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REVIEW

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Mycorrhiza in sedges—an overview

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Abstract Most terrestrial plants associate with root-colonising mycorrhizal fungi, which improve the fitness of both the fungal and plant associates. However, exceptions exist both between and within plant families failing to associate with mycorrhizal fungi or in the incidence and the extent of mycotrophy, which may vary greatly. Sedges are important pioneers of disturbed habitats and often dominate vegetations like wetlands, and arctic and alpine vegetations, in which the mycorrhizal inoculum in the soil is often low or absent. In the past, sedges were often designated as non-mycorrhizal, though limited reports indicated the presence of mycorrhiza in certain species. However, studies since 1987 indicate widespread occurrence of mycorrhiza in sedges. Based on these studies, the family Cyperaceae is no longer a non-mycorrhizal family, but the mycorrhizal status of its members is greatly influenced by environmental conditions. Further, sedges appear to have several morphological adaptations to thrive in the absence of mycorrhizal association. Though mycorrhizal associations have been noted in many sedge species, the ecological role of this association is not well documented and no clear generalisation can be drawn. Similarly, the role of mycorrhizal fungi on sedge growth and nutrient uptake or non-nutritional benefits has yet to be fully ascertained. This paper reviews the current information available on the incidence of mycorrhiza in sedges and the possible reasons for low mycotrophy observed in this family.

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Introduction

In natural ecosystems, plant roots are almost entirely mycorrhizal. Despite decades of investigation, the incidence of mycorrhiza in natural plant communities and the nature of the relationship between mycorrhizal fungi and plant species continue to intrigue ecologists. Despite the presence of mycorrhizas in the great majority of modern taxa, and in almost all ecosystems, some plant species never form mycorrhizal associations, while others do so rarely, sparsely or inconsistently (Newman and Reddell 1987; Tester et al. 1987). Such plant species do not occur randomly but tend to occur in particular families or genera. Members of the Cyperaceae, along with Brassicaceae, Caryophyllaceae, Juncaceae and Amaranthaceae, are assumed to lack mycorrhizal association or it is found only very rarely (Hirsch and Kapulnik 1998). In spite of the assumption that sedges are non-mycorrhizal, there have been several reports of mycorrhizal association in sedges (see Harley and Harley 1987; Tester et al. 1987). Mycorrhiza in sedges are predominantly of arbuscular mycorrhizal (AM) type and a few species (e.g. *Kobresia bellardii*) have ectomycorrhizal associations.

The early reports on mycorrhizal incidence in sedges were reviewed by Harley and Harley (1987), Tester et al. (1987) and Newman and Reddell (1987). Since that time, there is a lot more information on the incidence of mycorrhiza in sedges. Current interest is driven by the widespread observation of mycorrhiza in sedges and recent evidence suggests that the mycorrhizal status of the family Cyperaceae needs to be re-evaluated. This review aims to summarise the available information on mycorrhizal association in sedges and to highlight potential mechanisms involved in low mycorrhizal incidence.

Incidence and effect of mycorrhiza

Since 1987, information has become available for 221 sedge species, of which 88 (40%) are mycorrhizal, 24 (11%) are facultatively mycorrhizal and 109 (49%) are

Table 1 Sedge species reported to be mycorrhizal, facultatively mycorrhizal and non-mycorrhizal after 1987

Mycorrhizal

Bequerelia cymosa[37]
Bulboschoneus maritimus[7]
Bulbostylis cf. *conifera*[22]
Bulbostylis paradoxa[22]
Bulbostylis densa[28,29]
Carex annectens[26]
Carex baccans[9,28,29]
Carex bicknellii[26]
Carex blanda[26]
Carex brevior[26]
Carex buxbaumii[26]
Carex crawei[26]
Carex cristatella[26]
Carex fuscula[13]
Carex granularis[26]
Carex gravida[26]
Carex lindleyana[28,29]
Carex lurida[9]
Carex meyenii[18]
Carex myosurus[28,29]
Carex nigra[9]
Carex pensylvanica[26]
Carex rosea[26]
Carex speciosa[28,29]
Carex sp.[9]
Carex stipata[9,26]
Carex tetanica[26]
Carex tribuloides[9]
Carex vesicaria[46]
Carex vulpinoidea[9, 26]
Carex wahuensis ssp. *wuhensis*[18]
Caustis flexuosa[6]
Cladium amaicense[4]
Cyperus arenarius[32]
Cyperus brevifolius[29,28]
Cyperus clarkei[28,29]
Cyperus cyperinus[29,28]
Cyperus dubius[28,29]
Cyperus iria[14,15,16,28,29]
Cyperus laevigatus[3,32]
Cyperus ligularis[37]
Cyperus nutans[28,29]
Cyperus odoratus[37]
Cyperus paniceus[28,29]
Cyperus pilosus[14]
Cyperus platyphyllus[32]
Cyperus pygmaeus[32]
Cyperus sp.[9]
Cyperus squarrosus[28,29,37]
Cyperus stoloniferous[27,29,32]
Cyperus triceps[2,14,28,29]
Dulichinum arundinaceum[9]
Eleocharis acutangula[33,28,29]
Eleocharis dulcis[32]
Eleocharis geniculata[37]
Eleocharis ovata[9]
Eleocharis sp.[9]
Fimbristylis consanguinea[28,29]
Fimbristylis eragrostis[32]
Gahnia vitiensis subsp. *kauaiensis*[18]
Hypolytrum bullatum[37]
Hypolytrum pulchrum[22]
Isolepis nodosa[20]
Kobresia bellardii[23]
Lagenocarpus guianensis[22]
Lagenocarpus sp.[22]
Lepidosperma gracile[25]
Mariscus mariscoides ssp. *meyenii*[18]
Maricus meyenianus[18]
Oreobolus furcatus[18]
Ptilanthelium deustem[6]
Pycerus flavidus[32]
Pycerus pumilus[32]
Rhyncospora barbata[22]
Rhyncospora cf. *brasilensis*[22]
Rhyncospora cormbosa[37]
Rhyncospora pubera[37]
Rikliella squarrosa[32]
Schoenoplectus supinus[32]
Scleria lithosperma[28,29]
Scripus acutus[46]
Scripus atrovirens[9,46]
Scripus cyperinus[9]
Scripus fluviatilis[9,36]
Scripus maritimus[46]
Scripus robustus[9]
Scripus sp.[9]
Tetraria capillaris[25]

