Beneficial Role of Arbuscular Mycorrhizal Fungi on Florida Native Palms

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Mycorrhizas, the symbiotic associations of roots and soil fungi, are present in Florida native palms collected in the wild. However, the role of mycorrhizas in the growth of these palms is unclear. We studied seedlings of four palms native to the Everglades to see how mycorrhizas affect growth and uptake of phosphorus. Our findings will be helpful in proposed Everglades restoration projects.

The symbiotic fungi are called arbuscular mycorrhizal fungi (AMF) which are common and found in the majority of land plants including cycads, conifers (except the pine family), and most trees and crop plants, including palms. The fungi penetrate and grow inside the roots but are not visible on the root surface with the naked eye. They also do not form large, obvious reproductive bodies (i.e., mushrooms or truffles). Therefore, fungal presence can only be verified after clearing, staining and then observing the roots with a microscope. Within the root cells, the fungus forms tiny tree-like structures, called arbuscules, which are the places where nutrients and water are exchanged between the two organisms. The fungus cannot make its own food and receives organic nutrients (sugars and amino acids) from the photosynthetic plant. In return, the plant receives mineral nutrients and water through the fungi. Smith and Read (1997) and Wang and Qiu (2006) gave extensive reviews about the general biology of mycorrhizas.

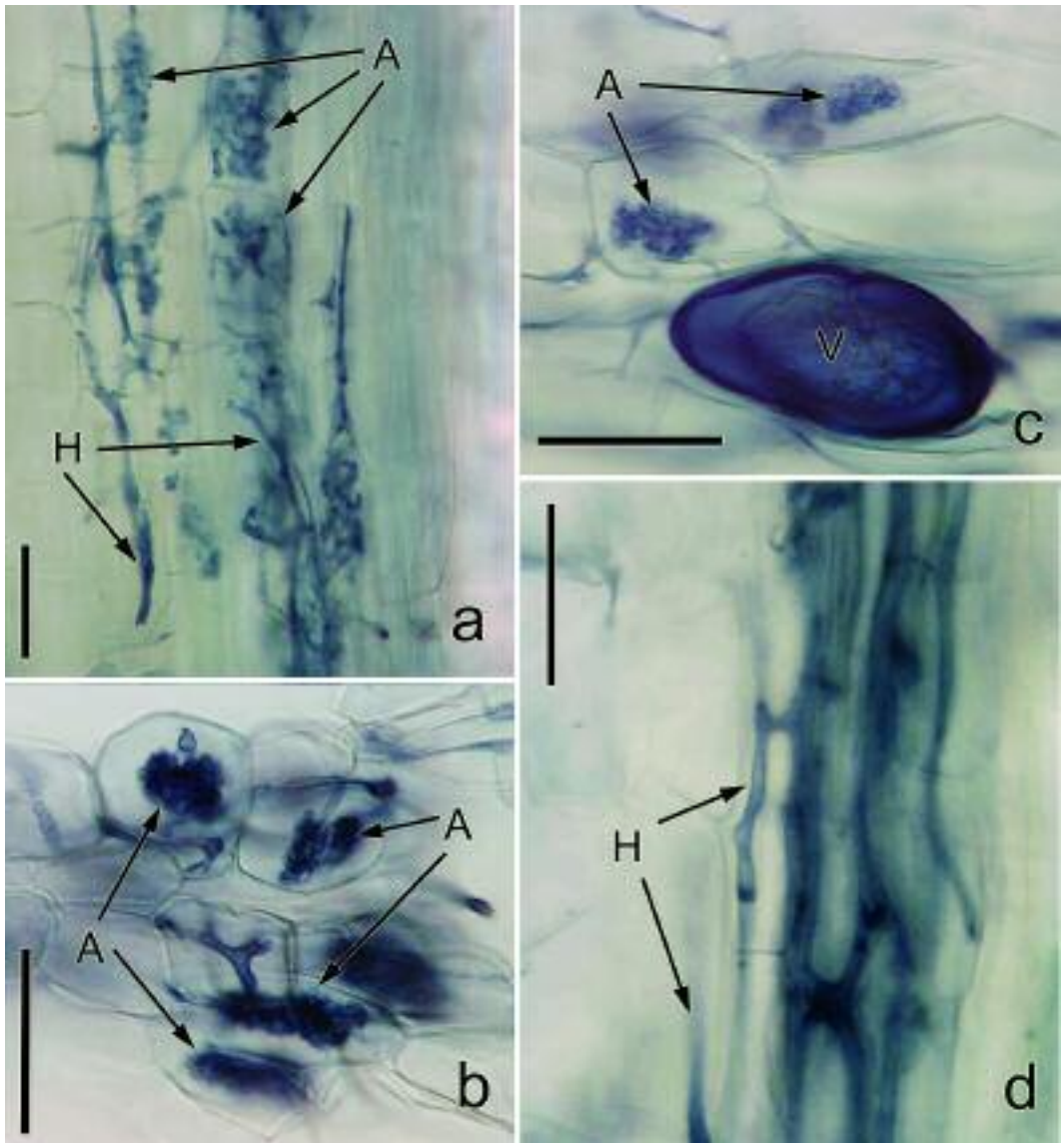
1. Representative plants of *Coccothrinax*, plants unpotted and washed free of soil. Treatments: 1 = no AMF, no microbes; 2 = no AMF, added microbes; 3 = live AMF, added microbes; 4 = no microbes, added 10 $mgkg^{-1}$ P.

