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Root structure and arbuscular mycorrhizal colonization of the palm *Serenoa repens* under field conditions

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Abstract

Serenoa repens (Bartr.) Small is a palm native to the southeastern USA. It is a common understory plant in pine communities on both acid sands and alkaline limestone. Roots have only primary growth and range in thickness from 8.0 mm (first order roots from the stem) to 0.8–2.9 mm (ultimate roots of third to fifth order). The thickest roots occur at soil depths >20 cm; fine roots (<1.2 mm) occur at all depths (1–60 cm). Some second and third order roots are negatively geotropic and grow up to the mineral soil surface. The epidermis of all roots has a thick, eventually lignified outer wall. Except for the thinnest, all roots have a single-layered, thick-walled exodermis, which is first suberized and later lignified. Root hairs are never present. A hypodermis composed of several layers of lignified cells (up to 8-cells-thick) is next to the exodermis and forms the outer cortex. Radial series of thin walled and slightly lignified cells sporadically occur in the outer cortex of the thinnest roots, but there are no passage cells in the exodermis, which is continuous. The remaining inner cortex is composed of unlignified parenchyma with air canals and a completely lignosuberized endodermis in old roots. Passage cells were seen the the endodermis of the some of the thinnest roots. Arbuscular mycorrhizal (AM) fungi occur in the outer one-third of the cortical parenchyma adjacent to the hypodermis. Fungal coils, arbuscules and vesicles are found most frequently in the thinnest roots, but also occur sporadically in all root orders. Cells a few mm from the apical meristem are sometimes colonized. At sites of appressoria, coils of AM hyphae occur within an epidermal cell and exodermal and hypodermal cells beneath. Intercellular hyphae with intracellular branch arbuscules (*Arum*-type) are common in the inner cortex. There is evidence of a dieback of the highest order roots during the winter dry season. Profiles of soil and roots have the highest density of AM spores in the surface 10 cm layer. Total AM spore density ranged from 130 to 1100 spores per 50 g soil in different samples. *Glomus* spp. dominated followed by *Gigaspora* spp. The findings are related to a more general understanding of growth and AM colonization in long-lived roots of tropical woody monocotyledons. Palm roots, in particular, are slow growing and are protected by massive hypodermal layers.

Introduction

Palms are woody perennial monocotyledons, whose roots are known to be mycorrhizal (St. John, 1988; Zona, 1996). Mycorrhizal colonization promotes palm growth on nutrient poor native soil (Janos, 1977) and is potentially significant in the ecology of wild palms and in the cultivation of ornamental palms. Although palm roots lack secondary growth, they are long-lived and often woody and massive in size. There are few descriptions of palm root architecture and little information on their arbuscular mycorrhizae (AM) association, possibly because palm roots are difficult to study because of lignified tissues and silica bodies, as well as their predominantly tropical distribution (Tomlinson, 1990).

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We report on root structure and mycorrhizae of *Serenoa repens* (Bart.) Small, the saw palmetto, a prostrate understory palm ranging from warm temperate to subtropical climates in the southeastern United States. The palm is common both in pine rockland vegetation on shallow alkaline soils over limestone and in pinelands on deep acidic sandy soil. It is often the dominant understory plant beneath various species of *Pinus*. *Serenoa* is also significant in producing fruit that has been shown to be of medicinal value (Bennett and Hicklin, 1998) and is becoming significant in local economies.

This study will provide a foundation for future experimental research on palm mycorrhizae. Therefore, the pathway of fungal penetration and relationship of root anatomy to the presence of AM are emphasized.

Materials and methods

Habitat

The research site is a remnant of undisturbed natural pine rockland vegetation in Miami-Dade County, Florida. The original overstory of *Pinus elliottii* Engelm. var. *densa* Little & Dorman was eliminated by a bark beetle outbreak in 1993 following Hurricane Andrew, five years before this study. Although dead pine trunks remain, there is little seedling regeneration. The following plants grow within 10 m of the collection site: *Bursera simaruba* (L.) Sarg., *Myrica cerifera* L., *Pithecellobium keyense* Britton ex Britton & Rose, *Quercus virginiana* Mill., *Rhus copallinum* L. The site was chosen because *Serenoa* plants grow in an area of deep sand and do not have other native palms (*Sabal palmetto* (Walter) Lodd. ex Schult. & Schult. f. and *Coccothrinax argentata* (Jacq.) L.H. Bailey) nearby which might complicate root sampling.

Soil

The site has shallow sandy soils over a bed of oölitic limestone. The surface 10 cm is a white sand; pH = 6.2–6.8; available P = 5.9–8.8 mg/kg; total P = 28–35 mg/kg (Bray and Kurtz, 1945). The soil at 20–50 cm depth is a yellow-orange sand; pH = 6.3–8.2; available P = 11.5–17.3 mg/kg; total P = 12–35 mg/kg.

Collection of roots and soil

Field study: A trench was dug perpendicular to a single prostrate palm trunk, starting about 20 cm behind its distal portion in contact with the soil, in late December 1997. This region of trunk had fully mature adventitious roots. Samples of soil (10×10×10 cm) and roots were cut from the trench wall and used for analyses of spores and root densities. The soil profile was sampled 0-50 cm deep and up to 120 cm from the trunk. The newly exposed trench wall was washed gently with a water spray to expose roots in natural positions.

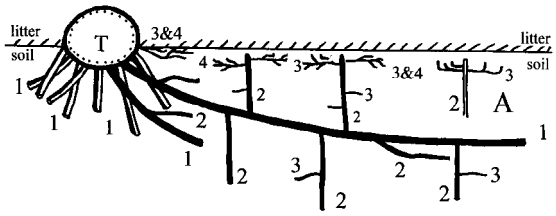


Figure 1. A. Diagram of root architecture. Soil surface and layer of litter (hatched) are indicated. Root orders (1–4) and horizontal trunk (T) are labeled. Order 2 roots may be horizontal or vertical (growing either up or down). Inset A shows a vertical Order 2 with its Order 3 & 4 roots becoming erect at their tips).

Soil samples (1 litre volume) from the side of the trench were wet sieved down to 32 μm particle diameter, and fungal spores were separated and counted by wet sieving (Brundrett et al. 1996). Root density was determined by washing roots free of soil in 1 litre soil samples, sorting into four diameter classes, and measuring total root length per soil volume for four root diameter classes using a morphometric video analysis system ('AgVision', Decagon Devices Inc., Pullman, WA).

