

DIOECY HOTSPOTS IN SOUTHEAST FLORIDA, U.S.A., ESPECIALLY SAW PALMETTO (*SERENOA REPENS*, ARECACEAE) THICKETS

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ABSTRACT

A survey of woody marshland hummocks, of Saw Palmetto (*Serenoa repens*, Arecaceae) thickets, and of additional Southeast Florida habitats revealed multiple sites with dioecy rates of 50–100%, especially in the Saw Palmetto thickets. These rates exceeded any encountered for woody species in a literature review globally or for Florida. A particularly notable feature of the thicket sites is extreme thick low-elevation palm frond canopy coverage, consistent with the historical perspective that a benefit of dioecy is sexual selection for seed quality where harsh ecological filters limit establishment.

KEY WORDS: Breeding systems, dioecy rates, hummocks, seedling recruitment, shade, Florida wetland ecology

RESUMEN

Un estudio de los mogotes leñosos de las marismas, de los matorrales de palma enana americana (*Serenoa repens*, Arecaceae) y de otros hábitats del sureste de Florida reveló múltiples lugares con tasas de dioecia del 50–100%, especialmente en los matorrales de palma enana americana. Estas tasas superaban las encontradas para especies leñosas en una revisión bibliográfica global o para Florida. Una característica particularmente notable de los matorrales es la cobertura de copas de palmeras a baja altitud, lo que concuerda con la perspectiva histórica de que un beneficio de la dioecia es la selección sexual para la calidad de la semilla donde los filtros ecológicos limitan el establecimiento.

Dioecy may be defined as the separation of staminate (“male”) and pistillate (“female”) flowers on different individuals of angiosperm species. Dioecy has evolved convergently worldwide many times, turning up in roughly half of flowering plant families (Renner & Ricklefs 1995; Sakai et al. 1995; Bruijning et al. 2017). Renner and Ricklefs (1995) estimated about 6 percent of angiosperm species to be dioecious, although woody plants in hot climates tend toward higher rates of 19–35(40) percent, essentially congruent with past Florida reports (Table 1). Within tropical woody floras commonly perceived correlates of dioecy are: small pale flowers (Fox 1985; Vamasi et al. 2003; Chen & Li 2008; Held 2017) having generalist pollinators (Bawa 1994; Lin et al. 2019, but see Renner & Feil 1993 for conflicting views), and small fleshy ornithochorous fruits (Bawa 1980; Givnish 1982; Vamasi et al. 2003; Held 2017) containing few seeds (Flores & Schemske 1984; Rohwer 1986; Held 2017). Dioecy tends to be abundant among woody climbers (Bullock 1985; Renner & Ricklefs 1995). It also is frequent on oceanic islands, where isolation likely promotes its evolution (Carlquist 1965, 1974; Lin et al. 2019).

Hummocks in Southeast Florida seasonal depression marshes inventoried at local sites prior to the present project revealed over half (8/14) of woody hummock angiosperms (on at least 2 of 100 inventoried hummocks) as dioecious or partly so. (Recalling the correlates mentioned above, the woody hummocks clearly have a strongly ornithochorous seed rain from perched birds.)

Saw Palmetto (*Serenoa repens* (W. Bartram) Small, Arecaceae) thickets bordering and extending into the study marshes had even higher woody plant dioecy rates than the hummock islands. These observations prompted a survey of several local *Serenoa* thickets (Fig. 1), and for comparative context, of multiple adjacent as well as separate non-*Serenoa* habitats. The results revealed multiple sites showing woody plant dioecy rates above any uncovered in a literature review. The primary purpose of the present paper is to report the unprecedented high-dioecy rates and their ecological setting. A secondary purpose is to examine the present results with respect to historical views on the selective forces for dioecy.

TABLE 1. "Dioecy" rates by region, Part A Globally, Part B. Florida.

Authors	Habitat/Locality	Percent Dioecy Reported	Comments
Part A Globally			
Flores & Schemske 1984	Puerto Rico	18.7–20.2%	Trees and shrubs
Bullock 1985	Mexico	24%	Trees
Matallana et al. 2005	Brazil	35%	Restinga woody vegetation
Sobrevila & Arroyo 1982	Venezuela	31%	Trees in montane forest
Bawa & Opler 1975	Nigeria	40%	Trees
Lin et al. 2019	Taiwan	24(to nearly 50%)	Varied localities
Chen & Li 2008	Yunan, China	25–27%	Woody angiosperms
Vamosi & Queenborough 2010	Costa Rica	30.5%	
Vamosi 2006	Volta Velha Preserve, Brazil	28%	Woody species
Vamosi et al. 2008	Peru	26%	Woody species
Queenborough et al. 2009	Ecuador	29%	Woody species
Oliveira 1996	Central Brazil	28%	Cerrado Region, woody species, this the top rate encountered
Croat 1979	Barro Colorado Island, Costa Rica	21%	Medium to large trees
Part B Florida			
Tomlinson 1974	South Florida	ca. 30%	Including polygamodioecy
Gillespie 2008	Florida	26%	Dry-forest trees S FL
Armentano et al. 2002	S Florida	26%	Everglades Tree Islands
Present study broad regional rate	Florida counties S of Lake Okeechobee N shore	22% (for species and separately likewise 22% for genera)	Estimate prepared for the present project for trees, shrubs, woody climbers S of Lake Okeechobee, includes polygamodioecy. Data and method of compilation in Appendix Notes.

MATERIALS AND METHODS

Field Sites, field data, and supplementary materials.—The work took place in Palm Beach and Martin counties, Florida. The preliminary hummock inventory is in the Supplementary Materials (Rogers 2024 item A). Field sites are listed with geocoordinates (item B) and with field data (item C).

Taxonomy and terminology.—Taxonomy followed Wunderlin et al. (2024). Having thick lignified stems, *Areaceae* and *Smilax* (*Smilacaceae*) were treated as “ecologically woody” despite not having a vascular cambium. Due to cases of partial dioecy, of polygamodioecy, and of uncertain absolute dioecy, the inclusive designation “dioecious” is placed in quotes hereafter to embrace such cases. South Florida “dioecious” species are listed in the Appendix which also cites the bases for their determinations as “dioecious.”