Facultatively mycorrhizal

Bulbostylis barbata[28,29,32,35]
Bulbostylis capillaris[18,22]
Carex atherodes[9,26,36,46]
Carex lasiocarpa[10,39,46]
Carex scoparia[9,26]
Carex strictata[9,26,46]
Cyperus articulatus[4,32,33]
Cyperus compressus[2,29,28,32]
Cyperus difformis[32,34]
Cyperus distans[15,28,29,32]
Cyperus halpan[4,31,32]
Cyperus kyllinga[21,28,29]
Cyperus ligularis[4]
Cyperus rotundus[3,18,28,29,32,37,38]
Cyperus surinamensis[4,37]
Fimbristylis falcata[28,29,32]
Fimbristylis miliacea[11,14,32,33]
Fimbristylis ovata[14,28,29,32]
Kobresia myusuroides[17,17,31]
Pleurostachys cephalotes[37]
Pycerus polystachyos[18,32,33]
Rhynchospora cephalotes[37]
Scleria latifolia[37]
Scleria melaleuca[37]

Non-mycorrhizal

Bulbostyli puberula[32]
Carex amphibola[26]
Carex acnescens[31]
Carex aff. *subantarticata*[13]
Carex albonigra[31]
Carex aphylla[12]
Carex aquatilis[39]
Carex bigelowii[41,45]
Carex boelckeiana[12]
Carex brizoides[42]
Carex caryophllea[30]
Carex cephalophora[26]
Carex ebenea[31]
Carex ericetorum[30]
Carex fillifolia[31]
Carex flacca[9,43]
Carex flava[10]
Carex gayana[13]
Carex hirta[30]
Carex hystericina[10]
Carex interior[26]
Carex lachenalii[44,45]
Carex madoviana[13]
Carex maritime[13]
Carex membranacea[8]
Carex mertensii[40]
Carex microchaeta[41]
Carex misandra[8]
Carex muricata[5]
Carex nardina[8,17]
Carex stenophylla ssp. *eleocharis*[31]
Carex sterilis[10]
Carex subspathecea[44]
Carex sylvatica[24]
Carex tenera[26]
Carex trifida[19]
Carex ursina[8,44]
Carex urticulata[39]
Carex wahuensis[31]
Caustis dioica[25]
Cyathochaeta avenccea[25]
Cyperus bulbosus[32]
Cyperus castaneous[32,35]
Cyperus decompositus[35]
Cyperus esculentus[32]
Cyperus exaltatus[32,33]
Cyperus haspan[37]
Cyperus javanicus[33,35]
Cyperus luzulae[37]
Cyperus pohlii [37]
Cyperus strigosus[31]
Cyperus tenuispica[32,33]
Eleocharis aff. *pachycarpa*[13]
Eleocharis geniculata[32]
Eleocharis scheuchezeri[8,17,17,44]
Eleocharis sp.[13]
Eleocharis tenius[10]
Eleocharis triste[8]
Eleocharis vaginatum[39]
Ficinia sp.[1]
Fimbristylis schoenoides[32]
Fimbristylis trachycarya[35]
Fimbristylis triflora[32]
Fuirena ciliaris[32]
Gahnia gahiniformis[31]
Isolepis antartica[1]
Isolepis aucklandica[19]
Kobresia simpliciuscula[31]
Kyllinga brevifolia[32]
Kyllinga bulbosa[32]
Kyllinga nemoralis[32]
Lagenocarpus sphacelata[32]
Maricus dubius[32]
Maricus paniceus[32]
Maricus squarrosus[32]
Mesomelaena pseudostygia[25]
Pycerus puncticulatus[32]
Rhynchospora ciliata[37]
Rhynchospora longisetis[35]
Schoenoplectus grossus[32]
Schoenoplectus juncoides[32]
Schoenoplectus senegalensis[32]
Schoenoplectus sp.[33]
Schoenus sp.[13]
Sclerya cyperina[22]
Scripus aff. perpusillus[13]
Scripus cespitosus[39]
Uncinia divaricata[19]
Uncinia hookeri[19]
Uncinia richleriana[12]

Table 1 (continued)

Mycorrhizal		
Carex pellita[26]	*Fimbristylis argentea*[32]	*Uncinia uncinata*[18]
Carex podocarpa[41]	*Fimbristylis bisumbellata*[32]	
Carex pumila[20]	*Fimbristylis complanata*[32]	
Carex rhynchophysa[31]	*Fimbristylis cymosa*[18,32]	
Carex rostrata[39]	*Fimbristylis cymosa* var. *spathaceae*[21]	
Carex rupestris[8,31]	*Fimbristylis dichotoma*[32]	
Carex scripoidea[17,17]	*Fimbristylis dipacea*[32]	
Carex sprengelli[26]	*Fimbristylis ferruginea*[32]	
Carex stans[8]	*Fimbristylis polytrichoides*[32]	

[1]Allsopp and Stock (1993); [2]Ammani et al. (1994); [3]Anwar and Jalaluddin (1993); [4]Aziz et al. (1995); [5]Barni and Siniscalco (2000); [6]Bellgard (1991); [7]Blaszkowski (1994); [8]Bledose et al. (1990); [9]Cooke and Lefor (1998); [10]Cornwell et al. (2001); [11]Dharmarajan et al. (1993); [12]Fontenla et al. (1998); [13]Fontenla et al. (2001); [14]Gupta and Ali (1993); [15]Harikumar (2001); [16]Jain et al. (1997); [17]Khon and Stasovski (1990); [18]Koske et al. (1992); [19]Laursen et al. (1997); [20]Logan et al. (1989); [21]Louis (1990); [22]Lovera and Cuenca (1996); [23]Massicotte et al. (1998); [24]Mayr and Godoy (1989); [25]Meney et al. (1993); [26]Miller et al. (1999); [27]Mohankumar et al. (1988); [28]Muthukumar and Udaiyan (2000); [29]Muthukumar et al. (1996); [30]Pawlowska et al. (1996); [31]Raab et al. (1999); [32]Ragupathy and Mahadevan (1993); [33]Ragupathy et al. (1990); [34]Raman et al. (1993); [35]Reddell and Milnes (1992); [36]Rickerl et al. (1994); [37]Silva et al. (2001); [38]Srivasta and Basu (1995); [39]Thorman et al. (1999); [40]Titus and del Moral (1998); [41]Treu et al. (1996); [42]Turnau et al. (1992); [43]van der Heijden et al. (1998); [44]Väre et al. (1992); [45]Väre et al. (1997); [46]Wetzel and van der Valk (1995)

