V**
Sagittaria graminea	An	+	+	21	H

Am = amphibious; S = submerged; F = free floating; An = anchored; W = wetland; H = hyphal; A = arbuscular; V = vesicular; EM = Ectomycorrhiza; AM = Arbuscular mycorrhiza. From Belik & Khan (1992, 1993a,b). (1) Relationship between mycorrhizal status of aquatic plants, presence or absence of root hairs, and root parenchyma must be re-evaluated. (2) Data regarding the trophic status (P-availability) of aquatic systems missing and rarely examined in aquatic macrophytes studied. (3) No true relationship was found between the root aerenchyma and AM colonization in the aquatic macrophytes studied— needs further evaluation. Terrestrial plants with few or no root hairs are obligatory mycorrhizal in P-deficient soils (Baylis, 1975; Belik & Khan, 1993b; Schwelger et al., 1995). Root hair–AM infection relationships in aquatic plants ??
[a] Roots possessed root hairs and heavily mycorrhizal.
[b] Roots lacked root hairs but non-mycorrhizal.
[c] Roots possessed root hairs and non-mycorrhizal.

due to increased availability of P from both the soil and the water columns. The relationship between P availability and mycorrhizal status has been rarely examined in aquatic macrophytes.

Aquatic plant growth in many freshwater ecosystems is limited by the phosphorus source, which is often from agricultural soils (Schindter, 1977) and the population surrounding many lakes (Gibson, 1997). No relationship was found between AM infection and trophic status of the British lakes (Farmer, 1985). Clayton & Bagyaraj (1984), who observed AM infections in submerged plants

from both oligotrophic and eutrophic lakes, also found no relationship between infection and trophic status of the lakes and the incidence of AM colonization. Rickerl et al. (1994), on the contrary, reported a high correlation between colonization levels and P for plants sampled from the dry regime and no correlation for plants sampled from the wet regime. Histological staining of *Vallisneria americana* roots revealed the widespread presence of arbuscules and thick-walled vesicles in its roots (Wigand & Stevenson, 1994). Lateral oxygen extrusion from the roots of aquatic macrophytes into the rhizospheres of submerged plants, which is regarded as necessary for the growth of aerobic AM fungi, may result in oxidation of iron to form distinct barriers to P uptake thus reducing the P availability in this zone. It may be that AM fungal hyphae facilitate P uptake by extending hyphae beyond this P-depletion zone in the rhizosphere and mobilizing adsorbed P in the rhizosphere; in return, submerged plants may promote the establishment of AM associations by lateral oxygen release (Wigand & Stevenson, 1994). Like their terrestrial counterparts, AM fungi in aquatic plants may also facilitate nutrient cycling, especially P. Wigand & Stevenson (1997) tested this hypothesis by using a submerged plant *Vallisneria americana* supplied with P^{33}-orthophosphate and recorded a greater incorporation of P^{33} into root cortex of the heavily infected roots (80%) of the mycorrhizal plants as compared to the fungicide-treated non-mycorrhizal plants. The authors also found that the level of P in the root tissue was over three times greater than in the sheath (iron hydroxide plaque) and six times greater than in the sediments surrounding the mycorrhizal plant, indicating that mycorrhizae facilitate P uptake of *V. americana* in the P-limited freshwater habitats. These observations suggest that AM fungal mediation was a major mechanism of facilitated P uptake and that the surrounding the mycorrhizal roots represent an additional mechanism of P assimilation by aquatic macrophytes.

In freshwater ecosystems, oxygen release into the rhizosphere can lead to the formation of mineral-hydroxide (Fe, Mn) sheath formation surrounding the roots (Wium-Andersen & Andersen, 1972; Wigand & Stevenson, 1997). This sheath results in P-absorption, making it less available for direct uptake (Jaynes & Carpenter, 1986). St-Cyr et al. (1993) also reported such a sheath for the submerged macrophyte, *Vallisneria americana*, which has also been described equipped with AM (Wigand & Stevenson, 1994). Sheath-thickness and composition vary among macrophytes due to variations in oxygenation, redox potentials and site (Wium-Andersen & Andersen, 1972; Sand-Jensen et al., 1982; Jaynes & Carpenter, 1986; Wigand & Stevenson, 1994).

