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Aquatic Botany 76 (2003) 281–290
Aquatic botany
www.elsevier.com/locate/aquabot

Growth response and phosphorus uptake by arbuscular mycorrhizae of wet prairie sawgrass

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Received 27 August 2002; received in revised form 21 March 2003; accepted 3 April 2003

Abstract

Sawgrass (*Cladium jamaicense* Crantz) is one of the dominant species of South Florida's wetland ecosystems. The objectives of this study were to investigate the mycorrhizal status of natural sawgrass in soils such as the Everglades organic peat, calcium carbonate marl, and low elevation pine rockland sandy soils and to determine the growth response and phosphorus uptake due to arbuscular mycorrhizal fungi (AMF) inoculation under different soil types. An initial survey revealed that AMF population near the root zone of sawgrass varied among the sites and soil types, ranging from 936 to 6214 spores per 50 g dry soil. The AMF colonization of sawgrass roots varied among sites and soil types, ranging from 0 to 41%. In a greenhouse pot experiment, AMF inoculation significantly ($P < 0.05$) increased sawgrass growth (14%), shoot (52%) and root (66%) biomass, and P uptake (58%) compared to control plants in organic peat soil under saturated conditions. Receding soil water levels during dry season in the Everglades wetland is potentially conducive for the beneficial sawgrass–AMF association.

Keywords: Sawgrass; Arbuscular mycorrhizae; Wetland soils; Phosphorus uptake

1. Introduction

The arbuscular mycorrhizal fungi (AMF) are important symbiotic root–fungus associations found in most terrestrial plants throughout the world, but their occurrence and the role in the nutrient uptake of wetland plants has long been questioned. However, in the last two and a half decades AMF have been reported in the roots of many plants in wetlands (Aziz et al., 1995; Wetzel and van der Valk, 1996; Miller, 1998; Miller et al., 1999), salt marshes

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0304-3770/$ – see front matter
doi:10.1016/S0304-3770(03)00075-5

(Read et al., 1976; Rozema et al., 1986; Cooke et al., 1993), and aquatic systems (Read et al., 1976; Bagyaraj et al., 1979; Clayton and Bagyaraj, 1984; Cooke et al., 1993; Wigand and Stevenson, 1994). Most of these studies concentrated on AMF survey, and reported the presence or absence of AMF spores and colonization. Exceptionally few studies described the role of AMF association in host plant nutrition in wetland systems (Tanner and Clayton, 1985; Secilia and Bagyaraj, 1994; Miller, 1998).

Sawgrass (*Cladium jamaicense* Crantz) is the dominant perennial sedge comprising 65–70% of the Florida Everglades (Loveless, 1959). Although several aspects of sawgrass, such as seed germination, floristics, structure and development, nutrient dynamics and production, and the effects of hydrology and fire (Ponzio, 1997; Stewart et al., 1997; Miao et al., 1997, 1998; Miao and Sklar, 1998), have been studied, little is known of the occurrence of AMF and its effects on the sawgrass growth and nutrient uptake (primarily phosphorus). The general perception among researchers is that these AMF are obligate aerobes and their ability to form successful symbiotic associations with wetland and aquatic plants would be limited.

In a terrestrial system, the plant supplies carbon for the AMF growth and in turn the fungus enhances the uptake of relatively immobile nutrients such as phosphorus, sulfur, copper, zinc, and boron (Smith and Gianinazzi-Pearson, 1988). In addition, under drought conditions, the plant water status and growth is improved by the presence of AMF (Hetrick, 1984). Arbuscular mycorrhizal/mycorrhizal plants are also less susceptible to infection by root pathogens and nematodes (Bagyaraj, 1984). While beneficial effects of AMF in nutrient uptake, drought tolerance, tolerance to extreme pH in soil, tolerance to heavy metals, suppression of root pathogen, and vegetation in disturbed areas have been well documented, few studies have demonstrated AMF's functional role in a wetland system. Aziz et al. (1995) were the first to report AMF in sawgrass roots. Although occurrence of mycorrhizal colonization in several plant communities including obligate wetland, facultative wetland, facultative upland, and obligate upland communities in the Everglades freshwater ecosystem, has been documented (Aziz et al., 1995), the functional role of these fungi was not studied.