Greenhouse study: Seedlings were first grown in sterilized soil mix for 12 months. They were transplanted into 2-liter pots with fresh, unsterilized native sandy soil taken from the field trench and contained wild *Serenoa* root fragments. After 5 months, roots were collected and used for histological study. Anatomical descriptions are based on both roots from wild, field-grown mature plants and roots of potted, greenhouse-grown seedlings colonized by AM fungi.

Microtechnique

Root anatomy was examined in both fresh and FAA-fixed roots using hand sections stained with aqueous toluidine blue. Histochemical stains were used following the procedures of (Perumalla et al., 1990): HCl-phloroglucinol for lignin; sudan IV for suberin; fluorescence of berberine sulfate and aniline blue combination (Brundrett et al., 1988), and natural auto-

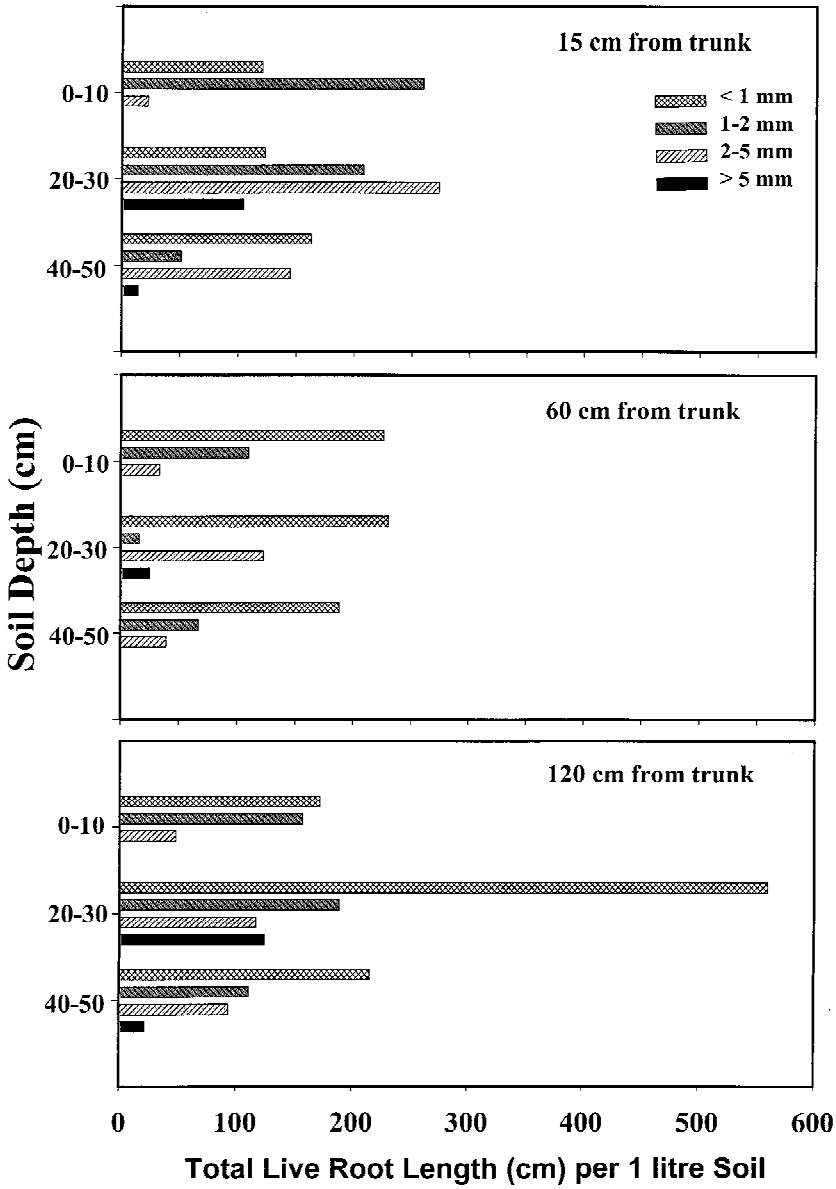


Figure 2. Total length of live roots found in 1 litre of soil in the profile of a trench from one plant. Bar graphs show four different root diameter classes at each of three soil depths at three distances from the trunk (above each other) along the trench. Bars are root diameter classes from thinnest (top) to widest (bottom): <= 1 mm; >1=2 mm; >2<5 mm; >=5 mm; respectively.

fluorescence for cell walls using a Leitz Ortholux II fluorescence system with wide band UV and narrow band blue filters.

For observing AM fungi, roots were cleared in KOH, bleached with NH_4OH-H_2O_2, and stained with trypan blue in acidic glycerol (Brundrett et al., 1996). The cortex of most roots was difficult to clear and observe through the thick lignified hypodermis. Whenever possible, roots were cut into longitudinal or transverse slices before processing.

Results

General mature architecture of root system and profile of root distribution

The stem of *Serenoa* is typically a horizontal axis ca. 8–15 cm in diameter. The plant produces vegetative lateral buds and eventually forms a cluster of prostrate trunks radiating from the original seedling site (Fisher and Tomlinson, 1973).

A generalized diagram of the root system of a mature, field-grown palm is shown in Figure 1. All roots are adventitious in origin on the lower one-third of the circumference of the horizontal trunk which is below the level of leaf litter. These roots are the thickest and are designated Order 1. They initially grow downwards or obliquely, and then become horizontal at soil depths >15 cm when not constrained by surface rocks (Figure 2). The living roots have a reddish surface color and are common in the 20–30 cm deep profile. The entire architecture is distorted by either very shallow soils or by localized deep pockets of sand which effectively act like deep flower pots.

Order 2 roots are either positively gravitropic, horizontal, or negatively gravitropic. Some erect Order 2 roots were more than 30 cm long. Order 3 roots are usually horizontal and eventually bear Order 4 roots as ultimate short feeder roots. This is especially noticable as the soil is removed where vertical Order 2 roots end within 1–2 cm of the soil surface, at the boundary of the compact humus layer and the loose leaf litter. The distal end of this non-growing, erect root may have a root cap or shows an aborted or damaged apex. Order 3 roots are clustered in the few cm behind the erect end. There is an obvious mat of horizontal fine roots (Orders 3 and 4) starting 6–7 cm below the soil surface and extending down to the 20–30 cm depth, as seen in Figure 2 especially in the fine roots at 120 cm distance. In some locations, Order 3 and 4 roots tend to bend up and end as an erect short root at the soil surface (inset A in Figure 1). Generally, the four diameter classes presented in Figure 2 represent Orders 1–4, respectively. However, root fragments are difficult to accurately classify. Roots <1 mm include both Order 4 and 5.