Christensen & Wigand (1998) found that the freshwater *Lobelia dortmanna* L. with low tissue P contents showed significantly higher mycorrhizal infection than plants with high tissue P contents, indicating that AM associations may be important in P assimilation by rooted aquatic plants in habitats with low P

availability. White & Charvat (1999) studied the effect of P availability on the AM status of an emergent aquatic, *Lythrum salicaria*, grown in hydroponic sand cultures at five P levels with or without AM fungal inoculum obtained from the wetland soil. The authors reported no infection in the control plants, the lowest or no AM infection in the roots of inoculated plants grown at the highest P levels, and the highest mycorrhizal colonization for plants grown at the lowest P levels. This pattern is consistent with that for terrestrial cereal crops (Khan, 1975). Further controlled studies mimicking natural conditions, as concluded by White & Charvat (1999), are needed.

Beck-Nielson & Madson (2001) reported AM infection in most submerged species sampled from oligotrophic lakes in Denmark, whereas no infection was found among submerged macrophytes sampled from eutrophic lakes. AM colonization may be an ecologically significant factor in soft water oligotrophic lakes, which have low P-availability in the sediments. Increased oxygenation and redox potential in the rhizosphere of plants growing in such ecosystems, lead to reduced P solubility (Christensen & Andersen, 1996; Christensen & Wigand, 1998). The presence of AM may ameliorate this problem by increasing surface area for nutrient uptake and acquiring P by hyphae.

Cornwell et al. (2001) found roots of *Typha latifolia* and *Carex lasiocarpa*, previously described as mycorrhizal in other wetland ecosystems, to be non-mycorrhizal in a phosphorus-poor fen in New York, suggesting that P availability may not be important in determining in which habitat these species form mycorrhizae. This further emphasizes the point that understanding the ecological functions of AM fungi in a given ecosystem requires further studies, requiring field surveys and manipulations in addition to green house experiments.

Many wetlands in the low-lying areas are very fertile because they receive nutrient inputs from surface runoffs and groundwater, while those on highly weathered and sandy or peat soils are nutrient poor. Few studies have considered fertility when attempting to relate mycorrhizal colonization to wetland characteristics. P input decreases a plant's dependency on AM fungi, regardless of the effects of flooding. Studies on effects of flooding on the role of AM fungi in wetlands are therefore likely to be more informative when conducted in less fertile areas or in P-rich habitats with low availability of P.

Miller & Sharitz (2000) suggested that AM fungal colonization has the potential to benefit grasses under wet conditions by increasing the size and P contents of wetland grasses under both dry and wet conditions, and that this is likely to increase with increased aeration from plant root or seasonal water drawdown. Tang et al. (2001) studied the relationship between P availability and AM colonization of *Typha angustifolia*, previously recorded by various workers to be non-mycorrhizal and provided clear evidence that AM fungi can colonize this

aquaphytic plant under controlled experimental conditions as a function of P availability.

Recently, some reports revealed AM in rice cultivated under waterlogged conditions. Rice plants were shown to be positively responsive to colonization by indigenous AM fungi (Dhillion, 1992). The author found that the higher availability of P in the high P soil did not completely eliminate AM infection of roots in the three rice varieties studied. Positive responses to AM-inoculation have been demonstrated in wetland rice (Solaiman & Hirata, 1996, 1998). Purakayastha & Chhonker (2001) achieved a high intensity of root colonization in wetland rice inoculated with the AM fungus *Glomus etunicatum* by raising seedlings in the upland nursery under aerobic conditions. The authors found that the colonization persisted when the same seedlings were transplanted into pots under waterlogged conditions. Secilia & Bagyaraj (1994) have shown that, like terrestrial crops, different strains and species of AM fungi differed in their ability to confer growth benefits to rice plants. Further studies are needed to evaluate the effectiveness of mycorrhizal inoculation of this wetland crop.