The objectives of the study were to: (1) survey the incidence of AMF in natural sawgrass populations in soils such as the Everglades organic peat, calcium carbonate marl, and low elevation pine rockland sandy soils and (2) assess the growth response and phosphorus uptake of AMF inoculated plants in different soil types of Florida Everglades.

2. Materials and methods

2.1. Habitat

For the initial survey study three research sites were selected. A tall sawgrass short hydroperiod wet prairie marsh was selected along Tamiami Trail (sites S1–S4; 25°45′30″ latitude North and 80°40′30″ longitude West) Shark Valley (sites S5–S9; 25°44′30″ latitude North and 80°45′30″ longitude West), Everglades National Park, Miami-Dade County, FL. The plant community consisted a mix of wetland species, *C. jamaicense*, *Eleocharis cellulosa*, *Salix carolianiana*, *Sesbania exaltata*, *Panicum hemitomon*, and *Typha dominigensis*.

The water depth during sampling was 30 cm from the surface, and it gets drier during winter season. The short hydroperiod wet prairie marsh is usually gets flooded for 2–6 months. A low elevation pine rockland site (sites S10–S12; 24°42′10″ latitude North and 81°23′10″ longitude West) was selected from lower keys (big pine key) of Monroe County, FL. This research site is an undisturbed natural pine rockland vegetation frequently flooded during summer months, usually 1–2 months. A typical pine rockland vegetation consists of dominant overstory of *Pinus elliottii* var. *densa*, a shrub layer of *Serenoa repens*, and several herbal species and sedges including sawgrass. The Tamiami Trail and Shark Valley sites are a combination of organic peat and calcium carbonate marl soils, whereas the low pine rockland site is shallow sandy soils over limestone.

2.2. Field sampling

Sawgrass roots were collected in September 1999 from Tamiami Trail and Shark Valley short hydroperiod wet prairie marsh in the Everglades (organic peat and calcium carbonate marl soils) and at low pine rocklands in lower keys (sandy soil), Florida. Three replicate plant samples were taken approximately 5 m apart from each plant at each sampling site. Whole plants were dug up with a spade, and roots and rhizosphere soil were carefully separated. The roots and rhizosphere soils were transferred to separate plastic bags, and transported to the laboratory, where they were kept at 4 °C until roots were examined for AMF colonization and soils were sieved for AMF spores. A portion of the soils were used for physicochemical analysis.

2.3. Laboratory procedures

Soil samples (50 ml volume dry weight basis) were wet sieved through a set of sieves followed by sucrose-density gradient (Brundrett et al., 1996). The AMF spores were separated and counted according to the diameter size (>250, 250–150, and 150–38 μm). The roots were cleared in 10% KOH at 90 °C for 15 min (Phillips and Hayman, 1970). After clearing, the root samples were stained in 0.05% trypan blue in lactoglycerol at 90 °C for 15 min. From each sample, 30 root segments of 1 cm length were examined for the presence of AMF colonization. Selected physicochemical analysis of the soil samples (moisture content, pH, labile P, total P) was conducted using standard soil analysis methods.

2.4. Greenhouse study

Seeds were collected from undisturbed native plants in the Everglades National Park, Miami-Dade County, FL. Seeds were surface sterilized with 1.0% sodium hypochlorite solution, scattered on the surface of new inorganic Perlite® in plastic pots, and placed under periodic mist watering. Seedlings at the first true leaf stage (10 cm tall) were transplanted into 6.5 cm × 24.5 cm plastic pots each filled with 720 g each of native wet prairie organic soil collected from short hydroperiod wet prairie sawgrass marsh area, sandy soil collected from pine rockland area, and calcium carbonate marl soil collected from sawgrass marsh near Homestead, FL. A layer of paper towel was placed at the bottom of the pots to prevent any soil loss during the experiment. The soils were twice steam pasteurized at 100 °C for 2 h with 24 h incubation between two cycles to eliminate most microorganisms.