Root 'branch angles' were not measured. However, we observed lateral roots arise at a wide range of angles, both with respect to gravity and to the orientation of the parent root. These different angles are show in Figure 1.

In vigorous root systems, Order 5 roots may occur, but they are short and often swollen or tubercle-like. Order 5 roots are more common in potted seedlings and in vigorous roots within deep natural sand pockets. When roots are sampled at the start of the dry season (December 1997), there are many detached dead or short and shriveled Order 5 roots which were lost and not counted. In the early rainy season (June 1998) there are many white and growing Order 4 and 5 roots, which were not seen when the soil samples were collected earlier (December). This observation suggests a seasonal die-back that may start in the drier surface soil layer and is reflected in the greater number of finest roots below 10 cm (Figure 2).

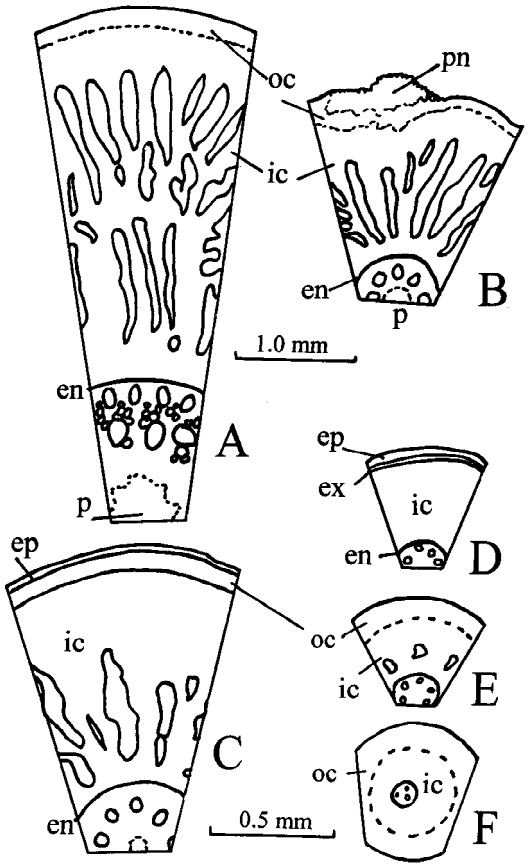


Figure 3. Serenoa roots, different orders in transverse section to show organization of tissues. **A**. Order 1 old root after epidermis is lost; **B**. Order 2 including a pneumathode region; **C**. Order 3; **D**. Order 4 with little lignification of the outer cortex; **E.** Order 4 with poorly defined exodermis and some lacunae in the cortex; **F.** Order 5 without a clearly defined exodermis. Abbreviations: en – endodermis, ep – epidermis, ex – exodermis, ic – inner cortex, oc – outer cortex, p – pith, pn – pneumathode. Scale line for A & B = 1.0 mm; for C–F = 0.5 mm.

Between the old dead leaf bases of the trunk, roots sometimes occur which are the size of Orders 2 and 3, apparently arising directly from the trunk. The ultimate roots are mainly Order 4 and sometime Order 5. However, it is unclear whether these are the only feeder roots or whether Order 3 are also feeder roots. Ultimate roots are very brittle and fragile; they easily detach during extraction. Thin roots, equivalent in diameter to Order 3 or 4, may also arise occasionally on Order 1 and 2 roots, respectively (Figure 1).

Table 1. Characteristics of different orders of roots of *Serenoa*

Features	Order 1	Order 2 Erect	Order 2 & 3	Order 4 & 5
Diameter (mm)	6.0 – 8.0	3.2 – 5?	1.4 – 4.0	0.87 – 1.18
Surface color	Reddish brown	Reddish brown	Brown	White to brown
Pneumathodes	Present	Present	Present	Rare
Exodermis	Present	Present	Present	Present but not always thickened
Outer cortex (= hypodermis)	Lignified	Lignified	Lignified	Sometimes unlignified
Inner cortex width (mm)	2.68	1.00	0.17 – 1.0	0.21 – 0.45
Inner cortex lacunae	Present	Present	Present	Present or absent
Endodermis	Present	Present	Present	Present ± passage cells
Stele diameter (mm)	2.0 – 2.13	0.93	0.51 – 0.60	0.10 – 0.18
Number phloem poles	28	18	12–13	4
Pith parenchyma	Present	Present	Present or absent	Absent

Anatomy and development roots of different orders

Although roots contain only primary tissues, significant changes occur during aging. The diversity of root size and histology for different Orders are summerized in Table 1 and diagramed in Figure 3.

Root caps remain attached after roots stop growth and their apical meristems have matured. The root surface shows regular, transverse rings of darkened, dead cells which represent root cap remains, perhaps due to rhythmic elongation. These dark collars of dead, pigmented root cap cells give palm roots a characteristic appearance. The root cap is formed by a distal layer and border cells of the apical meristem according to von Guttenberg (1968), although we did not confirm this. The root cap cells extend back to varying distances, sometimes forming a visible tubular sheath covering short longitudinal segments of the root. In inactive roots, the root cap is small and suberized, forming a restrictive cap. It seems that when a root resumes growth, the new tissues push through the suberized cap which is left behind, and a slight constriction in root diameter persists.

The epidermis (also called the 'rhizodermis') is one-celled thick, sometimes with remnant root cap fragments to the outside (Figure 4). All roots lack root hairs. The epidermal cells are papillose with a thickened but initially unsuberized and unlignified outer cell wall. In larger roots, the epidermis becomes lignified (Figure 8).

All root orders also exhibit an irregular longitudinal pattern of white rings of surface eruptions. These are a result of proliferation of subepidermal cells and a rupturing of the epidermis (Figure 3B). The proliferated cells are spherical, thin-walled, highly suberized, and with many intercellular spaces (Figure 9). Thick-walled exodermal and outer cortical cells appear to enlarge and may undergo one or two internal paradermal cell divisions. These lenticel-like structures are called pneumathodes (Seubert, 1997) because of their presumed function in gas exchange. They are most common in roots near the surface and on erect Order 2 roots.