Habitat inventories.—Assessing “dioecy” rates for each site (appearing in Fig. 3 in addition to list in supplementary data) consisted of recording every woody species encountered upon surveying the sites, then cross-checking the inventories with the “dioecy” data in the Appendix. (The author is generally familiar with the floras of most of the sites from several years leading class field trips, from additional projects there, and from a separate inventory of each site conducted for the present project.)

Serenoa repens is a generally shrub-sized palm, usually under 1.5–2.5(3) m tall. As Zona (1997) described, it “sometimes occurs in vast stands nearly excluding all other understory shrubs.” (In the study area the extensive stands are all or nearly all managed with prescribed burning, mechanical reduction, and sometimes herbicides. Such sites are not in the data.) In addition to the green canopy, the *Serenoa* thickets have layers of dead but intact fronds between the green layer and the ground. The inventoried thickets were typically under ca. one hectare each, although in all cases bordered entirely or in large part variably by large non-thicket marsh, pinewoods, or hammock natural areas. Every woody species penetrating the *Serenoa* thicket canopies was recorded within 1 m of each thicket edge along 60-m transects. The transect beginning point was taken

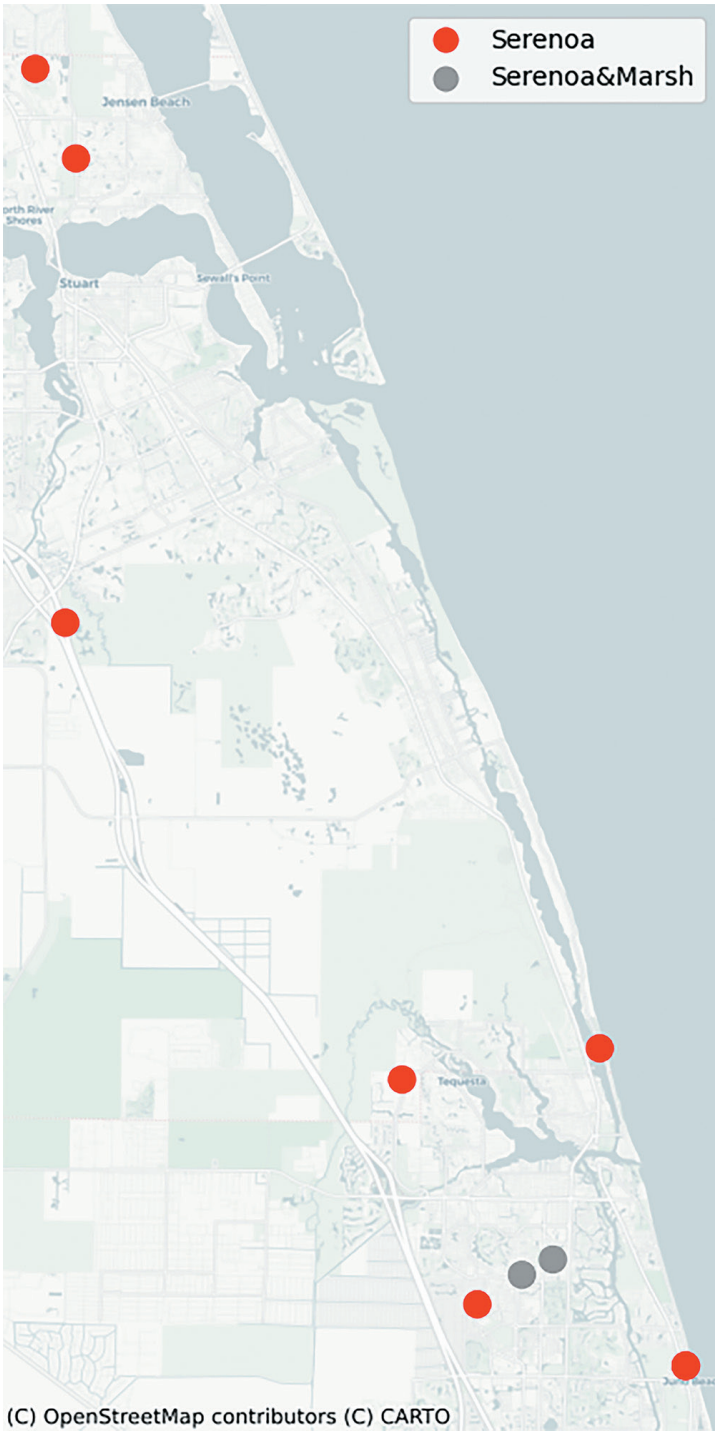


FIG. 1. *Serenoa* thickets, and two closely associated depression marshes. North (top) to south: Eagle Marsh, Green River, Halpatioke, Island Way (west dot), Blowing Rocks (east dot), Botanica (gray, to east), Paseos (gray, to west), Abacoa, Jupiter Dunes and Loggerhead (the last two neighboring sites under same dot).

to be the southeastern-most point of each thicket, proceeding then 60 m counterclockwise (northward/westward) insofar as physical circumstances permitted. Following the same protocol non-*Serenoa* woody habitats adjacent to the Abacoa, Halpatioke, and Island Way *Serenoa* thickets were tallied as comparative controls (Figs. 1, 3). To broaden the comparisons, additional sites having no connection to *Serenoa* thickets were also inventoried by recording every woody species present (Fig. 3).

Determinations of “dioecy.”—Dioecious species were pinpointed by consulting Tomlinson (1974), Gillespie (2008), Renner (2014), and the additional references cited in the resulting Appendix. Problem cases are discussed in the Appendix.

Light levels.—Light levels were recorded as lux, and graphed as transmittance (=measurement under canopy/measurement under open sky, Comeau 2000) measured using a Dr. Meter LX1330B light meter. The sensor on a coiled cable was placed face-up directly on the ground under whatever herbaceous growth and intact dead fronds occupied the designated spots. Thirty readings were recorded for each listed habitat type. For *Serenoa* thickets, the readings were taken at 2 m intervals measured along the perimeters, one m into the thickets from the edges. The marsh readings were taken at the same 2 m intervals. For hammock and pine-woods, the readings were taken along access pathways 3 m into the woods on both sides of 10 m intervals.

Software.—The graphs were prepared using R (R Core Team 2024) applying the magrittr and tidyverse libraries. Figure 1 was generated using Geopandas and the Matplot and Contextily libraries.