Although no comprehensive surveys of the palm family have been conducted, AMF have been found in every species of palm that has been studied. The first well documented description of a mycorrhiza in a palm and its beneficial effect on palm growth was given for the peach palm (*Bactris gasipaes* Kunth) by Janos (1977). Later, St. John (1988) presented an historical review of AMF in palms. AMF occur in all the three main commercial palms (African oil, coconut and date) and many wild palm species (reviewed in Fisher & Jayachandran 1999). Since this last review, AMF were reported in wild *Desmoncus* palms (Ramos-Zapata et al. 2006), wild Florida native palms (Fisher & Jayachandran 2005) and old cultivated date palms (Bouamri et al. 2006). But the mere presence of AMF does not tell us about the benefits of AMF for the plant. Although controlled experiments found that

addition of AMF to potted palms increased growth (reviewed later in detail), there have been no experiments with native Florida palms. Here, we report on several experiments with native palms that investigate some of the effects of AMF on palm seedlings that were grown in pots with native soil. This native sandy soil had low levels of phosphorus and other nutrients. We want to know if AMF promote growth and increase the uptake of phosphorus in these palms, similar to the effects of AMF on rare non-palms that were tested on the same native infertile soil (Fisher & Jayachandran 2002).

Our experimental study has practical implications for palms being grown for restoration and for palms growing naturally in the Greater Everglades ecosystem. Native palms are key species in both wetlands and uplands of pine forest and hardwood hammocks of this ecosystem. We need to understand the propagation and cultural requirements of the native palms better to improve their successful outplanting into natural environments. AMF may play an important role in the Everglades, a naturally low phosphorus (P) environment. Additions of P, as from nursery operations, can be

2. AMF in the cortex of ultimate feeder roots of palms. a. Intercellular hyphae and arbuscules in *Sabal*. b. Intracellular hyphae and arbuscules in *Sabal*. c. Vesicle and arbuscules in *Sabal*. d. Intercellular hyphae in *Acoelorrhaphe*. A, arbuscule; H, hypha; V, vesicle. Scale line = 50 µm.



ecologically disruptive (Fish & Wildlife Service 1999). AMF may be a potential substitute for fertilizers in nursery production of plants used in restorations if native palms respond to AMF.

Materials and Methods

Plants

In the Greater Everglades ecosystem in subtropical Florida, four species of palms are a visible and ecologically important component of the native plant communities. Wetlands have the Everglades or Paurotes palm [*Acoelorrhaphe wrightii* (Griseb. & H. Wendl.) H. Wendl. ex Becc.] and pine rocklands have the silver palm [*Coccothrinax argentata* (Jacq.) L.H. Bailey], the cabbage palm [*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f.], and the saw palmetto [*Senenoa repens* (W. Bartram) Small]. The last two palms also occur in plant communities transitional between wetland and pine rockland. Urban development, farming and nursery operations have eliminated much of these wetlands and upland communities.