The cell layer adjacent to the epidermis is first distinguished from the epidermis as an exodermis by the thickening of cell walls and development of suberin in the anticlinal walls. With age, all exodermal cell walls become equally thickened and both suberized and lignified (Figures 4, 7). We found no evidence of thin-walled or unsuberized passage cells.

The multilayered nature of the secondary wall and quality of staining with toluidine blue clearly distinguish these exodermal cells from adjacent outer cortical cells which are thick-walled with fewer or no wall layers (Figures 4, 5). Except for the highest order roots, these outer cortical cells mature into a hard, lignified hypodermis (Figures 4–8, 18). The thinnest Order 4 and 5 roots tend to lack a clear hypodermis and have a weakly developed exodermis (Figure 13), but some old Order 5 have a lignified hypodermis. In old roots, the epidermis disintegrates leaving the exodermis as the outer boundary with the soil.

The thickest roots have radially aligned lacunae in the inner cortex and variable number of cell layers between the lacunae and the endodermis. Thicker roots are aerenchymous but hard due to the thick shell of the hypodermis (Figure 3A–C).

As root tissues mature, endodermal cells opposite the protophloem poles are first to differentiate with the development of first suberin in the inner one-third of the radial cell walls followed by lignification of radial (Figures 12, 14) and then inner tangential walls (Figures 10, 11, 15). Differentiation of the endodermal cells progresses toward the xylem poles (Figure 11) and passage cells occur in young roots. Eventially, all endodermal cells become lignified and have thickened inner and thin outer tangential walls (Figure 10), although passage cells are found irregularly in the smallest roots (Figure 15).

The stele or vascular core has a one-layered pericycle and multiple protoxylem and protophloem poles, depending upon the diameter of the roots (Table 1; Figure 10). Wide metaxylem vessels remain immature with cytoplasm at a distance of several cm behind the apical meristem in wide roots. At these positions, the hypodermis, endodermis and central region of the stele are fully lignified. The stele center of thin roots has sclereids. Widest roots (> 2–3 mm) have a well-differentiated pith composed of large, thin-walled parenchyma surrounded by thick-walled, smaller sclereids (Figure 3).

Mycorrhizal fungal colonization

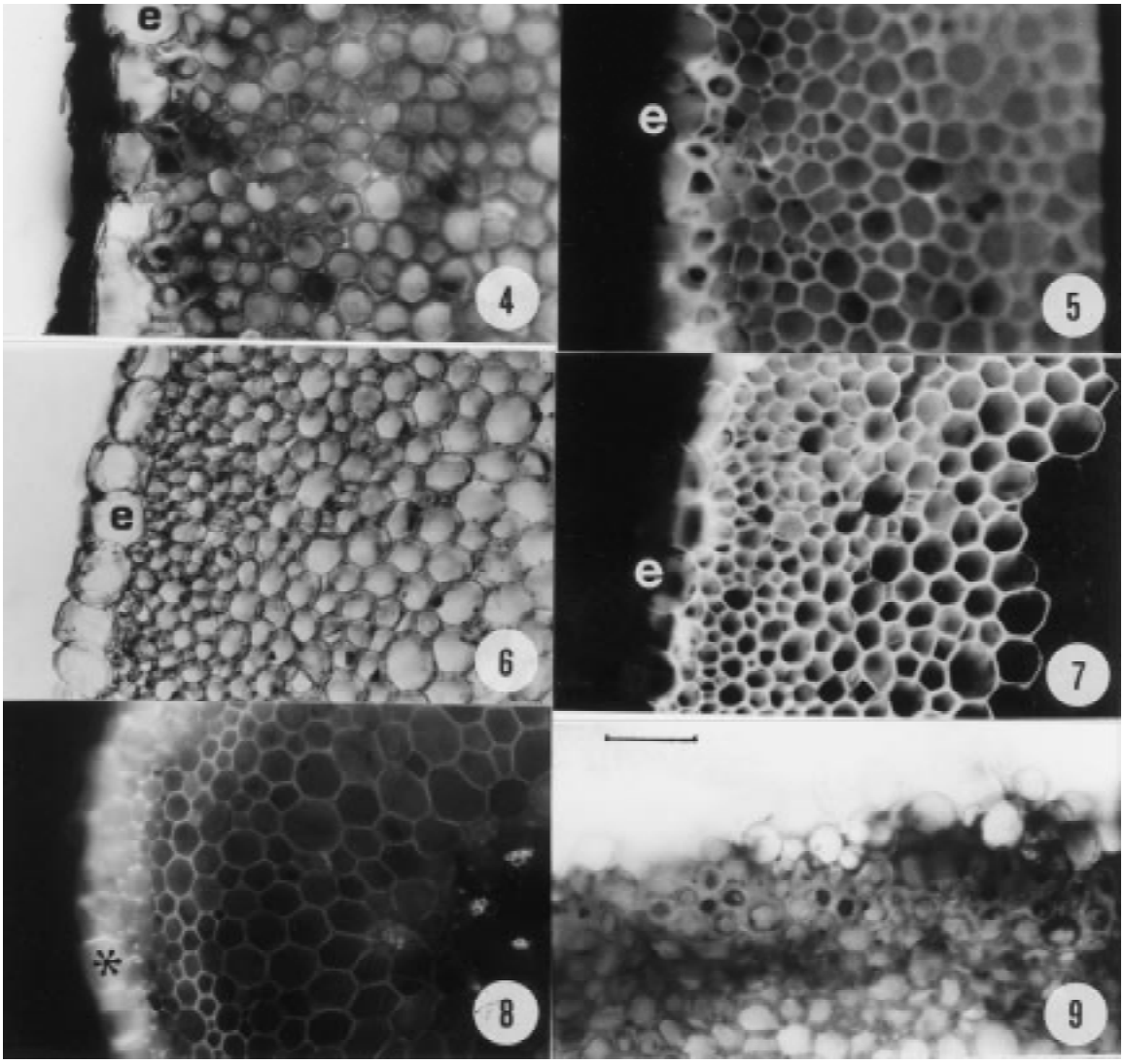
The root surface is covered with a variety of nonseptate fungal hyphae. Narrow, golden-brown hyphae anastomose in the valleys of the epidermal cells thus following the pattern of anticlinal epidermal walls. Wider unpigmented hyphae, which stain darkly with trypan blue, occur on the epidermal surface and on root cap remnants. Various forms of appressoria occur, ranging from a hyphal plexus with swelling on the epidermal surface (Figure 22) to an absence where a hypha enters directly into the epidermal cell with no external modification (Figures 18–20). The hyphae tend to form a coil within one (rarely two or three) adjacent epidermal cells and coils or loops within the adjacent exodermal and hypodermal cells (Figures 24–29). In surface view, there is no consistent pattern of appressoria on the root, which is consistant with a uniform epidermis and an exodermis that has no passage cells.