RESULTS

Percents “dioecy” for different *Serenoa* thickets recorded in the present study ranged from ca. 23% to 100% (Fig. 3). High rates were also in the depression marsh hummocks (mean “dioecy” = ca. 50% (8/14, 100 hummocks) and in and adjacent to most of the *Serenoa* thickets (Fig. 3). Species penetrating the *Serenoa* thicket canopies (Fig. 2) are listed in Table 2, with overall 30 species, 16 (53%) of them “dioecious.” The overall South Florida woody plant “dioecy” rate I calculated from recording all woody species South of the north edge of Lake Okeechobee was 22% calculated for species, as well as separately for genera (see notes following Appendix). Light transmittance levels under the canopy are compared with other local habitats in Figure 4.

DISCUSSION

General discussion.—Several of the rates reported in the present study, often exceeding 50% (Fig. 3), surpassed any discovered in the present literature review (generally well under 50%, Table 1), although the broad surveys in most literature reports would obscure localized single-habitat spikes such as those in the present project. As an exception to broadly compiled results, Lin et al. (2019) recorded single-site dioecy data on and near Taiwan. Even though they discussed the work mostly in terms of aggregate statistics, their scatterplots showed local samples with 40–nearly 50% dioecy.

In the present study the highest “dioecy” concentrated particularly in the *Serenoa* thickets on diverse substrates, including thickets on marsh/swamp margins (Paseos, Botanica, Eagle Marsh), on salty seashore (Blowing Rocks), on wet pinewoods (Halpatioke, Island Way), on a scrub-hammock ecotone (Juno Dunes), and on one scrub site (Loggerhead) (Fig. 3). (Even-aged burned *Serenoa* stands tended not to be penetrated by non-vining woody species other than varied small oaks (*Quercus* sp.) apparently rising from fire-resistant rootstocks.) Some non-*Serenoa* areas, mostly on wet sites, showed elevated (50%+) “dioecy” rates, collectively a little below the *Serenoa* thickets. These included the 100 woody marsh hummocks averaged, Delaware bald-cypress swamp, and the three non-*Serenoa* woody sites physically adjacent to *Serenoa* thickets (Fig. 3). High rates outside of thickets showed that the high thicket rates were not from *Serenoa* per se.

Selective forces for dioecy.—Two long-discussed non-mutually exclusive selective forces for dioecy are (1) suppression of inbreeding, and (2) sexual specialization, including reference to seedling recruitment in harsh habitats. General discussions of these dual outlooks are in Givnish (1982), Freeman et al. (1997), and Charlesworth (1999). An early discussion of the sexual selection viewpoint is in Darwin (1877), with more recent considerations in Barrett and Hough (2013), Réjou-Méchain and Cheptou (2015), Tonnabel et al.



Fig. 2. Overhead view of *Serenoa* thicket (Paseos site) with emerging woody vegetation, mostly *Ilex cassine* L. and *I. glabra* (L.) A. Gray (Aquifoliaceae).

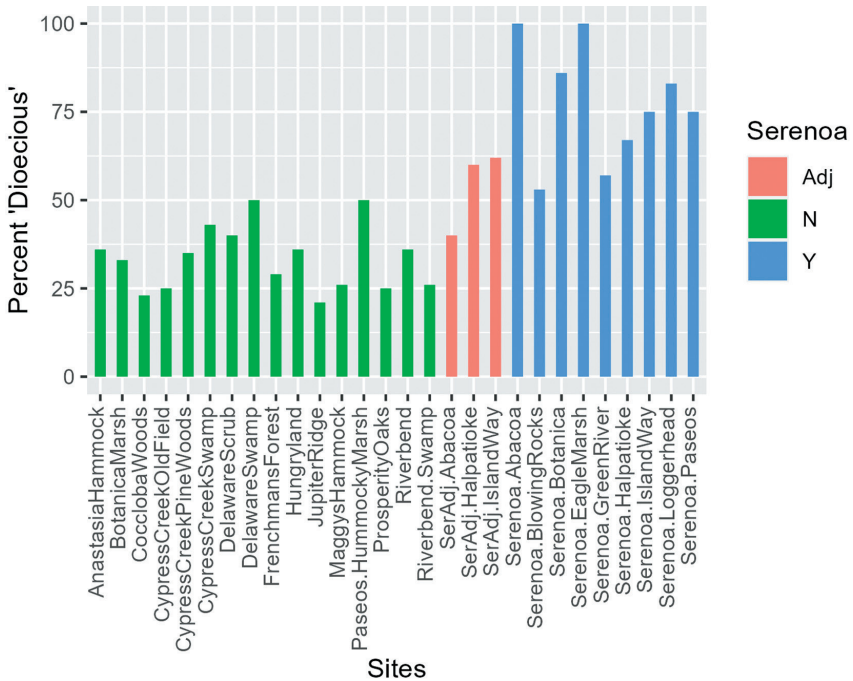


Fig. 3. Percents of woody (incl. *Smilax*) species “dioecious” at each study site. Blue bars = *Serenoa* thickets. Red bars = woody vegetation adjacent to *Serenoa* thicket, sampled in same fashion. Green bars = additional non-*Serenoa* sites. Anastasia represents a coastal hammock at Anastasia State Park in N Florida outside the study area. Delaware Scrub is the name of a local natural area, not a reference to the state. “*Serenoa*” along x axis = *Serenoa* thicket. “SerAdj” = adjacent to *Serenoa* thicket.

TABLE 2. Woody species penetrating *Serenoa* canopies. PD = present and "dioecious." PND = present and not "dioecious."

Species	A. Botanica Thickets bordering marsh	B. Juno Dunes Thicket on scrub adjoining hammock	C. Loggerhead Thicket on coastal scrub	D. Blowing Rocks Thicket on marine salt flat	E. Island Way Thicket along road in wet pinewoods	F. Abacoa Thicket in pine- woods	G. Eagle Marsh Thicket at edge of swamp	H. Green River Thicket along road at edge of wet pinewoods	I. Halpatioke Thicket in pinewoods	J. Paseos
<i>Acacia auriculiformis</i> A. Cunn. ex Benth. (Not native)										
<i>Baccharis</i> sp.			PD	PD						
<i>Bursera simaruba</i> (L.) Sarg.		PD		PD						
<i>Callitriche americana</i> L.			PD	PD		PND				
<i>Coccoloba uvifera</i> (L.) L.			PD	PND						
<i>Dalbergia ecastaphyllum</i> (L.) Taub.				PND						
<i>Ficus aurea</i> Nutt.				PND						
<i>Guajira discolor</i> (Spreng.) Little		PD		PD						
<i>Guilandina bonduc</i> L.		PD		PD						
<i>Hibiscus furcellatus</i> Desr.	PND									
<i>Ilex cassine</i> L.	PD				PD	PD				PD
<i>Ilex glabra</i> (L.) A. Gray	PD					PD	PD		PD	PD
<i>Lyonia fruticosa</i> (Michx.) G.S. Torr.					PND	PND	PND		PND	PND
<i>Lyonia lucida</i> (Lam.) K.Koch							PND			PND
<i>Metopium toxiferum</i> (L.) Krug. & Urb.		PD	PD							
<i>Morella cerifera</i> (L.) Small	PD				PD	PD	PD		PD	PD
<i>Myrsine cubana</i> A.DC.	PD									PD
<i>Parthenocissus</i> <i>quinquefolia</i> (L.) Planch.		PND	PND	PD		PD				
<i>Persea borbonia</i> (L.) Spreng.		PND		PND		PND				