Each pot received 20 g of either fresh or steam pasteurized inoculum maintained in nurse cultures of native AMF. Pigeon pea and sudan grass were used as the host plants for AMF nurse culture. Nurse cultures were at least 12-week-old before use. The inoculum samples showed heavily colonized (more than 75%) root fragments and many AMF spores (average 20,000 spores per 50 g of fresh inoculum). Soil and root fragments were mixed well and used as a mixed AMF inoculum. A part of the same inoculum was steam pasteurized for 2 h one time and used as an inoculum control for all treatments except AMF inoculum treatment. Soil filtrate consisted of 50 ml per pot of a soil solution derived from 500 g fresh soil shaken in 2000 ml distilled water, and passed through Whatman No. 1 filter paper. Treatments were as follows: control (soil + steamed inoculum); AMF (soil + fresh inoculum); and soil sievate (soil + steamed inoculum + soil filtrate). There were six replications for each treatment. Pots, each with one seedling, were arranged in a completely randomized design and grown under greenhouse conditions. During the experiment regular watering maintained the soil moisture at >90% of the water holding capacity (near saturation) and it was fertilized biweekly with Hoagland's solution without P at a rate of 50 ml per pot.

Plants were harvested after 16 weeks of growth. Plant height, number of tillers, shoot and root dry weights were recorded to evaluate treatment response. A small fresh root sample was used for AMF colonization after its fresh weight was measured. The final dry weight of the root was calculated based on the addition of the sample's proportion of the whole root system. Dried shoot and root samples were ground into powder. Phosphorus content of both shoot and root tissues were determined from pulverized dried tissues. Digestion and analysis of total P followed the dry-combustion and colorimetric method (Solorzano and Sharp, 1980). Total P uptake and root to shoot weight ratio were calculated from the measured parameters.

Statistical analysis was carried out using the SPSS Base 10.0 statistical software (SPSS Inc., Chicago, IL). Differences between treatments for sawgrass growth, biomass, and P nutrition parameters were determined by analysis of variance, and means were compared by the least significance difference test ($P < 0.05$).

3. Results

3.1. Soil characteristics

The short hydroperiod wet prairie marshes of the Everglades represent organic peat (decomposing plant material) and marl (precipitated calcium carbonate and calcareous periphyton mats) soils, and the low elevation pine rockland represents sandy soils (Table 1). In general, sandy soils are low in labile and total P compared to organic peat and marl soils. The pH of the sandy soils ranged from below neutral to neutral, whereas organic peat marl soils were predominantly alkaline pH. Organic peat and marl soils were under 30 cm water, whereas the sandy soils were closer to field capacity during sawgrass sampling for AMF spore population and root colonization.

Table 1
Selected physicochemical properties of soils surveyed for AMF

Site	Soil type	Moisture (%)	pH	Labile P ($mg\,kg^{-1}$ soil)	Total P ($mg\,kg^{-1}$ soil)
Tamiami Trail: Everglades					
S1	Peat	20.4	8.2	6.9	208
S2	Marl	28.7	8.5	9.9	251
S3	Peat	80.4	7.7	5.6	232
S4	Peat	26.5	8.2	7.9	227
Shark Valley: Everglades					
S5	Marl	35.4	8.5	6.1	265
S6	Peat	75.9	7.4	15.2	244
S7	Marl	68.3	8.1	14.9	261
S8	Peat	85.4	7.1	18.9	199
S9	Marl	36.8	8.4	12.5	269
Low elevation pine rockland					
S10	Sandy	31.2	6.9	5.3	39
S11	Sandy	28.6	7.0	6.5	48
S12	Sandy	32.0	6.9	7.8	51