Beneath each appressorium, a hypha invades an epidermal cell, an adjacent exodermal cell and then a radial series of outer cortex cells, which may have thick walls or may be part of the sporadic series of thin-walled cells. It is unclear if these cells were penetrated before or after adjacent exodermal and hypodermal cell walls were suberized and lignified. Intercellular hyphae were not observed in the compact cells of the outer cortex (Figures 16, 17). Hyphae travel mainly in the longitudinal intercellular spaces of the inner cortical parenchyma. Adjacent cortical cells, positioned both longitundinally and transversely to the root axis, are invaded by coils (Figures 21, 23), hyphal branches with arbuscules, and vesicles. Vesicles appear to be both inter- and intracellular.

In all root orders, hyphae and arbuscules are concentrated in the peripheral parenchyma cells of inner cortex (Figures 16, 17). AM hyphae are variously distributed, either completely around the circumference, in a sector when present in thin roots (orders 4–5), or in the peripheral half to three-quarters of the inner cortex. Fungi rarely occur within 2–3 parenchyma cells of both the endodermis and the thick-walled outer cortical cells. In thicker, higher order roots (Orders 1–3), limited AM fungi occur in the outer one-third or one-fourth of the inner cortex, to the exterior of the radial air lacunae.

AM fungi are never observed in the stele or endodermal cells. In old roots, hyphae (some septate and possibly saprophytic) grow on the surface of the lacunae and enter cells of the inner cortex adjacent to the endodermis but do not penetrate endodermal cells.

Because of the thick, lignified layer of exodermal and outer cortical cells, whole root segments can not be reliably cleared and stained to document presence of internal AM. Thick roots clear and stain well after they are cut into longitudinal slices to expose the cortex. Thin roots are problematic, especially when old and sclerified. Thick cross sections that are processed like whole roots are stained most reliably, but colon-

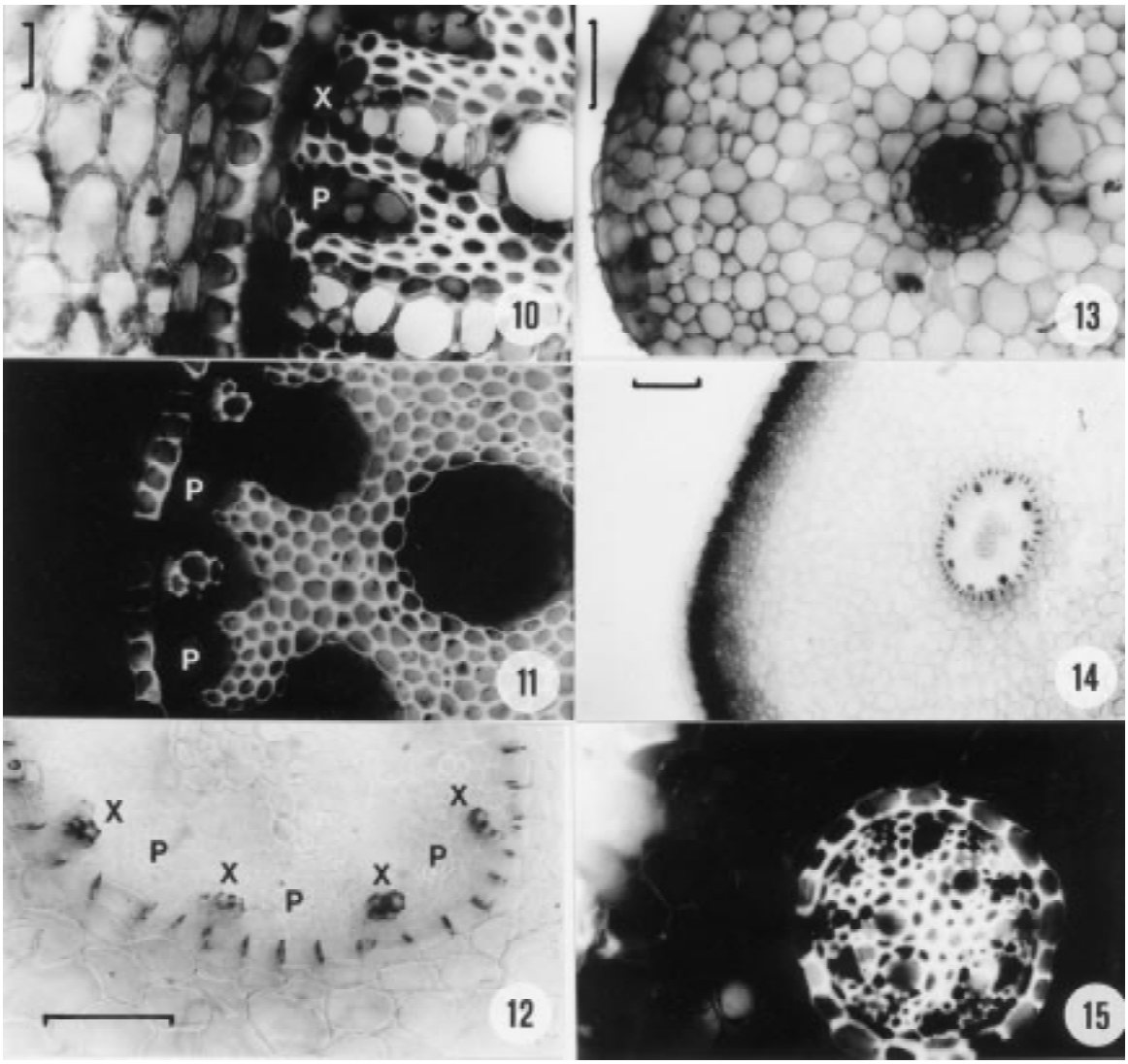


Figures 4–9. Roots in transverse section; all stained with berberine-analine blue. 4. Young Order 1 with epidermis on left and outer cortex on right; dark layer on the epidermis is the crushed remains of root cap; viewed with white light. 5. Same section viewed UV light; thick walls of exodermis are obvious, with no fluorescence of root cap and little for the epidermis. 6. Old Order 2 with exodermis and outer cortex similar in wall thickness when viewed with white light. 7. Same section viewed with UV light; walls of epidermis (inner walls only), exodermis and outer cortex all lignified. 8. Young Order 3 viewed with UV light; showing lignified epidermis and exodermis, inner cortex with some autofluorescence; endodermis with only casparian strips. 9. Surface of pneumathode region of Order 2 with surface dead cells and underlying thick-walled suberized cells; viewed with white light. Figures 4–9 same magnification. Scale line in Figure 9 = 50 μm. Asterisk (*) – lignified epidermis, e – epidermis.

ization along root length cannot be easily followed. Our inability to clear the exodermal/hypodermal layer prevents the use of the grid point method to determine percent colonization, which is standard practice for other plant species.