Soil

Soil samples for physicochemical analysis were collected from a pine rockland site containing wild plants of *Coccothrinax, Sabal* and *Serenoa*. The native pine rockland site had shallow sandy soils over a bed of oölitic limestone. Soil analysis (n = 3 at each depth) was carried out by a commercial testing service (A&L Southern Agricultural Laboratories, Pompano Beach, FL 33064). At the 0–5 cm. depth, color was white to gray; pH = 6.8–7.3; weak Bray test = 8 mg kg^{-1}P. At the 5–20 cm depth, color was white to yellow-orange; pH = 7.3–7.4; weak Bray test = 4–8 mg kg^{-1}P.

Soil used to fill pots for greenhouse experiments was dug from 5–20 cm depths and mixed. Soil was sieved through 6 mm mesh to remove stones and large root fragments. The average soil-solution P was 0.002 mg L^{-1} (SE = 0.0011, n = 4), as determined with a water extraction method by Olsen & Summers (1982). The average soil P (weak Bray test) from 0–20 cm depth = 6 mg kg^{-1}.

AMF inoculum

Nurse cultures of mixed native AMF from pine rockland were maintained on pigeon pea and sudan grass in 4 L pots containing fresh, unpasteurized soil from the native habitat of the species of interest. Nurse cultures were at least 12 wk old before use. The inoculum samples showed heavily colonized root fragments and many AMF spores. Spores collected on the 250 µm sieve were mostly the genus *Gigaspora* or *Scutelospora*; spores smaller than 250 µm were mostly *Glomus* spp. Soil and root fragments were mixed well and used as live inoculum (Treat. 3, below). A part of the same inoculum was steam pasteurized for 2 h one time and used as an inoculum control for all treatments without live AMF (Treat. 1, 2 & 4, below). Thus, all treatments received similar additions of organic and inorganic P found in the inoculum.

Experiment

Seeds were collected from wild plants, surfaced sterilized with 1.0% sodium hypochlorite solution for 15 min, rinsed in water, scattered on the surface of inorganic Perlite® medium in plastic pots, and placed under periodic mist watering. Seedlings with one or two green simple leaves (eophylls) were removed from the medium, roots trimmed to 4 cm length (to more easily fit into pots), and transplanted into 5 × 18 cm plastic pots (D40 Deepots™, Stuewe & Sons, Inc., http://www.stuewe.com) each filled with 600 g native sandy soil (see description above) that was twice steam pasteurized. Pots, each with one seedling, were grouped by species. Treatments were randomly arranged in frames and grown on benches in a glasshouse under ca. 50% shade. During the growing period, pots were periodically rearranged within and between species groups. Cross contamination was prevented by separation of pots and care in watering.

Four treatments were:

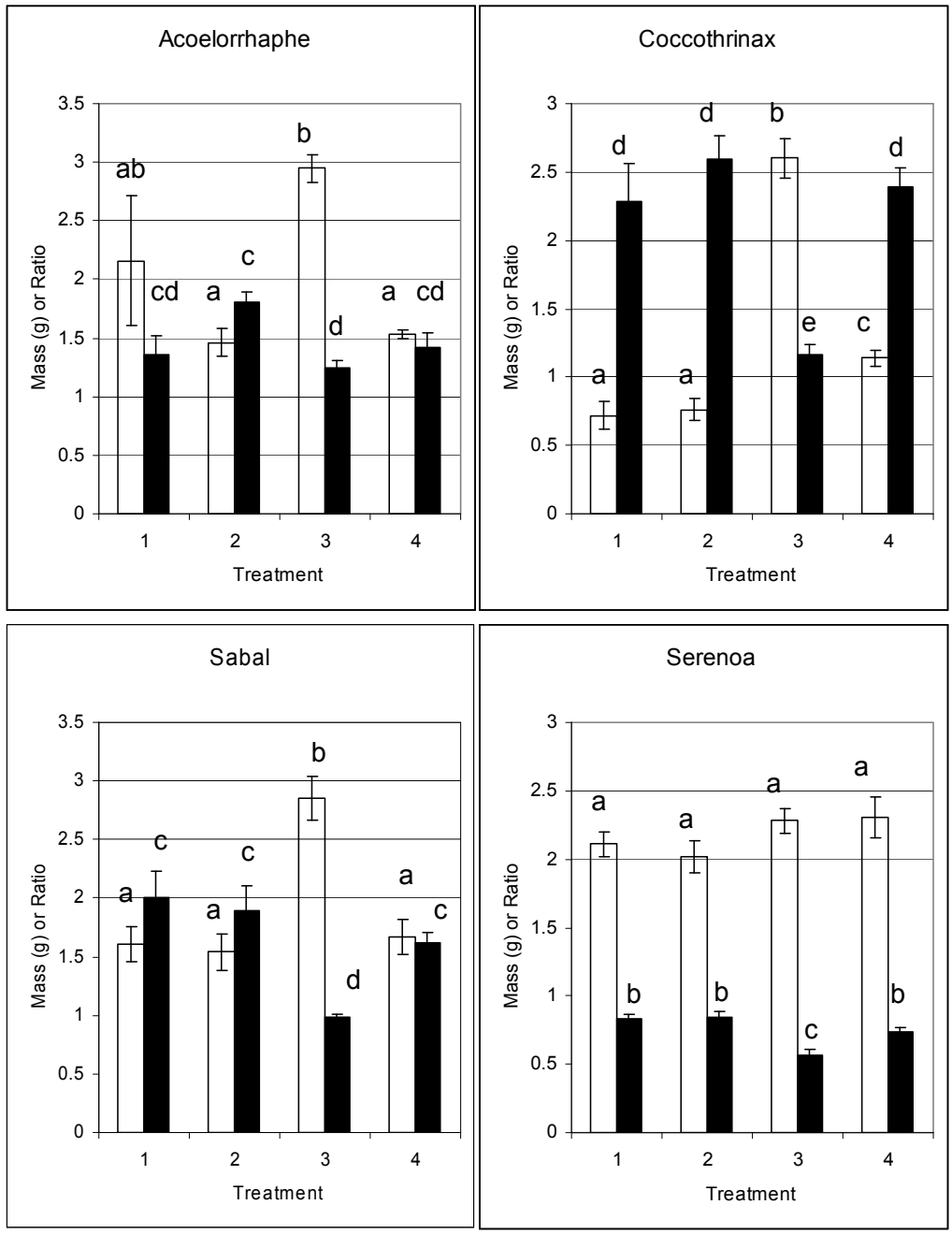
Treatment 1: no AMF; no soil microbes; no P

Treatment 2: no AMF; added soil microbes; no P

Treatment 3: live AMF; added soil microbes; no P

Treatment 4: no AMF; no soil microbes; added 10 mg kg^{-1} P

Each pot received 20 g of either live or dead inoculum (sterilized). Soil filtrate (containing soil microbes but not AMF) consisted of 30 ml per pot of a soil solution derived from 300 g fresh soil shaken in 2 L distilled water, and filtered through Whatman No. 1 filter paper. Phosphorus addition consisted of five treatments on alternating weeks beginning 3 or 4 wk after transplanting. This brought the



3. Plant dry mass of plants after 12 months for *Acoelorrhaphe*, 16 months for *Coccothrinax*, 12 months for *Sabal*, and 14 months for *Serenoa*. Treatments: (1) no AMF, no microbes; (2) no AMF, with microbes; (3) with AMF; (4) no AMF, no microbes, with added P. Open bar = whole plant dry mass; solid bar = root/shoot ratio. Mean values (± SE) given. Statistical comparisons made separately for dry mass and ratio. Bars having the same color and same letter are not statistically different ($\alpha = 0.05$).

total available P additions (in the form of KH_2PO_4) to the pot at 10 mg kg^{-1} (based on 600 g total soil). Hoagland's nutrient solution was prepared without P (Hoagland & Arnon 1950) and 50 mL added periodically to all pots of a species when plants became chlorotic (six times for *Coccothrinax* and *Serenoa*, four times for *Sabal*, three times for *Acoelorrhaphe*).