TABLE 2. continued

Species	A. Botanica Thickets bordering marsh	B. Juno Dunes Thicket on scrub adjoining hammock	C. Loggerhead Thicket on coastal scrub	D. Blowing Rocks Thicket on marine salt flat	E. Island Way Thicket along road in wet pinewoods	F. Abacoa Thicket in pine- woods	G. Eagle Marsh Thicket at edge of swamp	H. Green River Thicket along road at edge of wet pinewoods	I. Halpatioke Thicket in pinewoods	J. Pascoos
<i>Pithecellobium keyense</i> Britton ex Britton & Rose				PND						
<i>Quercus geminata</i> Small		PND				PND			PND	
<i>Quercus laurifolia</i> Michx.										
<i>Randia aculeata</i> L.				PD						
<i>Rhodomyrtus tomentosa</i> (Aiton) Hassk. (Not native)					PND					
<i>Rhus copallinum</i> L.					PD	PD				
<i>Sabal palmetto</i> (Walter) Lodd. ex Schult. & Schult.f.					PND					
<i>Schinus terebinthifolia</i> Raddi (Not native)					PD			PD		
<i>Smilax</i> sp.	PD	PD	PD		PD	PD		PD	PD	PD
<i>Vitis</i> sp.	PD	PD			PD	PD	PD	PD	PD	PD
<i>Ximenesia americana</i> L.										
<i>Zanthoxylum fagara</i> (L.) Sarg.				PND						

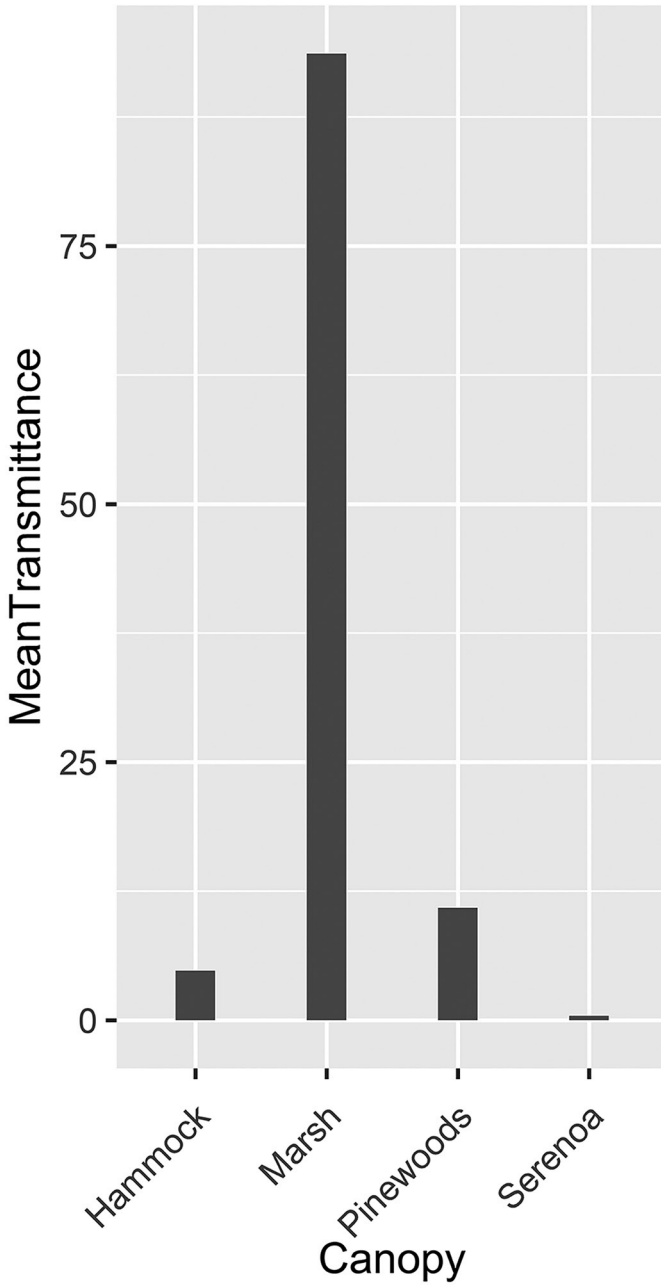


FIG. 4. Light transmittance under *Serenoa* thicket and additional canopies.

(2017), and Liu et al. (2021). Foreshadowing the present finding of high “dioecy” in high-stress habitats, Matallana et al. (2005) suspected “ecophysiological vigor” to be a competitive benefit of dioecious propagules in the oligotrophic Brazilian restinga, and Oliveira (1996) found dioecy associated with “dystrophic” conditions in the central Brazilian savanna (cerrado) woody vegetation.

The present results echoes prior workers finding high “dioecy” situated in sites consistent with sexual specialization facilitating seedling recruitment in harsh habitats. To the extent this is true, it exemplifies an environmental filter bringing together plants with similar traits conferring ability to recruit in the *Serenoa* thickets and the other elevated-dioecy habitat spots.

The obvious harshness in the *Serenoa* thickets is thick canopy coverage with deep shade (Fig. 4) coupled with altered spectral quality, rain penetration, evaporation, litter, soil biota, seed rain, and more, including direct blockage of rising seedlings. Adjacent sites and woody hummocks tending to have high rates were variably shaded (all sites woody, some hummocks covered with dense shrubs) and were all on wet substrates. It is not a contention of the present paper that dioecy *per se* is critical to assembling the thicket and other communities. It is likely, instead, that undetermined aspects of “seed quality” as a correlate of “dioecy” is in play.