7.6. Significance of Mycotrophy in Wetland Ecology and Management

The literature reviewed above suggests that the occurrence of AM in aquatic hydrophytes is common and is associated with fluctuating water, nutrients, and oxygen conditions. However, the consequences of severity and duration of hypoxia, and the anatomical and physiological adaptive features of hydrophytes are not yet fully understood in relation to VA mycorrhizae. Since each AM fungal species and isolate has specific ecological requirements, the screening of their diversity in aquatic environment is necessary in order to select the most superior, effective and efficient isolate for successful introduction into a habitat (Khan, 2002a,b). Several areas of inoculum production and application technology for wetland management merit further investigations.

Are AM fungi performing similar functions in wetlands as they are in drier habitats? Recent research by various workers reviewed in this article suggests that AM fungi may be advantageous to wetland plants: (1) during periods of low soil moisture associated with seasonal hydrology, that leaves them with reduced water levels or completely dry for short or long durations; and (2) in wetlands with low P. Details of the ecology of AM fungi in aquatic environments are not well understood and documented. Knowledge of interactions between AMF in submerged sediments and the mycorrhizospheres of fibrous plant roots can lead to improved management of wetlands and may be applicable to wetland plant establishment and later management.

The habitat sampled by various authors, listed above, ranged from mineral-rich groundwater-fed wetlands (such as fens and wet meadows) where soils are saturated during much of the year, to marshes with stagnate water, and to downward gradient of water as in may seasonal wetlands. There are many biochemical differences between these habitats, which affect the mycorrhizal status of their macrophytes. The plants, growing in the organic soils of groundwater-fed wetlands surveyed by Turner et al. (2000) for AM associations, were subjected to habitats with lower bioavailability of P contents than marshes and other similar nutrient accumulating wetlands. The authors found up to 61% AM colonization levels in 90% of the plant species sampled, and proposed that in wetlands with low P availability AM may tend to be more numerous than in wetlands that act as a sink for nutrients, and that plants may be more dependent on AM fungi for nutrient uptake under such conditions. The authors proposed that while preparing a site for restoration or creation of a new wetland, importance of AM should be considered as a contributing factor to the success of the project, especially if nutrient availability is low.

Presence of AM in rice plants is interesting but requires further studies with reference to AMF diversity and functionality in order to evaluate the effectiveness of mycorrhizal inoculation in this wetland crop.

Acknowledgements

References

Armstrong, W. (1979). Aeration in higher plants. In: H. W. Woolhouse (Ed.), *Advances in botanical research. VII* (pp. 225–232). Academic Press, London.

Armstrong, W., Justin, S. H. F. W., Beckett, P. M., & Lythe, S. (1991). Root adaptation to soil waterlogging. *Aquatic Botany*, **39**, 57–73.

Bagyaraj, D. J., Manjunath, A. M., & Patil, R. B. (1979). Occurrence of vesicular–arbuscular mycorrhizas in some tropical aquatic plants. *Transactions of the British Mycological Society*, **72**, 164–167.

Baylis, G. T. S. (1969). Host treatment and spore production by *endogone*. *New Zealand Journal of Botany*, **7**, 173–174.

Baylis, G. T. S. (1975). The magnoloid mycorrhiza and mycotrophy in root systems derived from it. In: F. E. Sanders, B. Mosse, & P. B. Tinker (Eds), *Endomycorrhizas* (pp. 373–389). Academic Press, New York.

Beck-Nielson, D., & Madson, T. V. (2001). Occurrence of vesicular–arbuscular mycorrhiza in aquatic macrophytes from lakes and streams. *Aquatic Botany*, **71**, 2, 141–148.