There were eight replicate pots per treatment for *Acoelorrhaphe, Sabal*, and *Serenoa* and ten replicates pots for *Coccothrinax*. Plants were

harvested after 12 mo (*Acoelorrhaphe, Sabal*), 14 mo (*Serenoa*) or 16 mo (*Coccothrinax*), and dry mass of roots and shoots were used to evaluate treatment response. In *Coccothrinax* and *Sabal*, phosphorus content was determined by the dry-combustion and colorimetric method (Solorzano & Sharp, 1980). Ultimate feeder root segments detached during washing (2–6 distal ends) were cleared in KOH, bleached, and stained with trypan blue (Brundrett et al. 1996) to observe AMF root colonization.

Differences among means of dry mass and P concentrations were tested with a one-way ANOVA. Differences between pairs of means were compared post hoc using a conservative Bonferroni test, if the Levene statistic indicated homogeneity of variances, or using a Games-Howell test if variances were not homogeneous using the SPSS Base 10.0 statistical software (SPSS Inc., Chicago, IL; http://www.spss.com).

Results and Discussion

Presence of AMF

AMF were present in small ultimate feeder roots (Fig. 1) of plants treated with live, mixed inoculum. All four species contained non-septate hyphae (Fig. 2a, b, d), arbuscules (Fig. 2a–c), and vesicles (Fig. 2c) in the root cortex, although not necessarily in the same root segment. Most commonly, AMF hyphae were intercellular (*Arum*-type morphology) (Fig. 2a), but occasionally intracellular hyphae were observed (Fig. 2b). Roots from other treatments did not show AMF colonization. However, quantitative assessment of fungal colonization could not be done with confidence because of difficulties in clearing roots with lignified epidermis and hypodermis.

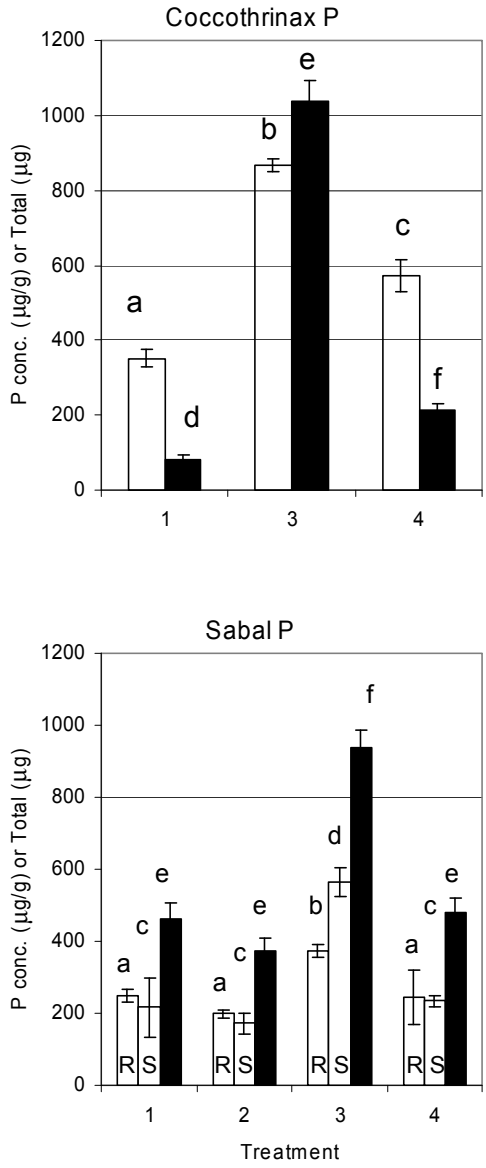
Previous publications have already illustrated AMF in wild collected roots of *Coccothrinax* (Fisher & Jayachandran 2005) and *Serenoa* (Fisher & Jayachandran 1999). In addition, the presence of AMF was reported in roots of six of the eight native Florida palm genera growing in the wild (Fisher & Jayachandran 2005). *Rapidophyllum* was not examined, and *Roystonea* was reported to have mycorrhizal colonization by Zona (1996), which has since been confirmed (J.B. Fisher, unpublished observations). All the major palm crops also have AMF in their roots under field conditions, e.g. African oil palm (Nadarajah 1980), beetle nut (Sengupta & Chaudhuri 2002), coconut (Lily 1975), date palm (Sabet 1940) and peach palm (Janos 1977).