3.2. AMF spores and colonization

A higher number of AMF spores were enumerated near the root zone in peat soils than in sandy soils (Table 2). The individual spore diameter of majority of the spore populations was between 38 and 150 μm in diameter. Fifteen species of AMF were isolated

Table 2
AMF spore populations and colonization (%) in the Everglades and low pine rockland sites

Site	Soil type	Spores per 50 g dry soil				Colonization (%)
		>250 (μm)	250–150 (μm)	150–38 (μm)	Total	
Tamiami Trail: Everglades						
S1	Peat	69	1489	4656	6214 (±1423)	41 (±10.4)
S2	Marl	0	132	947	1079 (±161)	17 (±2.9)
S3	Peat	51	1578	3763	5392 (±1103)	0 (±0)
S4	Peat	26	576	3156	3758 (±658)	34 (±9.2)
Shark Valley: Everglades						
S5	Marl	139	1223	3128	4490 (±573)	23 (±3.5)
S6	Peat	104	643	4098	4845 (±901)	11 (±2.3)
S7	Marl	0	63	2735	2798 (±397)	7 (±1.2)
S8	Peat	0	137	2177	2314 (±498)	9 (±1.7)
S9	Marl	32	570	3175	3777 (±530)	30 (±5.2)
Low elevation pine rockland						
S10	Sandy	16	165	856	1037 (±96)	27 (±3.5)
S11	Sandy	24	201	758	983 (±102)	31 (±4.6)
S12	Sandy	9	252	675	936 (±81)	38 (±5.8)

Numbers showed in parenthesis are standard errors.

Table 3
Selected physicochemical properties of pot experiment soils

Soil type	pH	Organic matter (%)	Labile P (mg kg^{-1} soil)	Total P (mg kg^{-1} soil)
Everglades peat	7.8	65	17.1	205
Low pine rockland sand	6.9	12.5	6.5	39
Everglades marl	8.1	2.5	9.0	250

by sucrose-density gradient method. Genus *Glomus* was the dominant one, followed by *Acaulospora*. A few species of *Gigaspora* and *Scutallospora* were also observed. Organic peat soils harbored higher AMF spores followed by marl and sandy soils. The AMF spores enumerated from short hydroperiod wet prairie marsh were darker than the spores from low elevation pine rockland habitat. Sawgrass root colonization by AMF ranged from 0 to 41% (Table 2). The AMF colonization of sawgrass root included abundant arbuscules and vesicles attached to non-septate hyphae (data not shown). The AMF root colonization tended to decrease with increasing in soil moisture content. Though root colonization levels were not high under flooded conditions in both marl and organic peat soils, reasonably good spore population (1079–6214 spores per 50 g soil) was enumerated from the same soils.

3.3. Growth effects and P uptake by AMF

Three different types of soils: organic peat, calcium carbonate marl, and low pine rockland sand, were used to study the growth and P uptake response of sawgrass to AMF inoculation. Selected physicochemical properties of these soils are listed in Table 3. Sawgrass seedlings did not survive in marl soil. The plants died 3 weeks after transplanting. The attempts to re-establish sawgrass on marl soil by re-potting and re-transplanting were not successful. So, the results are not reported. The experiments with the Everglades peat and low pine rocklands were harvested after 16-week growth. Table 4 shows the treatment effects on growth that have potential ecological significance: promotion of shoot and root dry weight by AMF versus control (treatment 2 versus treatment 1) and growth promotion by AMF versus soil sievate (treatment 2 versus treatment 3). Plant tillers were increased by AMF inoculation compared to controls and soil filtrate treatments in organic peat soils, but no

