NOTES ON THE NATURAL HISTORY OF *STILLINGIA AQUATICA* (EUPHORBIACEAE): WITH SPECIAL ATTENTION TO REPRODUCTIVE BIOLOGY

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ABSTRACT

Stillingia aquatica, a wetland shrub in the Southeastern U.S., was profiled in Southeast Florida from a natural history standpoint. The stem has exceptionally lightweight wood in common with other periodically root-inundated woody plants. Pseudowhorled tufts of conspicuous yellow leaves subtend the similarly colored spikelike thyrsoid inflorescences. The plants are monoecious, self-compatible, protogynous with respect to inflorescences, and with a mixed mating system. After a pistillate-only phase, pistillate and staminate phases overlap in time, and are positioned in close physical proximity within inflorescences. Then follows a prolonged phase of only staminate flowers plus maturing fruits. The inflorescences attract ants, bees, and especially abundant wasps, switching from mixed bees and wasps in the dry season to essentially just wasps in the wet season. Wind-pollination is minimal to none. Ants are often abundant in the inflorescences and believed to contribute to geitonogamy but are not necessary for fruitset. Agamospermy is none to negligible. The seeds often fail, with the failure rates varying between populations and between individual plants.

Key Words: caruncle, depression marsh, elaiosome, embryo abortion, Euphorbiaceae, Hippomaneae, geitonogamy, mixed mating system, protogyny

RESUMEN

Stillingia aquatica, un arbusto de humedales del sureste de los Estados Unidos, fue descrito en el sureste de Florida desde el punto de vista de su biología. El tallo tiene madera excepcionalmente ligera, al igual que otras plantas leñosas con raíces periódicamente inundadas. Grupos de hojas amarillas conspicuas y pseudoverticiladas subtienden las inflorescencias tirsoides, con forma de espiga de coloración similar. Con respecto a las inflorescencias, son plantas monoicas, autocompatibles, protoginas, y con un sistema de cruzamiento mixto. Después de una fase de solo pistiladas, las fases de pistilada y estaminada se superponen en el tiempo, y se ubican en estrecha proximidad física en las inflorescencias. Luego sigue una fase prolongada de solo flores estaminadas y frutos maduros. Las inflorescencias atraen hormigas, abejas y especialmente abundantes avispas, cambiando de abejas y avispas en la estación seca a esencialmente solo avispas en la estación húmeda. La polinización por el viento es mínima o nula. Las hormigas son a menudo abundantes en las inflorescencias y se cree que contribuyen a la geitonogamia, pero no son necesarias para la fructificación. La agamospermia es nula o despreciable. Las semillas a menudo fracasan, pero las tasas de fracaso varían entre las poblaciones y entre las plantas individuales.

INTRODUCTION

As Webster (1967) stated in the Generic Flora of the Southeastern United States, "almost nothing is known of the reproductive biology of the species of *Stillingia*." This has not changed by 2021. The goal of the present study has been to narrow that gap with a reproductive profile of *Stillingia aquatica* Chapm. augmented by limited attention to vegetative features.

The most recent full revision of *Stillingia* dates back to Rogers (1951), with updates in Esser (2012) and Huft (2016). Wurdack et al. (2005) placed *Stillingia* in Euphorbiaceae subfamily Euphorbioideae, tribe Hippomaneae. Members of subfamily Euphorbioideae characteristically have white latex, nonarticulated laticifers, flowers with neither disk nor petals, and distinctive molecular characters. Species of tribe Hippomaneae are mostly woody, and have staminodes and pistillodes absent, stigmas not cleft, inflorescences thyrsoid and elongate with pistillate flowers basal, numerous staminate cymules apically, small calyces, and immature flowers appressed to the inflorescence axis and covered by comparatively large and often glandular

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bracts. (The subfamily and tribal characteristics are from Esser 2012.) Wurdack et al. (2005) determined prior circumscriptions of tribe Hippomaneae and *Stillingia* to be paraphyletic. They placed *Stillingia* in a neotropical clade along with *Adenopeltis*, *Spegazziniophytum*, and *Sapium* s.s.