Effects of AMF

The effects of AMF, P and soil microbes on the dry mass (= dry weight) of roots, shoots and the entire plants and on the ratio of root to shoot mass are presented (Fig. 3). Roots and shoots were measured separately to calculate root/shoot ratio. However, for clarity of presentation, only the total plant mass is presented in the graphs. In *Acoelorrhaphe*, AMF (Treat. 3) produced large plants that were statistically different from Treat. 2 and 4, but not different from Treat. 1. For root mass only (not shown in Fig. 3), Treat. 3 was significantly different from Treat. 1, 2 and 4. The root/shoot ratio differed only between Treat. 2 and 3. In *Coccothrinax* (Fig. 3), AMF significantly increased whole plant mass over Treat. 1, 2 and 4. Treat. 4 plants were larger than the control Treat. 1 and 2 but did not equal Treat. 3. The root/shoot ratio in the AMF treatment was significantly smaller than the other treatments. In *Sabal*, AMF clearly promoted whole plant mass over all other treatments, which were not significantly different from one another. Similarly, root/shoot ratio was significantly smallest in Treat. 3. In *Serenoa*, no treatment differences were found in whole plant dry mass, although AMF and added P (Treat. 3 and 4) did significantly increase the shoot dry mass (not shown in Fig. 3). Seedlings of this species are notoriously difficult to transplant (J.B. Fisher, personal experience), and seedlings in this experiment appeared to be stunted in growth for the first few months after planting in pots.

Phosphorus content was determined for two experiments (Fig. 4). *Coccothrinax* had significantly higher P concentration in the shoot tissue of plants with AMF (Treat. 3) and with P (Treat. 4) compared to the soil microbes free control (Treat. 1). The soil level of P (10 mg kg^{-1}) was doubled to 20 mg kg^{-1} with P added, but this is still low relative to agricultural soils (Brady & Weil, 2002). Moreover, total shoot P was almost five-times greater with AMF than with addition of P. Treat. 2 and root tissues were lost during tissue analysis. In *Sabal*, P concentration of both shoots and roots were significantly greater for the AMF treatment compared to all other treatments. The total plant P was significantly greater in the AMF plants than in those of the other treatments and almost twice that of the P addition.

Working with *Bactris gasipaes* seedlings, Janos (1977) found that inoculated plants grew larger



4. Phosphorus uptake after 12 months for *Sabal* and 16 months for *Coccothrinax*. Treatments: (1) no AMF, no microbes; (2) no AMF, plus microbes; (3) plus AMF, plus microbes; (4) no AMF, no microbes, plus added P. Open bars = shoot P concentration (S) and root P concentration (R); solid bars = total plant P. Mean values (± SE) given. Statistical comparisons made separately for shoot, root and total plant. Bars having same color and same lower case letter are not significantly different ($\alpha = 0.05$).

and fewer died than controls growing in native unamended soil free of AMF. However, the difference in size did not appear until after ten months, presumably when nutrients stored in the seed were used up. Later, more varied pot experiments with *B. gasipaes* showed that three genotypes responded differently to a single species of AMF and added P (Clement & Habte 1995). Some palm genotypes were less dependent on AMF than others, i.e. some grew equally well at higher P levels with or without AMF. When *B. gasipaes* was grown in a field orchard, the results became more complicated and less clear (Bovi et al. 1998). A single plant genotype was used with different levels of fertilization. After five years, roots showed a difference in natural AMF colonization with more colonized at higher N levels. Degree of root colonization also showed an interaction between P and K fertilization.

Rattan palms (*Calamus simplicifolius* Wei, *C. tetradactylus* Hance, *C. tetradactyloides* Hance, and *Daemonorops margaritae* (Hance) Becc.) growing in plantations all had AMF in their roots (Gong et al. 2000). In two species (*C. simplicifolius* and *D. margaritae*), Gong et al. (1995, 2000) found that one year after the addition of AMF, there was an indication of increased shoot dry weight and P uptake both with and without added fertilizer. Unfortunately, replication was limited and differences were not tested statistically. Seedlings of African oil palm (*Elaeis guineensis* Jacq.) were grown for 12 months in non-sterile soil that had natural AMF spores (Sanni 1980). All plants eventually became colonized with AMF, but those inoculated with additional AMF spores were larger, presumably due to greater or more rapid AMF colonization.