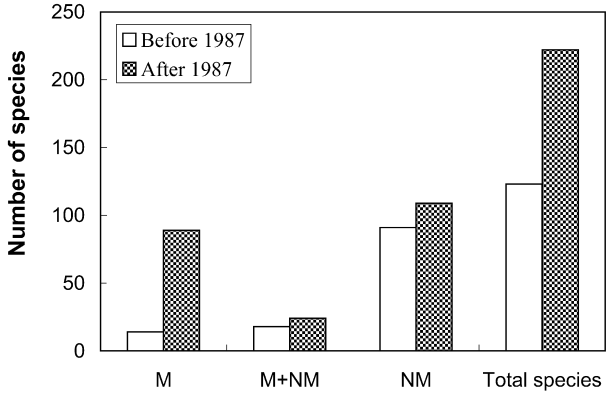

Fig. 1 Number of sedge species reported to be mycorrhizal (*M*), facultatively mycorrhizal (*M+NM*), non-mycorrhizal (*NM*) and total number of species examined for mycorrhiza before (from Newman and Reddell 1987) and after 1987

non-mycorrhizal (Table 1). There is a considerable increase in the percentage of mycorrhizal species (from 11% to 40%) and a decline in non-mycorrhizal species (from 74% to 49%) since 1987 (Fig. 1). Mycorrhizal association can either be restricted to a short period during the growing season (Meney et al. 1993) or it may be found throughout the growing season (Anwar and Jalaluddin 1994; Muthukumar 1996).

Since mycorrhizal fungi and their hosts have associations that occupy different positions on the "mutualism-parasitism continuum" depending on the environmental conditions (Johnson et al. 1997), the association may not always be clearly defined. Although the effects of mycorrhiza on sedge growth are little known, the abundance and widespread occurrence of this association in sedges from many ecosystems suggests an important ecological role in the natural environment. The non-mycorrhizal nature of *Carex coriacea* and *Uncinia divaricata*, even under extreme P-deficient conditions, tempted Powell (1975) to conclude that sedges, like rushes, are fundamentally non-mycotrophic. Sedges like *Carex flacca*, *Carex mertensii* and *Cyperus rotundus* do not benefit from mycorrhizal association and accumulate maximum biomass in substrates lacking mycorrhizal fungi (Muthukumar et al. 1997; Titus and del Moral 1998; van der Heijden et al. 1998). In addition, lack of mycorrhizal propagules in the substrate enhances the competitive ability of sedges over other facultatively mycotrophic plant species (Titius and del Moral 1998). Thus, it is essential to acknowledge the potentially important ecological role of these associations, however poorly known they might currently be.

Intraradical vesicles and hyphae are the AM fungal structures frequently reported in sedge roots. Reports on arbuscule occurrence are limited and the nutritional benefits of mycorrhizal association in sedges possessing arbuscules is yet to be ascertained (Fig. 2). In addition, AM fungal spores have been found both attached to roots (Muthukumar et al. 1997; Cooke and Lefor 1998) and within roots (Miller et al. 1999) (Fig. 2). This conclusively demonstrates that sedges would greatly improve the persistence and survival of AM fungal propagules in the soil. Further, inoculation of sedge roots containing AM fungal hyphae and vesicles induced functional mycorrhiza in mycorrhizal-dependent hosts like onion, cowpea and sunnhemp (Muthukumar et al. 1999). This suggests that mycorrhizal sedge roots can act as propagules like the roots of other mycorrhizal species. Such persistence of mycorrhizal fungi within roots may play a significant role in seasonal vegetation or in the disturbed and early successional plant communities where plant roots are sparse. Further, as sedges are perennials, the long-lived nature of the roots in some species may play a