Soil characterization and fungal spore density in profiles

The soil is typical of a sand pocket in the pine rockland community. The substrate is oölitic limestone that forms visible outcrops and generally has a shallow overlayer of sandy soil with a thin surface layer of organic litter, depending upon the length of time since the last burn of this fire climax community. Leaf litter

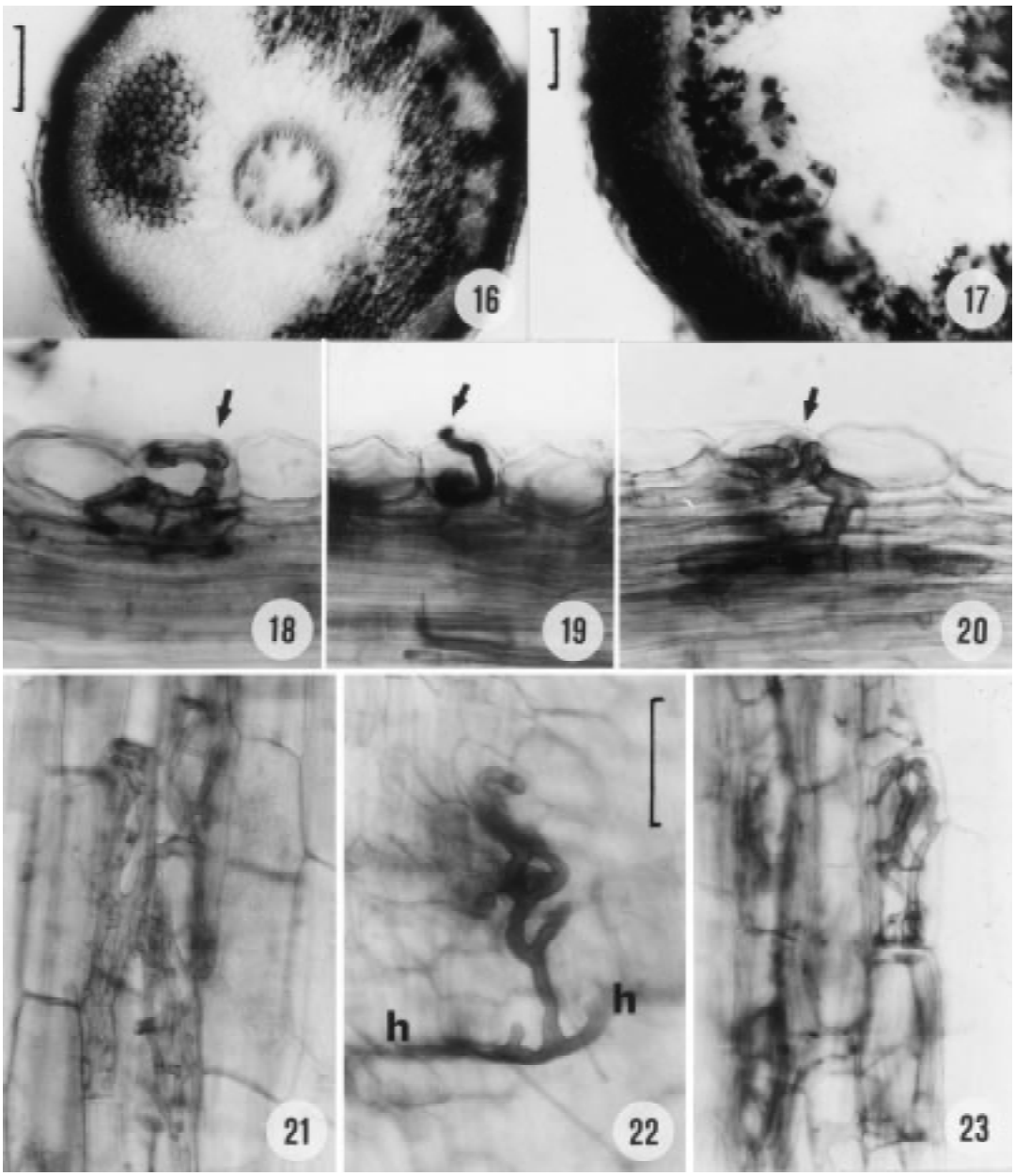


Figures 10–15. Root steles in transverse section; all stained with berbeine-analine blue, except for Figure 13 which is stained with toluidine blue. 10. Mature Order 1 with thick-walled lignified endodermis; viewed with white light. 11. Young Order 1 with developing endodermis that is thick-walled only opposite phloem poles; viewed with UV light. 12. Young Order 3 or 4; endodermis with only tangential walls lignified; lignin stained darkly at xylem poles (x); viewed with white light. 13. Mature Order 5 lacking a defined exodermis but with a clear endodermis; viewed with white light. 14. Young Order 3 or 4 with lignified outer cortex and radial walls of endodermis; lignin stained darkly; viewed with white light. 15. Mature Order 4 or 5, with lignified endodermis; viewed with UV light. Abbreviations: p – phloem pole, x – xylem pole. Scale lines = 200 μm in Figure 10; 50 μm in Figure 13; 100 μm in Figure 14; and 50 μm in Figures. 11, 12, 15.

and twigs reach a depth of 2 cm. The top soil layer is a white sand which changes to yellow-orange sand at about 20–30 cm depth. The pH is neutral to slightly acidic and is low in available phosphorus.

Frequency of AM fungal spores is presented in Figure 30. The highest spore counts were near the soil surface and nearest to the trunk, decreasing with depth and distance from the trunk. AM spore number (Figure 30) does not show a close correlation with root length distribution (= root density), especially with the thinnest size class at the 20–30 cm depth (Figure 2).