Table 4
Sawgrass response to AMF inoculation: growth

Soil type	Treatment	Tillers	Plant height (cm)	Shoot dry weight (g)	Root dry weight (g)	R:S ratio
Everglades peat	Control	2.5	56.4^{b}	1.4^{c}	1.9^{c}	1.3^{b}
	AMF	3.5	65.8^{a}	2.9^{a}	5.7^{a}	1.9^{a}
	Soil sievate	2.83	57.0^{b}	2.3^{b}	3.5^{b}	1.5^{a}
Low elevation pine rockland	Control	2.5	48.6^{b}	1.6^{a}	2.6^{a}	1.6^{a}
	AMF	2.17	62.3^{a}	1.9^{a}	2.9^{a}	1.7^{a}
	Soil sievate	2.67	57.3^{a}	1.9^{a}	2.7^{a}	1.5^{a}

Different letters (within columns) indicate significant difference (LSD, $P < 0.05$) between treatments within the corresponding soil.

Table 5
Sawgrass response to AMF inoculation: P uptake

Soil type	Treatment	Shoot P (%)	Root P (%)	Shoot P ($\mu g\, g^{-1}$ dry biomass)	Root P ($\mu g\, g^{-1}$ dry biomass)	Total P uptake ($\mu g\, g^{-1}$ dry biomass)
Everglades peat	Control	0.0025	0.0024	34.4^{b}	43.0^{c}	77.4^{c}
	AMF	0.0024	0.0022	68.9^{a}	116.8^{a}	185.7^{a}
	Soil sievate	0.0026	0.0023	58.7^{a}	79.9^{b}	138.6^{b}
Low elevation pine rockland	Control	0.0018	0.0022	28.2^{b}	57.5^{a}	85.7^{a}
	AMF	0.0022	0.0019	40.3^{a}	60.5^{a}	100.8^{a}
	Soil Sievate	0.0021	0.0021	38.1^{ab}	52.2^{a}	90.3^{a}

Different letters (within columns) indicate significant difference (LSD, $P < 0.05$) between treatments within the corresponding soil.

such trend was observed in sandy soils. In organic peat soil experiment, AMF significantly (LSD, $P < 0.05$) promoted more growth than the control and the soil sievate. The shoot and root dry weights were significantly (LSD, $P < 0.05$) higher than that of the control and the soil sievate. AMF recorded a double increase in shoot dry weight, and a triple increase in root dry weight over the control. In sandy soil, AMF and soil sievate showed significant increase (LSD, $P < 0.05$) in plant height over the control group, but there were no significant differences (LSD, $P > 0.05$) in the shoot and root dry weights (Table 4). The ratio of root to shoot dry weight was calculated for all plants. Table 4 shows that root/shoot ratio was either equivalent for all treatments (sand) or varied for all treatments (peat).

Concentrations of P (%) in shoot and root tissues were similar across treatments and soils. Thus shoot and root tissue P was increased by AMF due to a higher biomass. This increase is significantly different (LSD, $P < 0.05$) in peat soil (Table 5). Statistical analysis revealed that AMF inoculation significantly (LSD, $P < 0.05$) increased P uptake by AMF (185.65 μg) compared to control (77.44 μg) and soil sievate (138.64 μg) treatments in peat soil. There was an increase in P uptake by AMF (100.76 μg) compared to control (85.68 μg) and soil sievate (90.31 μg) in sandy soil, however it was not statistically significant (LSD, $P > 0.05$) (Table 5). The AMF root colonization was >75% in both soils inoculated with AMF, whereas no colonization was observed in the control or in the soil filtrate treatment.