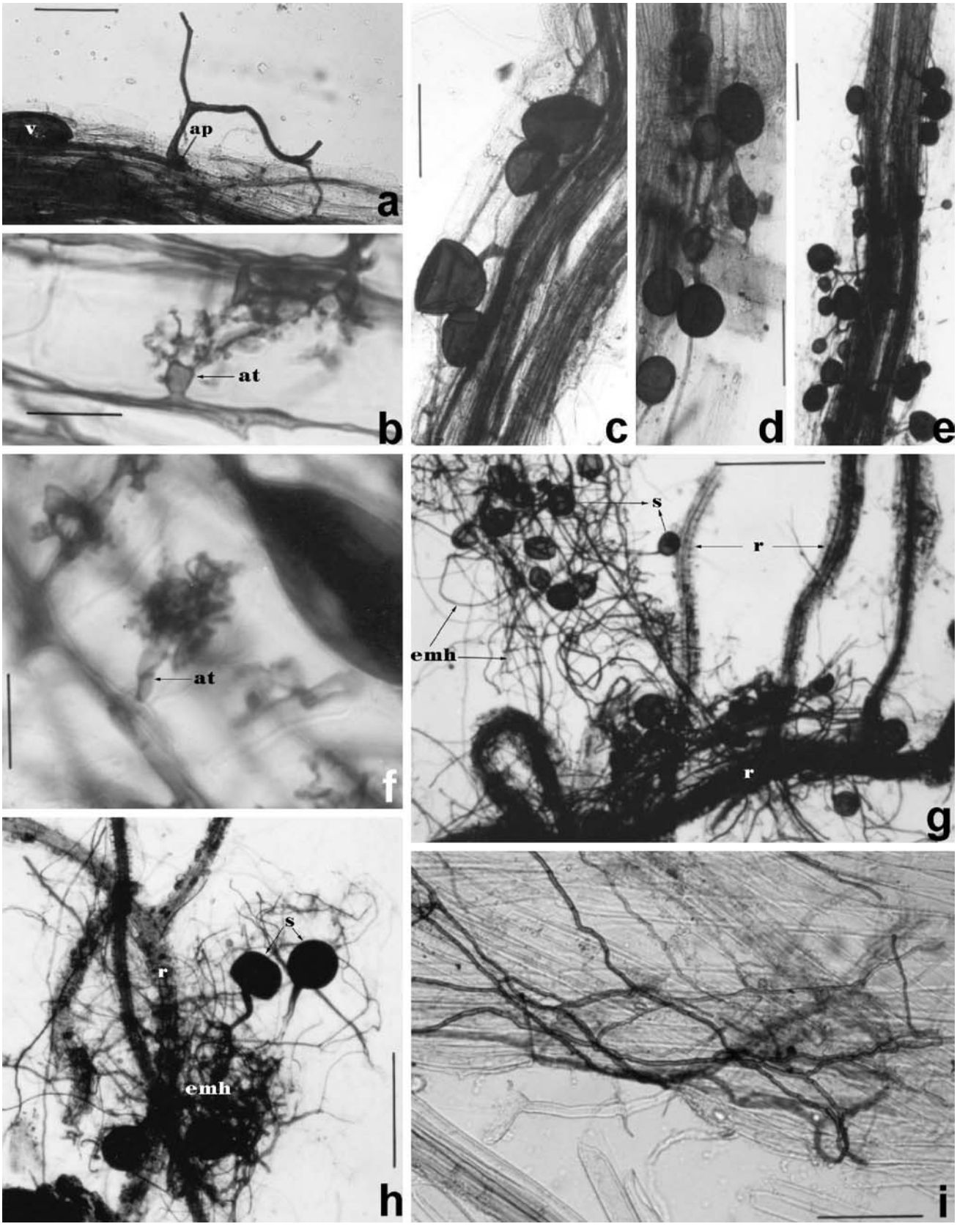

Fig. 2a–i Arbuscular mycorrhizal colonisation in sedges. **a** Appressorium (*ap*), intraradical hyphae and vesicle (*v*) in root of *Cyperus iria*. **b** Arbuscules in root cells of *Carex myosurus*; *at* arbuscular trunk. **c** Intraradical spores within *Cyperus iria* root. **d** Vesicles and spores within root of *Cyperus rotundus*. **e** Vesicles and intraradical spores in root of *Bulbostylis barbata*. **f** Arbuscules in root cells of *Carex baccans*; *at* arbuscular trunk. **g**, **h** Extramatrical hyphae (*emh*) and spores (*s*) of *Glomus aggregatum* (**g**) and *Glomus geosporum* (**h**) attached to *Cyperus rotundus* roots (*r*). **i** Dark septate fungi within root of *C. iria*. *Bars* **a**, **c–e**, **i** 100 μm; **b**, **f** 20 μm, **g** 400 μm, **h** 200 μm

Table 2 Tabulation of studies used in this review of habitat and soil factors with the availability of relevant data. + Data on that parameter(s) were taken from the reference given. *D* Disturbed, *UD* undisturbed, *Wt* wetland, *NWt* non wetland, *N* nitrogen, *P* phosphorus, *K* potassium, *OM* organic matter

Reference	Habitat type				Soil factor				
	D	UD	Wt	NWt	pH	N	P	K	OM
Allen et al. (1987)					+	+	+		+
Ammani et al. (1994)		+		+					
Anwar and Jalaluddin (1993)	+			+					
Aziz et al. (1995)		+		+					
Barni and Siniscalco (2000)		+		+					
Bellgard (1991)		+		+					
Blaszkowski (1994)		+		+					
Bledose et al. (1990)		+	+						
Cooke and Lefor (1998)	+	+	+						
Cornwell et al. (2001)		+	+						
Dharmarajan et al. (1993)		+	+		+	+		+	
Fontenla et al. (1998)		+		+					
Fontenla et al. (2001)		+	+						
Gupta and Ali (1993)	+			+					
Harikumar (2001)	+		+						
Jain et al. (1997)	+			+					
Khon and Stasovski (1990)		+		+					
Koske et al. (1992)	+	+	+	+					
Laursen et al. (1997)		+							
Lesica and Antibus (1986)					+	+	+	+	
Louis (1990)	+			+					
Lovera and Cuenca (1996)	+	+		+	+	+	+	+	+
Massicotte et al. (1998)		+							
Mayr and Godoy (1989)		+		+					
Meney et al. (1993)		+		+					
Miller et al. (1999)		+	+	+					
Mohankumar et al. (1988)		+		+					
Muthukumar and Udaiyan (2000)		+		+	+	+	+	+	+
Muthukumar et al. (1996)		+		+	+	+	+	+	+
Pawlowska et al. (1996)	+			+	+	+	+		+
Raab et al. (1999)		+							
Ragupathy and Mahadevan (1993)	+	+	+	+					
Ragupathy et al. (1990)			+						
Raman et al. (1993)	+			+					
Reddell and Milnes (1992)	+			+					
Rickerl et al. (1994)		+	+				+		
Thorman et al. (1999)		+	+						
Treu et al. (1996)		+		+					
Turnau et al. (1992)	+			+					
Väre et al. (1992)		+		+					
Väre et al. (1997)		+			+		+	+	+
Wetzel and van der Valk (1995)		+	+						

significant role in the persistence of propagules over space and time.

Reasons for low mycotrophy

The rare or non-mycorrhizal status of sedges is often attributed to the habitats they inhabit (Tester et al. 1987). However, as researchers in other studies have noted, there are several morphological, anatomical and physiological adaptations that could also contribute to the infrequent or rare presence of mycorrhiza in sedges. First, we consider habitat factors and then the various plant characters that might possibly contribute to the low mycorrhizal incidence found in sedges.