Belik, M., & Khan, A. G. (1992). Occurrence of vesicular arbuscular mycorrhizae (VAM) in submerged *Ruppia polycarpa* (Ruppiaceae). *International Symposium on Management of Mycorrhizas in Agriculture, Horticulture, and Forestry, 28 September–2 October, 1992*. The University of Western Sydney, Perth, Australia, Abstract (p. 4).

Belik, M., & Khan, A. G. (1993a). Vesicular arbuscular mycorrhizae in aquatic plants of Sydney, Australia. *Sixth International Congress of Plant Pathology, July 28–August 6, 1993*. Canada National Research Council, Montreal (Quebec), Canada, Abstract 8.2.4 (p. 139).

Belik, M., & Khan, A. G. (1993b). Relationship of root hair and arenchyma on the occurrence of mycorrhizae in submerged plants. *Ninth North American Conference on Mycorrhizae, August 8–12, 1993*. University of Guelph, Guelph, Ontario, Canada, Abstract (pp. 4–5).

Brown, A. M., & Bledsoe, C. (1996). Spatial and temporal dynamics of mycorrhizas in *Jaumea carnose*, a tidal salt marsh halophyte. *Journal of Ecology*, **84**, 703–715.

Brundrett, M. C. (1991). Mycorrhizas in natural ecosystems. *Advances in Ecological Research*, **21**, 171–313.

Brundrett, M. C. (2002). Coevolution of roots and mycorrhizas of land plants. *New Phytologist*, **154**, 275–304.

Christensen, K. K., & Andersen, F. O. (1996). Influence of *Littorella uniflora* on phosphorus retention in sediment supplied with artificial porewater. *Aquatic Botany*, **55**, 185–197.

Christensen, K. K., & Wigand, C. (1998). Formation of root plaques and their influence on tissue phosphorus content in *Lobelia dormanna*. *Aquatic Botany*, **61**, 2, 111–122.

Clayton, J. S., & Bagyaraj, D. J. (1984). Vesicular arbuscular mycorrhizas in submerged aquatic plants of New Zealand. *Aquatic Botany*, **19**, 251–262.

Cook, J. C., & Lefor, M. W. (1998). The mycorrhizal status of selected plant species from Connecticut wetlands and transition zones. *Restoration Ecology*, **6**, 214–222.

Cornwell, W. K., Bedford, B. L., & Chapin, C. T. (2001). Occurrence of arbuscular mycorrhizal fungi in a phosphorus-poor wetland and mycorrhizal response to phosphorus fertilization. *American Journal of Botany*, **88**, 10, 1824–1829.

DeAngelis, D. L., Post, W. M., & Travis, C. C. (1986). *Positive feedback in natural systems*. Springer-Verlag, Berlin.

Dhillion, S. S. (1992). Host-endophyte specificity of vesicular–arbuscular mycorrhizal colonization of *Oryza sativa* L. at the pre-transplant stage in low or high phosphorus soil. *Soil Biology & Biochemistry*, **24**, 2, 405–411.

Dhillion, S. S. (1994). Ectomycorrhizae, Arbuscular Mycorrhizae, and *Rhizoctonia* spp. of Alpine and Boreal *Salix* spp. in Norway. *Arctic and Alpine Research*, **26**, 304–307.

Duckett, J. G., & Read, D. J. (1991). The use of the fluorescent dye, 3,3'-dihexyloxacar-ococyanine iodide, for staining of ascomycete fungi associated with liverwort rhizoids and ericoid mycorrhizal roots. *New Phytologist*, **118**, 259–272.

Edwards, D., Wellman, C. H., & Axe, L. (1998). The fossil record of early land plants and relationships between primitive embryophytes: too little and too late? In: J. W. Bates, N. S. Ashton, & J. G. Duckett (Eds), *Bryology for the twenty-first century* (pp. 15–43). Maney Publishing and British Bryological Society, Leeds, UK.