AVENUES FOR FURTHER RESEARCH

The present study is a Florida step seeking relationships of plant breeding systems with ecological variables in small well-defined habitat sites, as opposed to the general trend of reporting dioecy rates for broad regions. In this connection, South Florida offers a heterogeneous patchwork of differentiated habitats. Indications of “seed quality” in prior publications, reappearing in the present work, invite additional study with respect to the level of connection, circumstances, mechanisms, teasing apart relevant variables, such as the roles of shade, poor edaphic conditions, and other stresses.

APPENDIX

"Dioecious" native woody species in South Florida in counties fully or mostly south of the north edge of Lake Okeechobee. For additional information see "Notes" below.

Species	Habitat	Dioecious?	Source for dioecy
<i>Alvaradoa amorphoides</i> Liebm.	hammock	Dioecious	Tomlinson (1974)
<i>Baccharis angustifolia</i> Michx.	marsh, beach, swale	Dioecious	Long and Lakela (1971)
<i>Baccharis dioica</i> Vahl	coastal hammock	Dioecious	Long and Lakela (1971)
<i>Baccharis glomeruliflora</i> Pers.	floodplain	Dioecious	Long and Lakela (1971)
<i>Baccharis halimifolia</i> L.	marsh, disturbed sites	Dioecious	Long and Lakela (1971)
<i>Batis maritima</i> L.	salt marsh, mangroves	Dioecious	Long and Lakela (1971)
<i>Berchemia scandens</i> (Hill) K. Koch	wet hammock, floodplain, wet flatwoods	Dioecious	Long and Lakela (1971)
<i>Bursera simaruba</i> (L.) Sarg.	hammock, midden	Dioecious	Tomlinson (1974)
<i>Casasia clusiifolia</i> (Jacq.) Urb.	hammock	Dioecious	Tomlinson (1974)
<i>Ceratiola ericoides</i> Michx.	scrub	Dioecious	Gibson and Menges (1994)
<i>Citharexylum spinosum</i> L.	pineland, hammock	Dioecious	Tomlinson (1974)
<i>Clusia rosea</i> Jacq.	hammock	Dioecious but nativity not certain	Tomlinson (1974). Wunderlin et al. (2024) listed this species as native, with doubts.
<i>Coccoloba diversifolia</i> Jacq.	hammock	Dioecious	Tomlinson (1974)
<i>Coccoloba uvifera</i> (L.) L.	hammock, beach strand	Dioecious or polygamodioecious	Tomlinson (1974), Madriz and Ramírez (1997)
<i>Conocarpus erectus</i> L.	tidal swamp	Dioecious	Tomlinson (1974)
<i>Consolea corallicola</i> Small Strittmatter et al. (2008)	seashore	Dioecious	Maguire et al. (2021)
<i>Diospyros virginiana</i> L.	flatwoods, hammock, sandhill	Dioecious	Tomlinson (1974)
<i>Dodonaea elaeagnoides</i> Rudolph ex Ledeb. & Alderst.	hammock, strand	Predominantly Dioecious	Gann et al. (2023)
<i>Dodonaea viscosa</i> Jacq.	dune, coastal pineland, hammock	Dioecious	Tomlinson (1974)
<i>Drypetes diversifolia</i> Krug & Urb.	hammock	Dioecious	Tomlinson (1974)
<i>Drypetes lateriflora</i> (Sw.) Krug & Urb.	hammock	Dioecious	Tomlinson (1974)
<i>Exothea paniculata</i> (Juss.) Radlk.	hammock, midden	Dioecious	Tomlinson (1974)
<i>Forestiera segregata</i> (Jacq.) Krug & Urb.	hammock, marsh, pineland, midden	Dioecious or mostly so	Tomlinson (1974)
<i>Fraxinus caroliniana</i> Miller	swampy wetland	Dioecious	Nesom (2010)
<i>Guapira discolor</i> (Spreng.) Little	hammock, pineland	Dioecious	Spellenberg (2003)
<i>Guapira obtusata</i> (Jacq.) Little	hammock	Dioecious	Spellenberg (2003)
<i>Guilandina bonduc</i> L.	coastal strand	Dioecious	Gillis and Proctor (1974) (See text for comment on <i>Guilandina major</i>)
<i>Gyminda latifolia</i> (Sw.) Urb.	hammock	Dioecious	Gillespie (2008)
<i>Heterosavia bahamensis</i> (Britton) Petra Hoffm.	hammock	Dioecious	Tomlinson (1974)
<i>Ilex ambigua</i> Torr.	hammock, scrub, sandhill	Dioecious or polygamodioecious	Wunderlin and Poppleton (1977) and Godfrey and Wooten (1981) described Florida <i>Ilex</i> species collectively as polygamodioecious.
<i>Ilex cassine</i> L.	hammock, flatwoods, pond margin, swamp	Dioecious or polygamodioecious	Wunderlin and Poppleton (1977) and Godfrey and Wooten (1981)
<i>Ilex glabra</i> (L.) A. Gray	bog, flatwoods, marsh margin, swales,	Dioecious or polygamodioecious	Wunderlin and Poppleton (1977), Buckley and Avila-Sakar (2013)
<i>Ilex krugiana</i> Loes.	pineland	Dioecious or polygamodioecious	Wunderlin and Poppleton (1997)
<i>Ilex opaca</i> Aiton	hammock	Dioecious or polygamodioecious	Wunderlin and Poppleton (1977) and Godfrey and Wooten (1981), Carr (1991)
<i>Metopium toxiferum</i> (L.) Krug & Urb.	hammock, pineland	Dioecious	Tomlinson (1974)