Habitat factors

The non-mycorrhizal property of sedges was attributed mostly to the wet and waterlogged or disturbed habitat they inhabit (Tester et al. 1987). A succession of sedge species, e.g. of the genera *Eriophorum*, *Carex* and *Scripus*, generally dominate different sections of the broad interval of soil moisture and pH from bogs to eutrophic fens, and sedges, together with grasses, are common in tundra wetlands (Bliss and Matveyeva 1992). The degree of seasonal water stress controls the extent of mycorrhizal colonisation in some wetland sedges. In a groundwater-fed study site with little variation in water level, sedges remained mostly non-mycorrhizal (Cornwell et al. 2001), but in marshes or prairie potholes, where there are greater seasonal fluctuations in water levels, sedges tend to become mycorrhizal (Wetzel and van der Valk 1995; Cooke and Lefor 1998; Miller et al. 1999). A χ^2 analysis of 201 entries (see Table 2), however,

indicated no significant differences (χ^2=0.147; P>0.05) in mycorrhizal incidence between sedges from wet and dry soils. This finding results from conflicting reports on mycorrhizal incidence of sedges pertaining to wetland or not wetland inhabitants. For example *Carex artherodes* is reported to be mycorrhizal in waterlogged soils (1 cm water depth) (Wetzel and van der Valk 1995), and non-mycorrhizal in dry soil (Rickerl et al. 1994). Likewise, Peat and Fitter (1993) indicated the absence of mycorrhiza in several sedges that were not wetland inhabitants.

Although the principal factors that directly or indirectly influence the extent of mycorrhizal colonisation in terrestrial ecosystems include soil variables and plant characteristics, the reason for decreased mycorrhizal incidence with increasing soil wetness is often unclear. If available soil oxygen is important to the survival of AM fungi then factors regulating colonisation in wetland sedges will also include soil redox potential and plant morphological features regulating oxygen diffusion into the root zone rather than the rhizosphere. It is possible that mycorrhizal fungi survive in the oxygenated portion of wetland sedge roots (Brown and Bledose 1996), but are inhibited outside the rhizosphere by lack of oxygen. Thus, the fungi may be slower to germinate from spores or to colonise new roots from the existing points of infection.

Reduced or lack of mycorrhizal inoculum in wet soils is often cited as a cause for the low incidence of mycorrhiza in sedges. In general, fewer AM fungal spores occur in wet and waterlogged soils (Rickerl et al. 1994). A recent study by Miller (2000) suggests that the inoculum potential of soil flooded for >1 year was similar to that of dry soil or soil intermittently flooded for the same period. This finding suggests that, in wet soils, the hyphal network retains viability mainly through connections to oxygenated roots of flood-tolerant plants.

Like wet and water-logged soils, frequently disturbed habitats, such as fallow, waste or croplands, generally have a large number of non-mycorrhizal species, including sedges, probably because disturbance causes both disruption of the mycelial network in the soil and scarcity of mycorrhizal species (Peat and Fitter 1993). Sedges are one of the pioneer colonisers of disturbed habitats along with other ruderals, which are slowly eliminated as the plant community stabilises. In this process, it is noteworthy that the well-developed ability of sedges to spread through vegetative means enables them to persist in closed turfs and in stable communities (Francis and Read 1994). A χ^2 analysis on the incidence of mycorrhiza in sedges from disturbed (including cultivated fields) and undisturbed habitats indicated no significant differences (χ^2=2.214; P>0.05). This finding results from the conflicting reports on mycorrhizal incidence of sedges in disturbed and undisturbed sites. Some sedge, like *Hypolystrum pulchrum* and *Bulbostylis paradoxa*, are reported to be mycorrhizal both in natural as well as in disturbed savannas (Lovera and Cuenca 1996), as is *Carex vitiensis* ssp. *kaualerisis* from recent volcanic substrates (Koske et al. 1992), and several sedges from cultivated fields are reported to be mycorrhizal. In contrast, some species, e.g. *Cyperus difformis*, are reported to be mycorrhizal in a disturbed site (Raman et al. 1993), but non-mycorrhizal in an undisturbed site (Ragupathy and Mahadevan 1993).

The benefit of a mycorrhizal association for a plant species depends on soil fertility and pH. The soil pH determines the solubility of many nutrients such as iron, manganese, phosphorus, zinc and molybdenum and therefore indirectly determines how much a plant can benefit from mycorrhizal association. Data on 65 entries were available for soil pH and mycorrhizal incidence in sedges. Spearman's rank correlation indicated a strong positive correlation (r=0.630; P<0.000) between soil pH and mycorrhizal colonisation level in sedges. The probability of mycorrhizal colonisation increases with increasing soil pH, as the availability of plant nutrients like P, Fe, Mn, Zn, Cu and Co are reduced with increasing soil pH (Brady 1990). Members of Cyperaceae often occupy infertile habitats to which they appear to be adapted. However, a Spearman's rank correlation analysis of soil nutrients like N, P, K and mycorrhizal colonisation levels indicate that colonisation levels in sedges are positively correlated to soil N (r=0.530; P<0.000; n=59), but negatively to soil P (r=–0.428; P<0.000; n=66) and K (r=–0.276; P<0.047; n=51). Likewise, a strong negative correlation also existed between soil organic matter and mycorrhizal colonisation levels in sedges (r=–0.355; P<0.006; n=59). It is now well established that sedges can use inorganic nutrients (as will be seen later), which renders them possibly less dependent on mycorrhizal fungi. However, further research is required to increase the understanding of these and other factors controlling plant-mycorrhizal association in sedges.

Plant adaptive mechanisms

Biomass allocation to roots and shoots

Limitations in nutrient acquisition could be overcome in infertile soils if sedges allocate more biomass to roots than shoots, thereby increasing the relative size of the nutrient acquisition system, or source, and decreasing the relative size of the nutrient utilising system, or sink. Biomass allocation to below-ground parts varies with nutrient availability and competition for nutrients. Many plant species, including grasses, adapt to nutrient-poor environments through increased allocation of biomass to roots (Schippers and Olff 2000). In contrast, sedges consistently invest greater biomass resources (20%–>80%) into root production regardless of soil nutrient levels (Aerts et al. 1992; Wetzel and van der Valk 1998) and the presence of AM fungi does not affect the allocation of biomass to the below-ground parts in sedges (Muthukumar et al. 1997).

Nutritional characteristics in sedges

Nutrients needed for plant growth are obtained either from the soil or from the stored reserves that are translocated and recirculated within the plant. Plants from nutrient-rich environments generally have higher potential to absorb nutrients and are more dependent on nutrient uptake than on internal nutrient circulation compared to plants from nutrient-deficient sites (Chapin 1980). In contrast, plants in nutrient-stressed soils may exhibit adaptations enabling them to use nutrients more efficiently by internal reallocation or to absorb nutrients more efficiently (Aerts et al. 1999; Jonasson and Shaver 1999).