Farmer, A. M. (1985). The occurrence of arbuscular–mycorrhiza in isoetid-type submerged macrophyte under naturally varying conditions. *Aquatic Botany*, **21**, 245–249.

Francis, R., & Read, D. J. (1995). Mutalism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure. *Canadian Journal of Botany*, **73**, 1301–1309.

Gibson, C. E. (1997). The dynamics of phosphorus in freshwater and marine environments. In: H. Tunney, O. T. Carton, P. C. Brooks, & A. E. Johnston (Eds.), *Phosphorus loss from soil to water*. CAB International, New York, pp. 119–135.

Hussain, R., Ayub, N., Gul, J., Chaudhary, A., & Khan, A. G. (1994). Incidence of vesicular–arbuscular mycorrhizal (VAM) fungi in aquaphytes growing in and around Islamabad. *Proceedings of the Third Asian Conference on Mycorrhizae (ACOM III), April 19–21, 1994*, Abstract 5.7, Seameo Biotrop, Yogyakarta, Bogor, Indonesia.

Hussain, R., Ayub, N., Gul, J., Chaudhary, A., & Khan, A. G. (1995). Incidence of vesicular–arbuscular mycorrhizal (VAM) fungi in aquaphytes growing in and around Rawalpindi/Islamabad. *Pakistan Journal of Phytopathology*, **7**, 2, 98–103.

Jamal, A., Ayub, N., Usman, M., & Khan, A. G. (2002). Arbuscular mycorrhizal fungi enhance zinc and nickel uptake from contaminated soil by soybean and lentil. *International Journal of Phytoremediation*, **4**, 3, 205–221.

Jaynes, M. L., & Carpenter, S. R. (1986). Effects of vascular and non-vascular macrophytes on sediment redox and solute dynamics. *Ecology*, **67**, 875–882.

Jumpponen, A., & Trappe, J. M. (1998). Dark septate endophytes: a review of facultative biotrophic root-colonizing fungi. *New Phytologist*, **140**, 295–310.

Justin, S. H. F. W., & Armstrong, W. (1987). The anatomical characteristics of roots and plant response to soil water-logging. *New Phytologist*, **106**, 465–495.

Kenrick, P., & Crane, P. R. (1997). The origin and early evolution of plants on land. *Nature*, **389**, 33–39.

Khan, A. G. (1974). The occurrence of mycorrhizas in halophytes, hydrophytes and xerophytes, and of endogone spores in adjacent soils. *Journal of General Microbiology*, **81**, 7–14.

Khan, A. G. (1975). Growth effects of vesicular arbuscular mycorrhiza on crops in field. In: F. E. Sanders, B. Mosse, & P. B. Tinker (Eds), *Endomycorrhizas* (pp. 419–436). Academic Press, New York.

Khan, A. G. (1991). Vesicular arbuscular mycorrhizae (VAM) in aquatic trees of N.S.W., Australia and their importance at land water interface. *Proceedings International Conference on Land Water Interactions, New Delhi, India, 8–13 December 1991*. National Institute of Energy, New Delhi, India, p. 16.

Khan, A. G. (1992). Occurrence of relationship between soil moisture gradient and pattern of VAM infection in *Csuarina cunninghamiana* growing in a transact on a creek embankment. *International Symposium on Management of Mycorrhizas in Agriculture, Horticulture, and Forestry, 28 September–2 October, 1992*. The University of Western Australia, Perth, Australia, Abstract.

Khan, A. G. (1993a). Vesicular arbuscular mycorrhizae (VAM) in aquatic trees of New South Wales, Australia, and their importance at land–water interface. In: B. Gopal, A. Hllbricht-Ilkowska, & R. G. Wetzel (Eds), *Wetlands and ecotones: studies on land–water interactions* (pp. 173–180). National Institute of Ecology, New Delhi, India.