APPENDIX continued

Species	Habitat	Dioecious?	Source for dioecy
Morella cerifera (L.) Small	hammock, swamp, cypress dome, flatwoods, forest, marsh	Dioecious	Tomlinson (1974)
Myrsine cubana A.DC.	hammock	Polygamodioecious	Tomlinson (1974)
Nyssa biflora Walter	swamp	Polygamodioecious	Balestri (2015) but see text for reservations
Picramnia pentandra Sw.	hammock	Dioecious	Tomlinson (1974)
Pisonia aculeata L.	hammock	Dioecious	Spellenberg (2003)
Pisonia rotundata Griseb.	hammock, pineland	Dioecious	Tomlinson (1974)
Randia aculeata L.	hammock	Mostly dioecious	Tomlinson (1974)
Rhus copallinum L.	sandhill, flatwoods, hammock	Dioecious or possibly sometimes polygamodioecious	Brizicky (1962)
Salix caroliniana Michx.	wet habitats	Dioecious	Tomlinson (1974)
Schaefferia frutescens Jacq.	hammock	Dioecious	Tomlinson (1974)
Simarouba glauca DC.	hammock	Dioecious	Tomlinson (1974)
Smilax auriculata Walter	sandhill, flatwoods, hammock, thicket	Dioecious	Ferrufino-Acosta (2010) generically for <i>Smilax</i>
Smilax bona-nox L.	flatwoods, floodplain, hammock, thicket	Dioecious	Ferrufino-Acosta (2010)
Smilax havanensis Jacq.	pineland, hammock	Dioecious	Ferrufino-Acosta (2010)
Smilax laurifolia L.	swamp, wet flatwoods	Dioecious	Ferrufino-Acosta (2010)
Smilax tannoides L.	moist hammock	Dioecious	Ferrufino-Acosta (2010)
Toxicodendron radicans (L.) Kuntze	hammock, forest, swamp, disturbed places	Dioecious	Gillis (1971)
Vitis aestivalis Michx.	hammock	Dioecious or polygamodioecious	Vanozzi et al. (2022) generically for <i>Vitis</i> , also Long and Lakela (1971), Wan et al. (2013), Kevan et al. (1988)
Vitis cinerea (Engelm.) Engelm. ex Millardet	hammock	Dioecious or polygamodioecious	Vanozzi et al. (2022), also Long and Lakela (1971), Wan et al. (2013), Barrett (1957)
Vitis rotundifolia Michx.	hammock, scrub	Dioecious or polygamodioecious	Vanozzi et al. (2022), also Long and Lakela (1971), Wan et al. (2013), Kevan et al. (1988)
Vitis shuttleworthii House	hammock	Dioecious or polygamodioecious	Vanozzi et al. (2022), also Long and Lakela (1971), Wan et al. (2013)
Zanthoxylum clava-herculis L.	hammock	Dioecious or polygamodioecious	Porter (1976) generically for <i>Zanthoxylum</i> (including examinations of all the species listed here), Correll and Correll (1982)
Zanthoxylum spinosum (Sw.) Sw.	hammock	Dioecious or polygamodioecious	Porter (1976), Correll and Correll (1982)
Zanthoxylum fagara (L.) Sarg.	hammock	Dioecious or polygamodioecious	Tomlinson (1974), Correll and Correll (1982)
Zanthoxylum flavum Vahl	hammock	Dioecious or polygamodioecious	Porter (1976), Correll and Correll (1982)

Appendix Notes:

The “dioecy” (see definition in text) estimate of 22% for South Florida was calculated during the present study to embrace every native woody species and every documented “dioecious” species in South Florida. A full list of native species in counties entirely or mostly south of the north edge of Lake Okeechobee was downloaded from the Wunderlin et al. (2024) website. Distinguishing the woody representatives there was based on designation as trees or shrubs in Long and Lakela (1971), or in Godfrey and Wooten (1981), or occasionally in additional resources. Determining “woodiness” for climbers was based on descriptions in the same references, on personal field experience, and on examination of online photographs. Fruit types, fleshiness, approximate size classes (“pea,” “grape,” “plum”), and numbers of “seeds” for every woody species in the list were determined from Long and Lakela (1971) supplemented occasionally with additional references and with field experience. “Dioecious” species listed above were pinpointed by consulting Tomlinson (1974), Gillespie (2008),

Renner (2014), and additional references cited in that table. This analysis yielded 61/280 (22%) South Florida woody angiosperm species (including "*Smilax* sp.") as "dioecious." Several genera in the study area, including dioecious genera (e.g., *Baccharis*, *Smilax*, *Vitis*), have multiple local species. The separate generic-level dioecy rate matched the species-level rate of 22% (38/173).

"Dioecy" problem cases:

"Dioecy" is often difficult to ascribe definitively to species. In addition to the sampling problems of widespread species traditionally studied pressed in herbaria, "dioecy" may be incomplete, cryptic, regionally varied, confounded by facultative apomixis, or labile. *Acer rubrum* L. (Aceraceae) across most of its range it is usually described as dioecious, as polygamodioecious, or as partly dioecious (Tomlinson 1974; Primack & McCall 1986; Renner et al. 2007), but for South Florida Tomlinson (1974) categorized it as "unequivocally" monoecious. "Dioecious" non-native woody species encountered during the field work included *Schinus terebinthifolia* Raddi (Anacardiaceae, Hogg et al. 2020 for its "dioecy"), and *Anacardiopsis cupanioides* (A. Rich.) Radlk. (Sapindaceae, inconsistently "dioecious" fide Adam & Williams 2001). *Guilandina major* (Medik.) Small (Fabaceae) is probably "dioecious," given the "dioecy" of its similar congener *G. bonduc* but unconfirmed. Reportedly polygamodioecious *Nyssa biflora* (Balestri 2015; Long & Lakela 1971; Godfrey & Wooten 1981) is included tentatively as "dioecious," but requires further study. Sacande and Vautier (2006) reported *Ximenia americana* L. (Ximeniaceae) in Africa as dioecious but it has perfect flowers, at least in the study area (pers. obs.)