4. Discussion

Until recently, it was believed that the roots of emergent macrophytes, specifically sawgrass, were not colonized by AMF (Meador, 1977), leading to the conclusion that the Everglades were a unique non-mycorrhizal ecosystem. Aziz et al. (1995) reported the occurrence of mycorrhizal colonization in several plant communities including obligate wetland, facultative wetland, facultative upland, and obligate upland communities in the Everglades freshwater ecosystem. In their study, sawgrass was one of the obligate wetland species, which indicated the presence of AMF. In our study, the Everglades short hydroperiod wet prairie sawgrass rhizosphere soils had AMF spore population in the range of 22–124 spores g^{-1}

soil, these results are in contrast to the Aziz et al. (1995) observations on the AMF spore population (2–12 spores g^{-1} soil) in the Everglades. The spore numbers in low pine rockland sandy soils were similar to those reported by Fisher and Jayachandran (1999) on AMF colonization of the palm, *S. repens*. However, since spore numbers are influenced by soil characteristics (Hetrick, 1984) and plant community structure (Janos, 1980; St. John and Coleman, 1981), we expected a lower number of spores because of the anaerobic conditions in the wetland. In a recent study, Miller (1998) observed that wetter parts of transects in Carolina Bay had higher spore numbers and spore volume than drier areas. The high spore numbers in our wetlands study sites suggest that the spores may have accumulated without further spore germination or maintained a higher sporulation rate due to a stress response of the fungi to the wet conditions (Rickerl et al., 1994).

We observed a decrease in AMF root colonization with increase in soil moisture content. A similar relationship was reported by Miller (1998) on two semi-aquatic grasses, *P. hemitomon* and *Leersia hexandra* grown in freshwater, nutrient poor Carolina Bay of the Southeastern Coastal Plains. A few other reports (Andesron et al., 1984; Rickerl et al., 1994) also documented a negative relationship between soil moisture and AMF root colonization.

Most wetlands and aquatic AMF studies concentrated on occurrence, describing which plant species were colonized by AMF. However, limited information is available on the functional role of AMF in wetland plants and its ecological significance. Here, we report the function of AMF in wetlands species sawgrass (*C. jamaicense*). The occurrence of arbuscules—the site of nutrient exchange between plant host and the fungus, in the present survey under inundated wetland conditions probably indicates the existence of active sawgrass–AMF symbiosis. The central question to our study was whether AMF play similar functions in wetlands as they do in terrestrial systems? Numerous studies have been conducted to show the effects of P on sawgrass (Steward and Ornes, 1975; Davis, 1991; Chiang et al., 1994; Newman et al., 1996). None of these studies have attempted to study the effects of AMF on sawgrass growth in relation to P nutrition. At the end of a 16-week growth period, AMF inoculation significantly increased sawgrass growth (height), shoot and root biomass, and plant P uptake in organic peat soil. A similar increase was observed in sandy soils, but the difference was not statistically different from control or soil sievate. Aziz et al. (1995) indicated that P uptake via AMF to wetland plants would be reduced, but in our study we clearly demonstrated that AMF benefits wetland plants by enhancing the uptake of P from peat soil under saturated water condition. Few studies (Tanner and Clayton, 1985; Secilia and Bagyaraj, 1994; Miller, 1998) have demonstrated the significance of AMF inoculation for wetland plants. An interesting observation in our study was that the AMF effect on sawgrass tillers paralleled with Secilia and Bagyaraj (1994) experiment on a rice paddy, where they showed AMF inoculation increased the number of rice paddy tillers over that of the uninoculated control. In conclusion, this study showed that AMF have the potential to provide nutritional benefit to sawgrass in the Everglades. The beneficial activity of AMF is most likely to be favored during the drier growing season, when the soil water content is near or below saturation. Therefore, further studies on sawgrass–AMF symbiosis under varying water levels in the Everglades are needed to elucidate the extent of nutritional benefits and to examine the influence of environmental conditions and habitat type on the association.

Acknowledgements

We thank Darcy Stockman for technical assistance. Jack Fisher helped with growing sawgrass seedlings and AMF nurse cultures. This paper is Southeast Environmental Research Center contribution number 200 and F.I.U. Tropical Biology Program contribution number 63.

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