Khan, A. G. (1993b). Occurrence and importance of mycorrhizae in aquatic trees of New South Wales, Australia. *Mycorrhiza*, **3**, 31–38.

Khan, A. G. (1993c). The influence of mycorrhizae in trees from wetland and waterlogged areas of New South Wales, Australia. *Ninth American Conference on Mycorrhizae, August 8–12, 1993*. University of Guelph, Guelph, Ontario, Canada, Abstract (p. 18).

Khan, A. G. (1995). Effects of various soil environmental stresses on the occurrence, distribution and effectiveness of arbuscular mycorrhizae. *Biotropia*, **8**, 39–44.

Khan, A. G. (2002a). The significance of microbes. In: M. H. Wong, & A. D. Bradshaw (Eds), *The restoration and management of derelict land: modern approaches* (pp. 80–92). World Scientific Publishing, Singapore, Chapter 8.

Khan, A. G. (2002b). The handling of microbes. In: M. H. Wong, & A. D. Bradshaw (Eds), *The restoration and management of derelict land: modern approaches* (pp. 149–160). World Scientific Publishing, Singapore, Chapter 13.

Khan, A. G., & Belik, M. (1995). Occurrence and ecological significance of mycorrhizal symbiosis in aquatic plants. In: A. Varma, & B. Hock (Eds), *Mycorrhiza: structure, function, molecular biology and biotechnology* (pp. 627–666). Springer-Verlag, Heidelberg.

Louise, I. (1990). A mycorrhizal survey of plant species colonizing coastal reclaimed land in Singapore. *Mycologia*, **82**, 772–778.

Malloh, D., & Malloh, B. (1981). The mycorrhizal status of boreal plants; species from Northern Ontario. *Canadian Journal of Botany*, **59**, 2167–2172.

Malloh, D., & Malloh, B. (1994). Ectomycorrhizae, arbuscular mycorrhizae, and *Rhizoctonia* spp. of Alpine and Boreal *Salix* spp. in Norway. *Artic and Alpine Research*, **26**, 304–307.

Miller, S. P. (2000). Arbuscular mycorrhizal colonization of semi-aquatic grasses along a wide hydrologic gradient. *New Phytologist*, **145**, 145–155.

Miller, S. P., & Bever, J. D. (1999). Distribution of arbuscular mycorrhizal fungi in stands of the wetland grass *Penicum hemitomon* along a wide hydrologic gradient. *Oecologia*, **119**, 586–592.

Miller, S. P., & Sharitz, R. R. (2000). Manipulation of flooding and arbuscular mycorrhiza formation influences growth and nutrition of two semiaquatic grass species. *Functional Ecology*, **14**, 6, 738–748.

Miller, R. M., Smith, C. I., Jastrow, J. D., & Bever, J. D. (1999). Mycorrhizal status of the genus *Carex* (Cyperaceae). *American Journal of Botany*, **86**, 4, 547–553.

Newman, E. I., & Reddell, P. (1987). The distribution of mycorrhizae among families of vascular plants. *New Phytologist*, **106**, 745–751.

O'Conner, P. J. O., Smith, S. E., & Smith, F. A. (2002). Arbuscular mycorrhizas influence plant diversity and community structure in a semiarid herbland. *New Phytologist*, **154**, 209–218.

Pedersen, O., Sand-Jensen, K., & Revsbech, N. P. (1995). Diel pulses of O_2 and CO_2 in sandy sediments inhabited by *Lobelia dormanna*. *Ecology*, **76**, 1536–1545.

Phipps, C. J., & Taylor, T. N. (1996). Mixed arbuscular-mycorrhizae from the Triassic of Antarctica. *Mycologia*, **88**, 707–714.

Proctor, C. F. (2000). Mosses and alternative adaptations to life on land. *New Phytologist*, **146**, 1–3.