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REFERENCES

- ADAM, P. & G. WILLIAMS. 2001. Dioecy, self-compatibility and vegetative reproduction in Australian subtropical rainforest trees and shrubs. *Cunninghamia* 7:89–100.
- ARMENTANO, T., D. JONES, M. ROSS, & B. GAMBLE. 2002. Vegetation pattern and process in tree islands of the southern Everglades and adjacent areas. In: F. Sklar & A. van der Velk, eds. *Tree islands of the Everglades*. iv + 541 p. Kluwer Academic Publishers, Dordrecht, Boston and London, U.K. Pp. 225–281.
- BALESTRI, F. 2015. Horticultural potential of *Nyssa biflora* Walt. (swamp tupelo). Masters Thesis. Iowa State University. 81 p.
- BARRETT, H. 1957. *Vitis cinerea* as a source of desirable characters in grape breeding. *Proc. Amer. Soc. Hort. Sci.* 70:165–168.
- BARRETT S. & J. HOUGH. 2013. Sexual dimorphism in flowering plants. *J. Exp. Bot.* 64:67–82.
- BAWA, K. 1980. Evolution of dioecy in flowering plants. *Annual Rev. Ecol. Syst.* 11:15–39.
- BAWA, K. 1994. Pollinators of tropical dioecious angiosperms: a reassessment? No, not yet. *Amer. J. Bot.* 81:456–460.
- BAWA, K. & P. OPLER. 1975. Dioecism in tropical forest trees. *Evolution* 29:167–179.
- BRIZICKY, G. 1962. The genera of Anacardiaceae in the southeastern United States. *J. Arnold Arbor.* 43: 359–375.
- BRUIJNING, M., M. VISSER, H. MULLER-LANDAU, S. WRIGHT, L. COMITA, S. HUBBELL, HANS DE KROON, & E. JONGEJANS. 2017. Surviving in a cosexual world: A cost-benefit analysis of dioecy in tropical trees. *Amer. Naturalist* 189:297–314.
- BUCKLEY, N. & G. AVILA-SAKAR. 2013. Reproduction, growth, and defense trade-offs vary with gender and reproductive allocation in *Ilex glabra* (Aquifoliaceae). *Amer. J. Bot.* 100:357–364.
- BULLOCK, S. 1985. Breeding systems in the flora of a tropical deciduous forest in Mexico. *Biotropica* 17:287–301.
- CARLQUIST, S. 1965. *Island life: A natural history of the islands of the World*. Natural History Press, Garden City, New Jersey, U.S.A.
- CARLQUIST, S. 1974. *Island biology*. xii + 660 pp. Columbia University Press, New York, U.S.A.
- CARR, D. 1991. Sexual dimorphism and fruit production in a dioecious understory tree, *Ilex opaca* Ait. *Oecologia* 85:381–388.
- CHARLESWORTH, D. 1999. Theories of the evolution of dioecy. In: M. Geber, T. Dawson, and L. Delph, eds. *Gender and sexual dimorphism in flowering plants*. Springer, Berlin, & Heidelberg. Pp. 33–60. https://doi.org/10.1007/978-3-662-03908-3_2
- CHEN, X.-S. & Q.-J. LI. 2008. Sexual systems and ecological correlates in an azonal tropical forest, SW China. *Biotropica* 40:160–167.
- COMEAU, P. 2000. Measuring light in the forest. *British Columbia Minist. Forests Extens. Note* 42:1–7.
- CORRELL, D. & H. CORRELL. 1982 [reprinted 1996]. *Flora of the Bahama Archipelago*. Gantner, Vaduz, Germany.
- CROAT, T. 1979. The sexuality of the Barro Colorado Island flora (Panama). *Phytologia* 42:319–348.
- DARWIN, C. 1877. The different forms of flowers on plants of the same species. John Murray, London, UK.

- FERRUFINO-ACOSTA, L., 2010. Taxonomic revision of the genus *Smilax* (Smilacaceae) in Central America and the Caribbean Islands. *Willdenowia* 40:227–280.
- FLORES, S. & D. SCHEMSKE. 1984. Dioecy and monoecy in the flora of Puerto Rico and the Virgin Islands: ecological correlates. *Biotropica* 16:132–139.
- FOX J. 1985. Incidence of dioecy in relation to growth form, pollination and dispersal. *Oecologia*. 67:244–249.
- FREEMAN, D., J. DOUST, A. EL-KEBLAWY, K. MIGLIA, & E. MCARTHUR. 1997. Sexual specialization and inbreeding avoidance in the evolution of dioecy. *Bot. Rev. (Lancaster)* 63:65–92.
- GANN G., C. ABBOTT C., K. HINES, & COLLABORATORS. 2005–2023. Natives for your neighborhood. The Institute for Regional Conservation. Delray Beach, Florida. Website <https://www.regionalconservation.org/beta/nfyn/default.asp> [accessed 1/22/2024].
- GIBSON, D. & E. MENGES. 1994. Population structure and spatial pattern in the dioecious shrub *Ceratiola ericoides*. *J. Veg. Sci.* 5:337–346.
- GILLESPIE, T. 2008. Sexual systems and fruit types in native dry forest trees in South Florida. *Florida. Sci.* 71:370–382.
- GILLIS, W. 1971. The systematics and ecology of poison-ivy and the poison-oaks (*Toxicodendron*, Anacardiaceae). *Rhodora* 73:72–159 (with subsequent installments).
- GILLIS, W. & G. PROCTOR. 1974. *Caesalpinia* subgenus *Guilandina* in the Bahamas. *J. Arnold Arbor.* 55:425–430.
- GIVNISH, T. 1982. Outcrossing versus ecological constraints in the evolution of dioecy. *Amer. Naturalist* 119:849–865.
- GODFREY, R. & J. WOOTEN. 1981. Aquatic and wetland plants of Southeastern United States. Dicotyledons. Univ. Georgia Press, Athens, Georgia, U.S.A.
- HELD, B. 2017. Ecological correlates with dioecy in the flora of a tropical premontane wet forest in Costa Rica. Undergraduate Distinction Papers. 53.
- HOGG, B., K. STOKES, M. RAYAMAJHI, J. GEIGER, & P. PRATT. 2020. Foliar lifespan, phenology and seasonal dynamics of the invasive shrub *Schinus terebinthifolia*. *Weed Res.* 60:212–220.
- KEVAN, P., D. BLADES, U. POZLUŠZNY, & J. AMBROSE. 1988. Pollen dimorphism and dioecy in *Vitis aestivalis*. *Vitis* 27:143–146.
- LIN, H.-Y., Y.-H. TSENG, C.-F. HSIEH, & J.-M. HU. 2019. Geographical distribution of dioecy and its ecological correlates based on fine-scaled species distribution data from a subtropical island. *Ecol. Res. (Tokyo)* 35:170–181.
- LIU, M., H. KORPELAINEN, & C. LI. 2021. Sexual differences and sex ratios of dioecious plants under stressful environments. *J. Pl. Ecol.* 14:920–933.
- LONG, R. & O. LAKELA. 1971. A flora of Tropical Florida. Univ. Miami Press, Coral Gables, Florida, U.S.A.
- MADRIZ, R. & N. RAMÍREZ. 1996, 1997. Biología reproductiva de *Coccoloba uvifera* (Polygonaceae) una especie poligamodioica. *Rev. Biol. Trop.* 44:105–115.
- MAGUIRE, L., D. BARRIOS, E. DIAZ, B. ZUMWALDE, W. TESTO, & V. NEGRÓN-ORTIZ. 2021. Pleistocene aridification underlies the evolutionary history of the Caribbean endemic, insular, giant *Consolea* (Opuntioideae). *Amer. J. Bot.* 108:1–16.
- MATALLANA, G., T. WENDT, D ARAUJO, & F. SCARANO. 2005. High abundance of dioecious plants in a tropical coastal vegetation. *Amer. J. Bot.* 92:1513–1519.
- NESOM, G. 2010. Taxonomy of the water ashes: *Fraxinus caroliniana*, *F. cubensis*, and *F. pauciflora* (Oleaceae). *Phytoneuron* 2010-39:1–13.
- OLIVEIRA, P. 1996. Dioecy in the cerrado vegetation of Central Brazil. *Flora* 191:235–243.
- PORTER, D. 1976. *Zanthoxylum* (Rutaceae) in North America North of Mexico. *Brittonia* 28:443–447.
- PRIMACK R. & C. MCCALL. 1986. Gender variation in a Red Maple population (*Acer rubrum*; Aceraceae): a seven-year study of a “polygamodioecious” species. *Amer. J. Bot.* 73:1239–1248.
- QUEENBOROUGH, S., S. MAZER, S. VAMOSI, N. GARWOOD, R. VALENCIA, & R. FRECKLETON. 2009. Seed mass, abundance and breeding system among tropical forest species: do dioecious species exhibit compensatory reproduction or abundances? *J. Ecol.* 97:555–566.
- R CORE TEAM. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- RÉJOU-MÉCHAIN, M. & P. CHEPTOU. 2015. High incidence of dioecy in young successional tropical forests. *J. Ecol.* 103:725–732.
- RENNER, S. 2014. The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *Amer. J. Bot.* 101:1588–1596.
- RENNER, S. & J. FEIL. 1993. Pollinators of tropical dioecious angiosperms. *Amer. J. Bot.* 80:1100–1107.
- RENNER, S. & R. RICKLEFS. 1995. Dioecy and its correlates in the flowering plants. *Amer. J. Bot.* 82:596–606.