Preliminary observations with the dissecting microscope indicated that spores collected on the 250 μm sieve were mostly the genus *Gigaspora* or *Scutellospora.* These spores were typically large with a bulbous base. Spores smaller than 250 μm were mostly *Glomus* spp. We did not observe obvious *Acaulospora*, *Entrophospora*, or *Sclerocystis.*

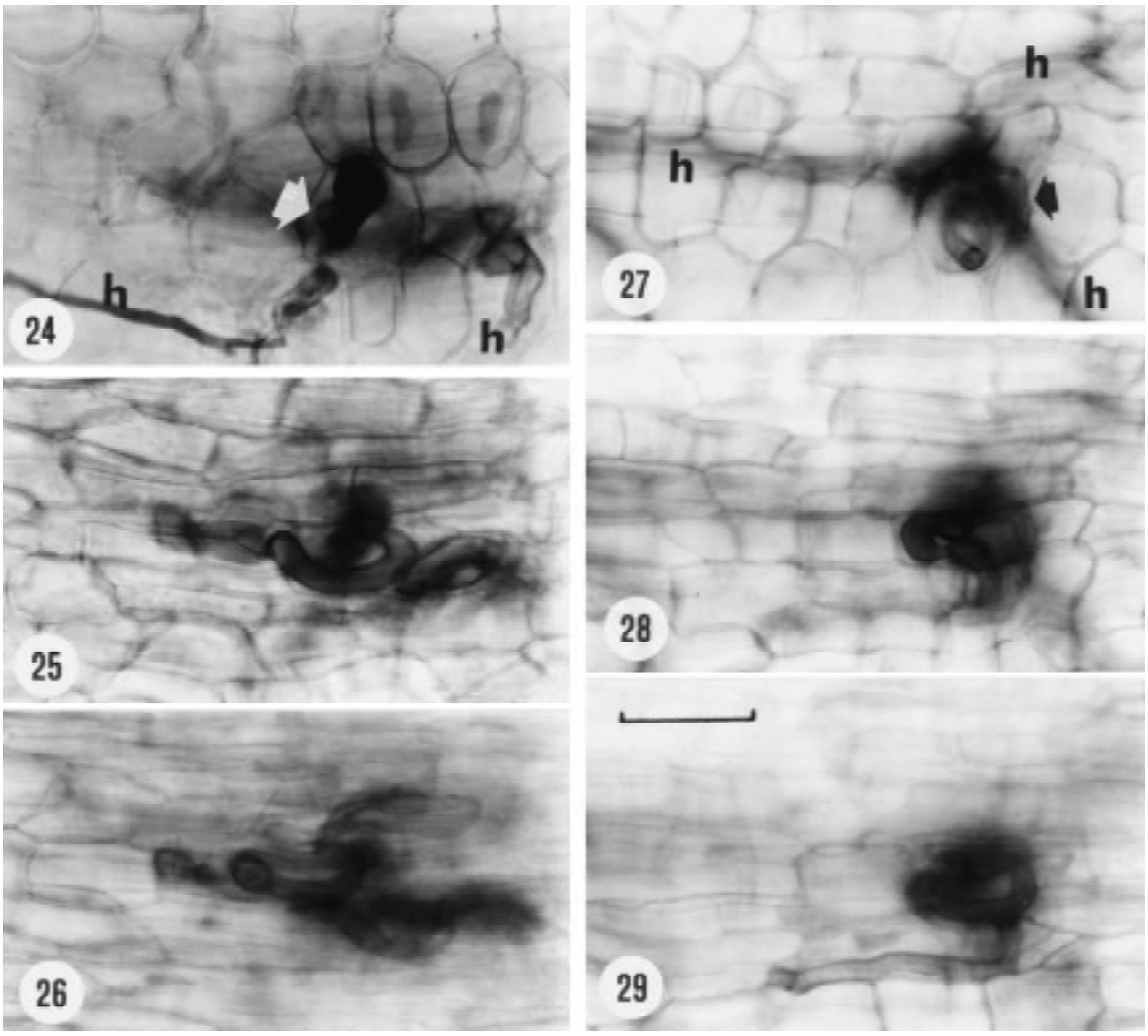


Figures 16–23. Roots in thick transverse and longitudinal sections; all stained with trypan blue and viewed with white light. 16. Order 3 with patchy distribution of AM fungi in cortex. 17. Order 3 or 4 with AM fungi in peripheral region of outer cortex. 18–20. Hyphal penetration of three different epidermal cells; in longitudinal view with epidermis at top. 21. Cortical cells with intracellular hyphae. 22. External hypha at site of appressorium (microscope focused above the epidermal surface). 23. Cortical cells with inter- and intracellular hyphae. Scale line = 200 μm in Figure 16; 100 μm in Figure 17; and 50 μm in Figures 18–23. Arrow – site of hyphal penetration, h – hyphae external to root and continuing out of focus.

Discussion

Root structure

The architecture and distribution of roots within the soil profile are similar to those described for African oil palm (*Elaeis guineensis*) by Purvis (1956) and Jourdan and Rey (1997), although the finest roots (presumably feeder roots) of *Serenoa* occur more evenly in all soil depths (0–50 cm) rather than mainly in the surface 20 cm reported for *Elaeis* (Tailliez, 1971) and



Figures 24–29. Roots in surface view; all stained with trypan blue and viewed with white light. 24–26. Three images of the same appressorium at focal planes of the epidermis, exodermis and next cell below, respectively. 27–29. Three images of the same appressorium at focal planes of the epidermis, exodermis, and next cell below, respectively. All at same magnification. Scale line in Figure 29 = 50 μm. Arrow – site of hyphal penetration, h – hypha external to the root and continuing out of focus.

Bactris (Vandermeer, 1977; Ferreira et al., 1990; Ferreira et al., 1995). The more uniform distribution of fine roots in *Serenoa* may be due to the well-drained sandy substrate as opposed heavy clay. However, the distribution of feeder roots may vary during the growing season. We found many old and senescing Order 4 and 5 roots in December (end of wet season) and many new, growing higher order roots in June (start of wet season), suggesting an annual turnover of feeder roots. This observation must be substantiated by following feeder root growth and death throughout the year. Thus, the distribution of living (non-shriveled and solid) roots in Figure 2 may only represent the winter state of live roots, in which few or no roots $<$ 1 mm were found. In *Elaeis*, the finest roots elongated more slowly in adult plants than in seedlings, i.e. short lateral roots in Table 3 versus 1 in Jourdan and Rey (1997). In addition, these workers found that Order 4 roots (= 'ultimate unbranched roots') were self-pruning, living for one month or less (Jourdan and Rey, 1997: Table 4). *Serenoa* may also have short-lived Order 4 and 5 roots which would account for the observation of white fine roots growing near the surface during the rainy season.