Purakayastha, T. J., & Chhonker, P. K. (2001). Influence of vesicular–arbuscular mycorrhizal fungi (*Glomus etunicatum* L.) on mobilization of zinc in wetland rice (*Oryza sativa* L.). *Biology Fertility Soil*, **33**, 323–327.

Rabatin, S. C. (1980). The occurrence of the vesicular–arbuscular mycorrhizal fungus *Glomus tenuis* with Moss. *Mycologia*, **72**, 191–195.

Rickerl, D. H., Sancho, F. O., & Ananth, S. (1994). Vesicular arbscular endomycorrhizal colonization of wetland plants. *Journal of Environmental Quality*, **23**, 913–916.

Russell, R. S. (1977). *Plant root system*. McGraw-Hill, London.

Saif, S. R. (1981). The influence of soil aeration on the efficiency of vesicular–arbuscular mycorrhizae. I. Effect of soil oxygen on the growth and mineral uptake of *Eupatorium odoratum* (L.) inoculated with *Glomus macrocarpus*. *New Phytologist*, **88**, 649–659.

Saif, S. R. (1983). The influence of soil aeration on the efficiency of vesicular–arbuscular mycorrhizae. II. Effect of soil oxygen on the growth and mineral uptake in *Eupatorium odoratum* L., *Sorghum bicolour* (L.) Moench, and *Guizotia abyssinica* (L.f.) Cass. Inoculated with vesicular arbuscular fungus. *New Phytologist*, **95**, 405–417.

Sand-Jensen, K., Prabl, C., & Stokohlm, H. (1982). Oxygen release from roots of submerged aquatic macrophytes. *Oikos*, **38**, 349–354.

Schindter, D. W. (1977). Evolution of phosphorus limitation in lakes. *Science*, **195**, 260–262.

SchuBler, A. (2000). *Glomus claroideum* forms an arbuscular mycorrhiza-like symbiosis with the Hornwort *Anthoceros punctatus*. *Mycorrhiza*, **10**, 15–21.

Schwelger, P. F., Robson, A. D., & Barrow, N. J. (1995). Root hair length determines beneficial effect of a *Glomus* species on shoot growth of some pasture species. *New Phytologist*, **131**, 247–254.

Secilia, J., & Bagyaraj, D. J. (1994). Selection of efficient vesicular–arbuscular mycorrhizal fungi for wetland rice — a preliminary screen. *Mycorrhiza*, **4**, 265–268.

Sharma, A. K., Singh, R., & Singh, V. A. (1998). Effect of vesicular–arbuscular mycorrhiza on uptake of phosphorus and zinc in rice (*Oryza sativa* L.). *Current Science*, **57**, 901–902.

Shuja, N., Gilani, U., & Khan, A. G. (1971). Mycorrhizal associations in some angiosperm trees around new university campus, Lahore. *Pakistan Journal of Botany*, **24**, 367–374.

Simon, L., Bousquet, J., Levesque, R. C., & Lalonde, M. (1993). Origin and diversification of endomycorrhizal fungi and coincidence with vascular land plants. *Nature*, **363**, 67–69.

Smith, S. E. (1980). Mycorrhizas of autotrophic higher plants. *Biological Reviews*, **55**, 475–510.

Smith, S., & Read, D. (1997). *Mycorrhizal symbiosis*. Academic Press, London.

Solaiman, M. Z., & Hirata, H. (1996). Effectiveness of arbuscular mycorrhizal colonization at nursery stage on growth and nutrition in wetland rice (*Oryza sativa* L.) after transplanting under different soil fertility and water regimes. *Soil Science and Plant Nutrition*, **42**, 561–571.

Solaiman, M. Z., & Hirata, H. (1998). *Glomus*-wetland rice mycorrhizas influenced by nursery inoculation techniques under high fertility soil conditions. *Biology and Fertility of Soils*, **27**, 92–96.