Other workers showed more clearly that AMF promoted nutrient uptake by palms. In a more controlled experiment with *Elaeis*, Blal et al. (1990) found that micropropagated plantlets (which unlike seedlings lacked stored nutrients in the seed endosperm) responded to AMF inoculation with greatly increased growth and increased P uptake when grown on two different acidic tropical soils. AMF also promoted growth and uptake of P from two sources of P (rock phosphate and super phosphate fertilizers). In date palm (*Phoenix dactylifera* L.) seedlings, AMF increased plant growth and uptake of P after nine months (Oihabi et al. 1993). Other species of *Phoenix* were also affected by AMF. Two-year-old seedlings of *P. roebelenii* O'Brien inoculated with AMF were larger but did not have significantly higher concentrations of P when they were harvested two years later (Jaizme-Vega & Díaz-Pérez 1999). Seedlings of *P. canariensis* Chabaud were inoculated separately with three different species of AMF (all species of *Glomus*) and grown for one year on a

peat:pine bark substrate in pots (Morte & Honrubia 2002). In unfertilized plants, one AMF species had higher rates of colonization and larger plants than the control or the other two AMF species. In addition, fertilized plants were larger than unfertilized ones. Plants were also analyzed for the concentration of minerals in the shoot tissues. In fertilized conditions, where nutrient levels were presumably less limiting, the AMF increased P only in the shoot. However, in unfertilized conditions, where there was a greater limitation of nutrients, AMF significantly increased the concentration of P, K, Mg, Na and Mn (Morte & Honrubia 2002). Thus, AMF can improve growth and nutrient uptake in palms, especially when soil nutrients limit growth.

The peach palm was considered by Janos (1977, 1996) to be an obligate mycotroph that required a symbiosis with AMF to survive in nature. Yet palms do not always require AMF, especially under high nutrient conditions of ornamental horticulture. Many ornamental palms are grown successfully in sterilized soil or artificial nursery mixes with external input of all required nutrients. Some 20-years-ago, St. John (1988) reviewed the presence of mycorrhizae in palms and suggested that AMF could be beneficial in palm horticulture, possibly when there are problems with nutrient uptake.

Our results with the effect of AMF on Florida native palms are consistent with these pervious publications. AMF generally improved growth and increased concentration and total plant P as compared to the AMF-free plants. The addition of soil microbes (Treat. 2) did not significantly affect growth or P concentration over the soil microbes-free control (Treat. 1). Addition of P that doubled the soil P level (from 10 to 20 mg kg^{-1}) increased the shoot P concentration in *Coccothrinax* and *Sabal*. Addition of P increased the whole plant mass of only *Coccothrinax* over the controls (Treat. 1, 2) but was still less than the AMF (Treat. 3). In the other three species, addition of P did not affect plant mass. We have no information on effects of greater additions of P.

The ratio of root/shoot mass is a measure of resource allocation in a plant. In *Coccothrinax, Sabal* and *Serenoa*, root/shoot ratios of plants inoculated with AMF were significantly smaller than controls or addition of P (Fig. 3). In *Acoelorrhaphe*, the ratio was significantly different only between AMF and Treat. 2, the control with soil microbes. Colonization by AMF also lowered the root/shoot ratio in other Florida natives (Fisher & Jayachandran 2002). Such a decrease in root/shoot ratio in AMF plants was found previously in many species (Vaast et al. 1996), although considerable variation in the effect of AMF on root/shoot ratios occurred in other species (Allen 1991, Corkidi & Rincón 1997, Janos et al. 2001).