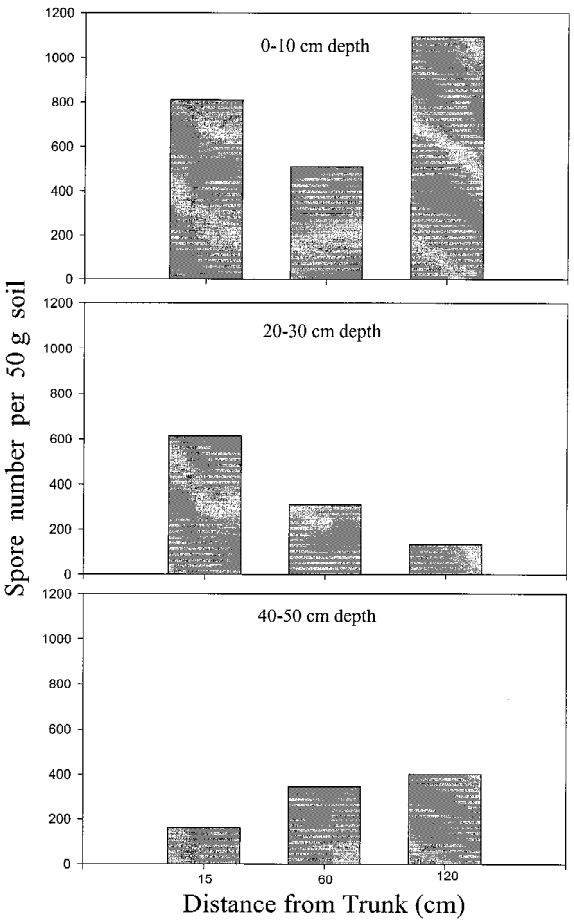


Figure 30. Spore number as bar graph at three distances from the trunk, repeated for the three soil depths. Only AM spores >32 μm diameter were counted per 50 g fresh soil taken from the same trench as in Figure 2.

Root anatomy conformed to the descriptions by Seubert (1997). Suberization of the exodermis occurred later than that of the endodermis and before maturation of the hypodermis, which is also lignosuberized (as defined by Peterson and Enstone, 1996). Throughout development and in old roots, the exodermis remains distinct from hypodermal cells in terms of cell size and cell wall staining. Therefore, we consider the exodermis as single layered, uniform, and without passage cells.

The regular production of dark rings of root cap remnants and periodic slight constrictions in root diameter indicate rhythmic extension growth or individual roots. We have no information on whether such periodicity is synchronized within the entire or a part of the root system.

The zone of epidermal absorption appears to be limited because ultimate roots (Orders 4 and 5) are usually short (<= 1 cm) and higher order roots (Orders 2 and 3) have thick exo- and hypodermal layers with all cells walls lignosuberized within a few cm of the root tip. This surface area limitation is especially probable because root hairs are absent. Water continuity between the soil and living cell membranes is probably maintained by mycorrhizal hyphae that pass through suberized cell walls of the outer cortex (exo- and hypodermis). However, we did not determine the extent of living external hyphae along the length of a root. In old thick roots, the epidermis is lost, and only the exodermis remains as the outer root-soil boundary.

Mycorrhizae

Although the species of AM fungi have not been identified, a description of colonization by these endosymbionts are useful in understanding the biology of palm roots and will serve as a foundation for future descriptive and experimental studies of AM in *Serenoa* and other palms. The approach of Merryweather and Fitter (1998) in identifying the species of AM fungi within a root system is needed for *Serenoa*. The presence and identity of spores (*Glomus*, *Gigaspora*, and *Scutelospora*) in adjacent soil does not confirm which AM fungi are present in colonized *Serenoa* roots.

The hyphae of AM fungi penetrate the root of *Serenoa* through a single epidermal cell and then form intracellular coils within epidermal, exodermal and hypodermal cells, similar to both *Arum*- and *Paris*-type mycorrhizae (Smith and Smith, 1997). The infection unit expands laterally after reaching the thinner-walled cells of the inner cortex. Intercellular hyphae predominate in this region where hyphae grow in the longitudinal intercellular spaces and lacunae. Thus, the bulk of colonizing root hyphae are of the *Arum*-type with arbuscules produced by hyphal branches that enter cortical cells. This form of root colonization is similar to that reported for wild temperate herbaceous monocots by Brundrett and Kendrick (1990b) and in cultivated *Allium porrum* (Brundrett et al., 1985). However, we did not observe hyphal projections (bobbits) described by Widden (1996) in some Liliaceae. In their literature review, Smith and Smith (1997: Table 1 Arecaceae) noted that both *Arum*- and *Paris*-types of AM have been reported in palms. Our observation of thin brown hyphae on *Serenoa* root surfaces that

form arbuscules in adjacent epidermal cells needs to be expanded and documented.

We could not determine the state of the exodermis at the time of earliest hyphal penetration because the roots could not be cleared adequately. Continued hyphal penetration occurs at some distance (5 mm or more) from the root tip, but we do not know if the exodermis was fully suberized in this region. Brundrett and Kendrick (1990a, b) found that most AM hyphal penetration of the epidermis in wild plants occurred before the exodermis was fully suberized, i.e. before paradermal walls were suberized. They and we assume that fungal penetration cannot occur after the exodermis and hypodermis are suberized and lignified, but this must be verified in palms. We are currently trying to improve techniques so that these critical stages of hyphal penetration can be described better.

It now appears that AM are widespread among palms (St. John, 1988; Zona, 1996), and a few studies have clearly shown enhanced nutrient uptake and growth promotion by AM colonization in several palms (Janos, 1977; Blal et al., 1990; Clement and Habte, 1995). The native soil is sandy, well-drained, and low in phosphorus. Thus, AM could be ecologically significant in phosphorus and water uptake (Smith and Read, 1997). However, the role of AM in the ecology of native palms and the significance of AM for the horticulture of palms will only be clarified by future descriptive and experimental studies.

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