Sondergaard, M., & Laegaard, S. (1977). Vesicular mycorrhiza in some aquatic plants. *Nature*, **268**, 232–233.

Stahl, M. (1949). Die mycorrhiza der lebermoose mit besonderer berucksichtigung der thallosen formen. *Planta*, **37**, 103–148.

St-Cyr, I., Fortin, D., & Campbell, P. G. (1993). Microscopic observations of the iron plaque of submerged aquatic plant (*Vallisneria americana* Michx). *Aquatic Botany*, **46**, 155–167.

Stenlund, D. L., & Charvat, I. D. (1994). Vesicular arbuscular mycorrhizae in floating wet land mat communities dominated by typha. *Mycorrhiza*, **4**, 131–137.

Stevens, K. J., & Peterson, L. R. (1996). The effect of a water gradient on the vesicular arbuscular mycorrhizal status of *Lythrum salicaria* L. (purple loosestrife). *Mycorrhiza*, **6**, 99–100.

Stewart, M. N., & Rothwell, G. W. (1993). *Paleobotany and the evolution of plants*. Cambridge University Press, Cambridge.

Tang, F., White, J. A., & Charvat, I. (2001). The effect of phosphorus availability on arbuscular–mycorrhizal colonization of *Typha angustifolia*. *Mycologia*, **93**, 1042–1047.

Tanner, C. C., & Clayton, J. S. (1985). Vesicular arbuscular mycorrhiza studies with a submerged aquatic plant. *Transactions of the British Mycological Society*, **85**, 683–688.

Taylor, T. N., & Taylor, E. L. (1993). *Biology and evolution of fossil plants*. Prentice Hall, Englewood Cliff, NJ.

Thormann, M. N., Currah, R. S., & Bayley, S. E. (1999). The mycorrhizal status of the dominant vegetation along a peatland gradient in Southern Boreal Alberta, Canada. *Wetlands*, **19**, 438–450.

Trappe, J. M. (1987). Phylogenetic and ecologic aspects of mycotrophy in the angiosperms from an evolutionary standpoint. In: G. R. Safir (Ed.), *Ecophysiology of VA mycorrhizal plants* (pp. 5–25). CRC Press, Boca Raton, FL.

Treu, R., Laursen, G., Stephenson, S. L., Landolt, J. C., & Densmore, R. (1996). Mycorrhizae from Denali National Park and Preserve, Alaska. *Mycorrhiza*, **6**, 21–29.

Turnau, K., Ronikier, M., & Unrug, J. (1999). Role of mycorrhizal links between plants in establishment of liverworts thalli in natural habitats. *Acta Societatis Botanicorum Poloniae*, **68**, 63–68.

Turner, S. D., & Friese, C. F. (1998). Plant–mycorrhizal community dynamics associated with a moisture gradient within a rehabilitated prairie fern. *Restoration Ecology*, **6**, 44–51.

Turner, S. D., Amon, J. P., Schneble, R. M., & Friese, C. F. (2000). Mycorrhizal fungi associated with plants in ground water fed wetlands. *Wetlands*, **20**, 200–204.

White, J. A., & Charvat, I. (1999). The mycorrhizal status of an emergent aquatic, *Lythrum salicaria* L., at different levels of phosphorus availability. *Mycorrhiza*, **9**, 191–197.

Wigand, C., & Stevenson, J. C. (1994). The presence and possible ecological significance of the sub-merged macrophyte *Vallisneria americana*. *Estuaries*, **17**, 206–215.

Wigand, C., & Stevenson, J. C. (1997). Facilitation of phosphate assimilation by aquatic mycorrhizae of *Vallisneria americana* michx. *Hydrobiologia*, **342–343**, 35–41.

Wium-Andersen, S., & Andersen, J. M. (1972). The influence of vegetation on the redox profile of the sediment of Grange Langso — a Danish *Lobelia* Lake. *Limnology and Oceanography*, **17**, 948–952.