Foraging for nutrients and water

Distribution of nutrients and moisture in soils is very patchy, and physical obstacles like boulders or rocks in hilly terrains may prevent root penetration (Schlesinger et al. 1996). Many sedge species have foraging rhizomes or stolons (Callaghan et al. 1990) to overcome these problems of nutrient and water acquisition. These sedges display an architecture that increases the probability of locating nutrient-rich pockets and escapes competition for nutrients and water from more aggressive plant species. Mycotrophic sedges like *Eriophorum vaginatum* are non-mobile and have little effect on nutrient spatial heterogeneity (Heal et al. 1989). However, the non-mycorrhizal *Carex bigelowii* exhibits an opportunistic "phalanx" strategy in large nutrient-rich pockets, whereby modules with short internodes proliferate and efficiently utilise the resources (Kershaw 1962). This type of foraging strategy results in the physiological integration of clonal plants, which refers to the processes whereby resources are exchanged between potentially independent ramets through structures such as rhizomes and stolons (de Kroon and van Groenendael 1997). Sharing of water, nutrients or carbohydrates seems especially profitable under circumstances where these resources are heterogeneously distributed in space (Hutchings and Wijesinghe 1997). For example, in the non-mycorrhizal *Carex flacca*, water and nitrogen are translocated towards the stressed ramet from the ramet receiving ample water and nitrogen through a rhizome (de Kroon et al. 1998). Similar translocation of water and nutrients through stolons or rhizomes has been demonstrated in several non-mycorrhizal sedges (Jònsdòttir and Callaghan 1990; de Kroon et al. 1996). The benefits of integration to ramets under nutrient-poor conditions (the recipients) outweigh the costs to the ramets under nutrient-rich conditions (the donors) (de Kroon et al. 1998; Dhereteteldt and Jónsdóttir 1999).

Utilisation of organic nutrient sources

Sedge-dominated wet and cold ecosystems are poor in inorganic plant-available nutrients, which frequently limits plant growth, as mineralisation in these soils is restricted due to low temperatures and anoxic soils. Mineralisation of organic N and P is controlled by microbial activity and these processes are slow in soils at low temperatures. This reduced microbial activity at low soil temperatures limits the availability of inorganic nutrients to plants in cold soils. Recent research has shown that sedges can compensate for the low availability of inorganic N by direct uptake of organic N as low-molecular-mass amino acids (Chapin et al. 1993; Kielland 1994; Jonasson and Shaver 1999).The concentration of amino acids in the soils of sedge-dominated plant communities is high, often several-fold higher than the concentration of inorganic N (Kielland 1994), thus representing an important source of plant N.

Sedges take up several amino acids, such as glycine, glutamic acid, aspartic acid, alanine and arginine, that are released during decomposition of soil organic matter simultaneously but at different rates (Chapin et al. 1993; Kielland 1994; Raab et al. 1996, 1999). This variation in the uptake of amino acids among sedges resides in the availability of the amino acids in the soil rather than in the ability of sedge roots to absorb these organic compounds. By directly absorbing and utilising amino acids, sedges acquire an energetically favourable source of N under non-mycorrhizal conditions and short-circuit the mineralisation processes considered as bottlenecks in nutrient cycling in certain ecosystems. Recently, Lipson et al. (1999) demonstrated that ectomycorrhiza could transfer an average of 1.3% N from the amino acid glycine to the roots of the alpine sedge *Kobresia myosuroides*, which clearly indicates that ectomycorrhizal association also has an important role in N nutrition in addition to the ability of roots to absorb organic N.

The root surface phosphatase activity capable of hydrolysing organic phosphate compounds in sedges suggests a more direct utilisation of organic P sources than previously believed. Roots of *E. vaginatum* hydrolyse organic phosphate at approximately one-third of the rate at which they take up inorganic P (Kroehler and Linkins 1991). Calculated estimates also indicate that the root surface phosphatase activity could provide approximately 20–70% of the annual P demand in *Eriophorum*. In addition, root surface phosphatase activity appears to be relatively temperature-independent at low temperatures, as sustained root surface phosphatase activities have been detected in *Eriophorum* roots at just above freezing temperatures. This phosphatase activity at low temperatures coupled with low temperature-adapted phosphate absorption (Chapin 1974) could be advantageous for sedges throughout the growing season under non-mycorrhizal conditions.

Tissue longevity and nutrient resorption

Sedges in nutrient-deficient environments are often adapted to high nutrient resorption to minimise nutrient losses rather than having adaptations to promote nutrient uptake (Berendse and Jonasson 1992). In nutrient-poor

wetlands and arctic sites dominated by non-mycorrhizal sedges, the constraints on nutrient uptake are particularly strong due to the short growing season and the wet and cold soil conditions. Traits that promote high internal nutrient retention time within the plants have high adaptive significance. Increased leaf longevity may be particularly important in conserving nutrients in relation to high resorption (Aerts 1995). However, as leaf longevity declines, resorption should theoretically gain importance (Jonasson 1989; Aerts 1995). Sedges like *E. vaginatum* compensate for relatively short leaf longevity through high nutrient proficiency, mycorrhizal association and leaf-level nutrient-use efficiency, as leaf litter N and P concentrations are reduced to about 0.4% and 0.03%, respectively.

Sedges have also been shown to reabsorb nutrients efficiently. *E. vaginatum* has among the most efficient resorption measured among vascular plants. Its reabsorption efficiency results from a combination of its leaf growth patterns and nutrient translocation within leaves (Jonansson and Chapin 1985). In an Alaskan muskeg, *E. vaginatum* formed two to three leaves sequentially at about 1.5-month intervals during the growing season. A new leaf appeared when the previous leaf had grown near maximum length; as the new leaf appeared, the previously formed one started to transport nutrients, which consequently became available to the new leaf (Jonasson and Chapin 1985). Before senescence, the plant typically had reabsorbed more than 90% of the leaf P and 80% of the leaf N content, and the annual uptake requirements to replenish the canopy nutrient lost to litter were reduced to ~10% of the peak season's leaf P pool and 20% of the N pool (Jonasson and Chapin 1991). Thus, *E. vaginatum* could rescue nutrients at a near-constant rate during the entire period of growth simply by transporting nutrients from old leaves to new ones.