- RENNER, S., L. BEENKEN, G. GRIMM, A. KOCYAN, & R. RICKLEFS. 2007. The evolution of dioecy, heterodichogamy, and labile sex expression in *Acer*. *Evolution* 61:2701–2719.
- ROGERS, G. 2024. "Data for dioecy hotspots in southeast Florida, especially Saw Palmetto (*Serenoa repens*) thickets." Mendeley Data, V1, doi: 10.17632/jt9frcrgfm.1
- ROHWER, J. 1986. Some aspects of dioecy in *Ocotea* (Lauraceae). *Pl. Syst. Evol.* 152:47–48.
- SACANDE, M. & H. VAUTIER. 2006. *Ximenia americana* L. *Univ. Copenhagen Seed Leaflet*. 112.
- SAKAI, A., W. WAGNER, D. FERGUSON & D. HERBST. 1995. Origins of dioecy in the Hawaiian flora. *Ecology* 76:2517–2529.
- SOBREVILA, C. & M. ARROYO. 1982. Breeding systems in a monotane tropical cloud forest in Venezuela. *Pl. Syst. Evol.* 140:19–37.
- SPELLENBERG, R. 2003. In: *Flora of North America* Editorial Committee, eds. 1993+. *Flora of North America North of Mexico* [Online]. 22+ vols. New York, U.S.A and Oxford, UK. Vol. 4. <http://floranorthamerica.org/Nyctaginaceae> [accessed 6/7 2023].
- STRITTMATTER, L., R. HICKEY, & V. NEGRÓN-ORTIZ. 2008. Heterochrony and its role in sex determination of cryptically dioecious *Consolea* (Cactaceae) staminate flowers. *Bot. J. Linn. Soc.* 156:305–326.
- TOMLINSON, P. 1974. Breeding mechanisms in trees native to tropical Florida—a morphological assessment. *J. Arnold Arb.* 55:269–290.
- TONNABEL, J., P. DAVID, & J. PANNELL. 2017. Sex-specific strategies of resource allocation in response to competition for light in a dioecious plant. *Oecologia* 185:675–686.
- VAMOSI, J., S. OTTO, & S. BARRETT. 2003. Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *J. Evol. Biol.* 16:1006–1018.
- VAMOSI, S. 2006. A reconsideration of the reproductive biology of the Atlantic forest in the Volta Velha reserve. *Biodivers. & Conservation* 15:1417–1424.
- VAMOSI, S. & S. QUEENBOROUGH. 2010. Breeding systems and phylogenetic diversity of seed plants along a large-scale elevational gradient. *J. Biogeogr.* 37:465–476.
- VAMOSI, S., S. MAZER, & F. CORNEJO. 2008. Breeding systems and seed size in a Neotropical flora: testing evolutionary hypotheses. *Ecology* 89:2461–2472.
- VANOZZI, A., F. PALUMBO, M. LUCCHINI, & G. BARCACCIA. 2022. Dioecy in flowering plants: From the first observations of Prospero Alpini in the XVI Century to the most recent advances in the Genomics Era. *Agriculture* 12:<https://doi.org/10.3390/agriculture12030364>.
- WAN, Y., H. SCHWANINGER, A. BALDO, J. LABATE, G.-Y. ZHONG, & C. SIMON. 2013. A phylogenetic analysis of the grape genus (*Vitis* L.) reveals broad reticulation and concurrent diversification during Neogene and Quaternary climate change. *Evol. Biol.* 13:141. <https://doi.org/10.1186/1471-2148-13-141>.
- WUNDERLIN, R., B. HANSEN, A. FRANCK, & F. ESSIG. 2024. Atlas of Florida plants (<http://florida.plantatlas.usf.edu/>). [S.M. Landry and K.N. Campbell (application development), USFWater Institute.] *Inst. Syst. Bot., Univ. South Florida, Tampa, U.S.A.*
- WUNDERLIN, R. & J. POPPLETON. 1977. The Florida species of *Ilex* (Aquifoliaceae). *Florida Sci.* 40:7–21.
- ZONA, S. 1997. The genera of Palmae (Arecaceae) in the southeastern United States. *Harvard Pap. Bot.* 2:71–107.