Significance for Conservation and Restoration

In southern Florida, soils generally have low available P (Myers & Ewel 1990). Phosphorus appears to be a limiting nutrient in coastal and pine rockland soils, as was shown in the native endangered species of *Jacquemontia reclinata* and *Amorpha crenulata* (Fisher & Jayachandran 2002), in which AMF facilitated growth and P uptake. The present results confirm this beneficial effect of AMF in native palms. Arbuscular mycorrhizal fungi (AMF) appear to help native Florida palms gather the low levels of nutrients (and perhaps moisture) found in nutrient poor soils. Palms may require AMF to survive in the wild but not when grown in pots or in the soil of gardens where they are fertilized. This fact may already be obvious to palm growers: most palms grow perfectly well in sterilized soil mixes with added fertilizer. Nutrient deficiencies or poor growth in cultivated palms are commonly related to the extremes of high or low soil pH, temperatures or light intensity, and presumably not a lack of soil microorganisms.

Janos (1996) classified the peach palm as an obligate mycotroph because seedlings would not survive in their natural habitat without AMF, as opposed to facultative mycotrophs which can survive in the absence of AMF. More recently, he clarified the relationship by distinguishing between "response" to and "dependence" upon mycorrhizas (Janos 2007). A species must be grown on a wide range of soil P concentrations to verify these distinctions. Since *Coccothrinax* showed a significant enhancement of growth by P addition (Treat. 4), it may be less dependent upon AMF than the other species which did not respond to this level of P. We have results from only two P concentrations and cannot evaluate these four species for certain. However, *Acoelorrhaphe, Sabal* and *Coccothrinax* are definitely responsive to AMF, as shown by increased growth in Treat. 3. Because our AMF-free control plants (Treat. 1 and 2) were small and chlorotic, we suspect that they would not survive, but we do not know for certain. Plants

with additional P (Treat. 4) were healthier. Past experience with growing these four species in a nursery mix without AMF inoculation but with fertilization indicates that they grow well in a high nutrient environment, presumably lacking AMF (unpublished observations). Gemma et al. (2002) suggested that this type of responsiveness to AMF under very low natural soil P levels should be referred to as "ecological mycorrhizal dependency." The four palms can be ranked by their relative responsiveness (called "relative mycorrhizal dependency" by Baon et al. 1993), as determined by the percentage increase in average dry mass of entire plant ([Treatment 3 - Treatment 2]/Treatment 2) based on native soil P concentration. The RMD are as follows: *Coccothrinax* = 241%; *Sabal* = 84%; *Acoelorrhaphe* = 47%; and *Serenoa* = 13%. However, because there were different growth periods for the one-time measurement, these rankings are still tentative. The relative ranking is the same if RMD of each species is divided by the number of growing months for that species.

Because P and other nutrients are limiting in natural sites in southern Florida (Myers & Ewel 1990), we assume that natural seedling establishment depends upon AMF colonization. In natural sites occupied by palms, AMF can be expected to be ubiquitous in the roots of most plants and adjacent soil. Thus, any new seedlings that develop will quickly become colonized by AMF. In certain situations , where natural AMF inoculum could be absent or present only in low propagule numbers (e.g., cleared roadsides, sites where top soil was removed, reclaimed urban landscapes or where soil from non-vegetated sources is added, as in canal waste or coastal areas "enriched" with marine dredgings), the resulting soil environment would be similar to the classic low AMF habitats: mine tailings, strip mining disturbance or volcanic eruption (Allen 1991). In such cases, natural seedling establishment could be slowed or prevented by lack of natural AMF colonization. Nursery grown seedlings may lack AMF and successful establishment would require fertilization until AMF colonize the palm. However, use of fertilizers can be an issue in restoration projects in natural areas or preservations. Because the Everglades hammocks and pine rocklands are naturally low P environments (Chen et al. 2000), any use of P fertilizer is a major concern for land managers (U.S. Fish & Wildlife Service 1999). Therefore, acceptance of phosphate fertilization is very unlikely for plants grown for Everglades ecosystem restoration since P is such a significant pollutant in these habitats (Fish & Wildlife Service 1999). The use of native AMF is an ecologically sound method for conservation horticulture and may be a valuable tool in future restoration plans. AMF inoculation is a non-polluting way to improve growth of native plant seedlings without the need of additional P in situations where natural AMF is limiting growth, including nursery production.

Acknowledgments

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