Root characters

Plant parameters like root length, root diameter, root surface area: shoot-to-root ratio, and root hair density, length and diameter have been considered important for uptake of low-mobility ions such as phosphate (Hetrick 1991). Clearly, a plant that produces the greatest interface with the soil has the greatest uptake potential, but this is balanced against the cost to the plants of growing and maintaining roots (Fitter 1987). In this context, fine roots offer greater return for the investment, but fine roots have limited growth potential (Lyford 1975), life span (Reynolds 1975), and transport capacity, and are vulnerable to physical damage, desiccation and grazing by soil-borne micro arthropods or pathogens (Fitter 1987). Soil flooding results in a variety of stresses for plants among which oxygen deficiency to roots is often the underlying factor (Drew 1997). These low oxygen concentrations, caused by low gas diffusion in water-saturated soil (Jackson 1985), reduce nutrient uptake during flooding resulting in lower biomass production (Trought and Drew 1980). It is possible for a given plant species to increase its specific root length in response to flooding (Rubio et al. 1997), thereby either reducing the dependence on mycorrhizal fungi, exhibiting an apparent decrease in the percent colonised root length with the actual colonised length remaining the same, or showing some combination of these responses. Sedges have various mechanisms to overcome nutrient limitations under these conditions.

Anatomical modifications

Sedges tend to alter their root morphology and structure in response to soil moisture changes in soil structure and chemistry. To ensure transport of oxygen to roots, flood-tolerant sedges increase their root thickness and partially replace their root systems with either lysigenous (e.g. *Carex extensa*) or schizogenous aerenchyma (e.g. *Carex pseudocyperus* and *Carex remota*) (Moog 1998; Visser et al. 2000). Roots of most *Carex* species and other sedges like *Eriophorum* consist of typical aerenchyma known as 'spider web' or 'cyperacean' aerenchyma in response to flooding (Justin and Armstrong 1987) through the development of radial files of cells initially interconnected by remnants of tangential walls (Moog 1998; Visser et al. 2000). The presence of thick, mostly unbranched, roots containing aerenchyma represents an extensive network of air spaces throughout the root cortex that is a typical feature of sedges growing in regularly or permanently flooded soil (Jackson and Armstrong 1999). The amount of aerenchyma tends to increase with oxygen deficiency and is related to the flooding frequency (Justin and Armstrong 1987). Although aerenchymatous roots provide the root cells with much needed oxygen, they deprive roots of nutrients by forming insoluble phosphate and nitrogenous compounds when the excess oxygen leaks from the roots at low temperatures (Moog and Brüggermann 1998). However, flood-tolerant sedges like *C. pseudocyperus* and *C. remota* develop intact cortex or cortex with fine intercellular spaces throughout most of the root system under anaerobic conditions (Moog 1998). This root structure enables efficient nutrient uptake and plant growth during anaerobiosis in these flood-tolerant *Carex* species. Although the occurrence of sparse AM colonisation has been reported in the flood-tolerant *C. remota* (Harley and Harley 1987), mycorrhizal fungi generally do not colonise the aerenchymatous cortex of the wetland sedges (see http://www.ffp.CSIRO.au/-research/mycorrhizal).

Root hairs

The occurrence of root hairs increases nutrient uptake, and the abundance of root hairs has been shown to increase under low-nutrient conditions (Föhse and Jungk 1983). In addition, root hair diameter, length and abundance determine the extent of AM colonisation levels in sedges (Muthukumar et al. 1999). Miller et al. (1999)

identified unique root hairs with a bulbous swelling base associated with the non-mycorrhizal condition. This character gives the roots a fuzzy appearance and this fuzziness has been used as a specific character in the description and identification of certain *Carex* species (Reznicek 1986). The occurrence of bulbous root hairs appears to be related to soil moisture levels, as *C. atherodes*, *Carex interior*, *Carex pellita* and *Carex stricta*, examined by Miller et al. (1999), with bulbous root hairs were obligate wetland species. However, mycorrhizal colonisation in *C. atherodes* and *C. stricta*, which are known to develop bulbous root hairs, has been reported by Wetzel and van der Valk (1995) and Cooke and Lefor (1998). So the non-mycorrhizal status associated with bulbous root hairs in wetland sedges observed by Miller et al. (1999) may be a habitat-induced condition.

Cluster roots

An alternative to the development of root hairs is the production of cluster roots—a strategy used by plants to acquire nutrients in infertile soils (Lamnot 1982). Analogous root clusters have been recognised in most members in the tribes Cariceae and Rhyncosporaceae of the Cyperaceae both in Australia and elsewhere (Davies et al. 1973; Lamnot 1993; Meney et al. 1993). The rootlets are swollen (dauciform) with obvious gaps between them, and appear even hairier than proteoid roots; however, to date nothing is known of their physiology (Dinkelaker et al. 1995).

Root clusters appear to have superior capacity over unmodified roots in absorbing nutrients from the soil surface horizons. Root clusters enhance the release and uptake of nutrients as they are preferentially formed in the decomposing litter—the part of the soil profile that is the main source of nutrients in leached soils. However, evidence that root clusters assist the decomposition of litter has yet to be obtained. Unequivocally, the dense cover of long root hairs ensures good contact with the soil and litter particles, enabling immediate uptake of nutrients as they are released. The A_0 soil horizon, which is most prone to sudden and prolonged drying out, is an environment more suited to root hair formation than to mycorrhizal fungal growth (Lamnot 1993). Lamnot (1982) indicated that plant species with root clusters are rarely mycorrhizal. In contrast, Meney et al. (1993) recorded the highest AM colonisation levels among sedges in the dauciform roots of *Lepidosperma gracilis*. Additionally, the presence of non-AM endophytic fungi in modified roots of *L. gracilis* suggests the possible involvement of microorganisms other than mycorrhizal fungi in stimulating the formation of such specialised roots.

Root longevity

Long-lived roots increase nutrient usage efficiencies and carbon invested in root biomass. In addition, slow-growing and long-lived roots are better synchronised with the slow, temperature-limited decomposition rates in soils of tundra regions where the activity of fast-growing and short-lived roots would be limited by the rate at which nutrients become available (Chapin et al. 1978). The roots of mycorrhizal *Eriophorum anguistifolium* and *E. vaginatum* grow at the surface of the frozen soils and recede down the profile towards the permafrost during summer (Billings et al. 1977). Roots of *E. anguistifolium* die when the soil freezes in winter (Shaver and Billings 1975) and are therefore functional for only one growing season. In contrast, non-mycorrhizal sedges like *Luzula nivalis*, *Luzula confusa* and *Carex aquatilis* have longer lived roots, which can survive between 7 and 10 years (Shaver and Billings 1975; Bell and Bliss 1978). Isotopic ^{14}C studies by Jònsdòttir and Callaghan (1990) indicate that 11-year-old non-mycorrhizal roots of *C. bigelowii* can receive carbon from young photosynthesising tillers and in turn take up and transport nutrients, especially N, to the young tillers (Jònsdòttir and Callaghan 1990).

Dark septate fungi

The roots of sedges are extensively colonised by dark septate fungi (DSF) in environments where mycorrhizal fungi do not proliferate (Khon and Stasovski 1990; Treu et al. 1996). In alpine habitats, DSF are the dominant fungal symbionts of sedges, and in less extreme environments dual infection with AM fungi is common (Read and Haselwandter 1981; Bledose et al. 1990; Khon and Stasovski 1990; Väre et al. 1992; Treu et al. 1996). *Uncinia meridensis*, in the subantarctic, has been reported to possess abundant DSF colonisation in addition to heavy colonisation by AM fungi (Christie and Nicolson 1983). In contrast, the roots of sedges in arctic Canada are colonised by hyaline translucent septate or non-septate fungal hyphae (Khon and Stasovki 1990). Healthy lateral roots of alpine *Carex* species are frequently infected by fungi with dark septate surface hyphae that produce weakly staining, hyaline hyphal extensions in the tissues (Davies et al. 1973). The occurrence of DSF is widespread among sedges of peatlands in Canada (Thormann et al. 1999), prairie savannas characterised by sandy soils with low moisture content (Miller et al. 1999) and in different habitats in Western Ghats, southern India (Muthukumar and Udaiyan 2002) (Fig. 2).

The functional relationship between DSF and plants may be comparable to that between ectendomycorrhizal fungi or AM fungi and their hosts. Infection with DSF seems to be mutualistic rather than parasitic, as suggested by Haselwandter (1987). Experiments examining the role of DSF in the ecology of *Carex* species of high alpine communities indicated that colonisation of roots enhanced the biomass of *Carex firma* and P-relations of both *C. firma* and *C. sempervirens* after 12 weeks of growth (Haselwandter and Read 1982). However, specific fungal structures like arbuscules as in AM fungi or convoluted coils as in ericoid mycorrhiza are absent in DSF associ-

ation. Thus, it is premature to conclude DSF as an alternative to mycorrhizal fungi in sedges. However, DSF have the ability to produce extracellular enzymes like laccases, lipases, amylases and polyphenol oxidase necessary to process complex detrital macromolecules into usable subunits (Cladwell et al. 2000). This fungal activity allows sedges to access N and P in environments where nutrients accumulate in organic pools.

Secondary metabolites

Competition for nutrients can be reduced through the production of chemical substances that affect the growth of other plants in the community. Members of Cyperaceae are known to accumulate tannins, proanthocyanins, alkaloids and flavonoids (Cronquist 1981). These allelochemicals may affect nutrient availability through their effects on symbiotic microbes. Though sedges have evolved a wide variety of secondary metabolites, the function of these chemicals is unknown. Potential roles include interaction with other plants, herbivores and pathogens (Bell 1981). However, sedges are also known to tolerate or remain unaffected by the secondary metabolites produced by other plant species. *Cyperus esculentus* is resistant to allellopathic cover crops like *Secale cereale* and *Vicia villosa*.

The presence of fungitoxic compounds in root cortical tissue or in root exudates may reduce susceptibility of plants to mycorrhization (Tester et al. 1987). There is reason to believe that many of the secondary metabolites (cyanogenic glucosides, betalains, alkaloids, etc.) accumulated in non-mycorrhizal families can be antagonistic to fungi. Flavonoids present in sedges include a diverse group of common root constituents, some of which have been implicated in plant protection from fungal pathogens, insects and nematodes, as well as allellopathic interactions (Rao 1990).

Though the influence of plant secondary metabolites on mycorrhizal fungi in certain non-mycorrhizal families like Brassicaceae, Chenopodiaceae, etc., has been extensively studied, nothing is known about the influence of these chemicals on mycorrhiza in Cyperaceae. Purple nutsedge or nut grass (*Cyperus rotundus*) accumulates sesquiterpenes that are known to affect growth and productivity of co-existing plant species (Komai et al. 1991). However, AM colonisation in mycorrhizal-dependent hosts tends to be unaffected when they are grown along with purple nutsedge (Muthukumar et al.1997). Similarly, Titus and del Moral (1998) also found no significant variation in AM colonisation levels in coexisting plant species in response to the presence of the non-mycorrhizal *Carex mertensii*. These reports clearly indicate that sedge root chemicals do not affect mycorrhizal formation in coexisting mycorrhizal host species like in members of some non-mycorrhizal families. However, more detailed studies on the role of secondary metabolites may highlight the possible role of these chemicals in the mycotrophic status of sedges.

Conclusions and future considerations

On the basis of the available evidence it is possible to conclude that Cyperaceae is not strictly a non-mycorrhizal family. However, the mycorrhizal status of its members could be influenced strongly by environmental conditions. Further, sedges have several adaptations allowing them to become established and survive in the absence of mycorrhizal association. However, key experiments remain to be done, chiefly the need to test the nutritional benefit to the sedges. The ecology and importance of mycorrhizal association in sedges are largely unknown and most of the assumptions are based on sparse evidence.

An interesting question is the role of non-functional mycorrhiza (intraradical hyphae and *Glomus*-type vesicles) in sedges. Despite the detection of arbuscules in several sedges, it remains unclear whether sedges actually benefit from mycorrhizal association in their natural environment. Mycorrhizal association may diverge from easily recognisable benefits to other non-nutritional benefits, which are yet to be recognised for sedges under natural conditions. Thus, a primary research focus in the future should be the functional aspects of the type and nature of interaction between sedges and mycorrhizal fungi involved in the association. Furthermore, a detailed understanding of the systematics of the family may also unearth valuable clues as to the interaction between mycorrhizal fungi and sedges.

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