Stillingia consists of about 28 generally woody species distributed mostly from the southern U.S. through South America, with a small presence in the Indian Ocean, Oceania, and China (Esser 2012; Huft 2016; Li et al. 2017). Several species are narrow endemics. Most tend toward dry conditions, and some are succulents. *Stillingia aquatica* is the only aquatic species.

A conspicuous characteristic of *Stillingia* is an element referred to as the carpidiophore or gynobase, a stiff three-pronged structure at the capsule base remaining on the pedicel after dehiscence (Fig. 1A). *Adenopeltis* and *Gradyana*, also in Hippomaneae, have a carpidiophore as well. Noteworthy, although not unique to *Stillingia,* are large goblet-shaped nectar glands on the inflorescence bracts.

Two species live in South Florida, *Stillingia aquatica* and *S. sylvatica* L. The latter, "queen's delight," ranges across much of the southern U.S. Rogers (1951) suggested introgression between *S. sylvatica* and *S. aquatica*. *Stillingia sylvatica* differs by preferring upland habitats, by being a short-lived rhizomatous sprawling subshrub (vs. a long-lived woody taprooted shrub), by tending toward larger seeds, and by lacking conspicuous lenticels (Rogers 1951; Webster 1967).

Stillingia aquatica (Fig. 1B), water-toothleaf, corkwood, ranges from South Carolina to Alabama and South Florida in open seasonally inundated marshes and shores, and when not inundated, in perpetually moist soil. In South Florida it is a prominent component of depression marshes mostly flooded during the summer-autumn rainy months and mostly not inundated during the drier late winter-spring months. *Stillingia aquatica* and *Hypericum fasciculatum* Lam. are the main woody residents of the depression marshes in the study area, accompanied variably by *Ilex cassine* L., *Morella cerifera* (L.) Small, and *Cephalanthus occidentalis* L. rising above a mixed wetland herbaceous layer with abundant periphyton. *Stillingia aquatica* in the study area is most abundant where the highwater level is ca. 15–25 cm, and has not been observed where that depth exceeds 40 cm.

MATERIALS AND METHODS

Several sites in and near Jupiter, Palm Beach County, Florida, were data sources: Botanica Wetland Preserve (an exceptionally large population in an extensive depression marsh), C-18 (a small population marginal in a large depression marsh at the NW corner of the C-18 Canal and Beeline Highway), Hungryland (a vast marsh within the John C. and Mariana Jones/Hungryland Wildlife and Environmental Area), Canal Road (a small population in a ditch along a dirt maintenance road berm within a slash pine wet savanna, part of the Mariana Jones/Hungryland Wildlife and Environmental Area), Jones Creek Headwaters Preserve (small population in an intermittently flooded depression surrounded mostly by a wet meadow and slash pine woods), Pine Glades Natural Area (small population in a small depression pond surrounded mostly by slash pine woods), and Cypress Creek (a cluster of approximately seven individuals in a bald cypress swamp). The sites were free of standing water during the late winter and spring 2020 until all flooded in the last days of May. Except for the Jones Creek site, they all remained flooded from late May through December 2020, with water levels dropping sharply in January 2021.

Pollen Trapping.—Pollen trapping was applied to assess wind pollination. The traps were microscope slides coated with petroleum jelly on one side in a patch approximating a 22 × 22 mm microscope coverslip. The slides were suspended to simulate natural inflorescence spacing at the Botanica site during abundant flowering. Two different spots were sampled, one before inundation, the other in standing water.

Each slide after trapping was heated gently, and a drop or two of glycerine added to soften and spread the jelly smoothly before adding a coverslip. The entire coverslip area was searched using a compound microscope at 400× in successive linear searches across the whole area under the coverslip. A comparison slide was prepared with *Stillinga* pollen added manually and otherwise treated in the same fashion. The dates of pollen trapping were May 14–23, 2020, pre-inundation, then repositioned post-inundation May 30–Jun 2, 2020. The

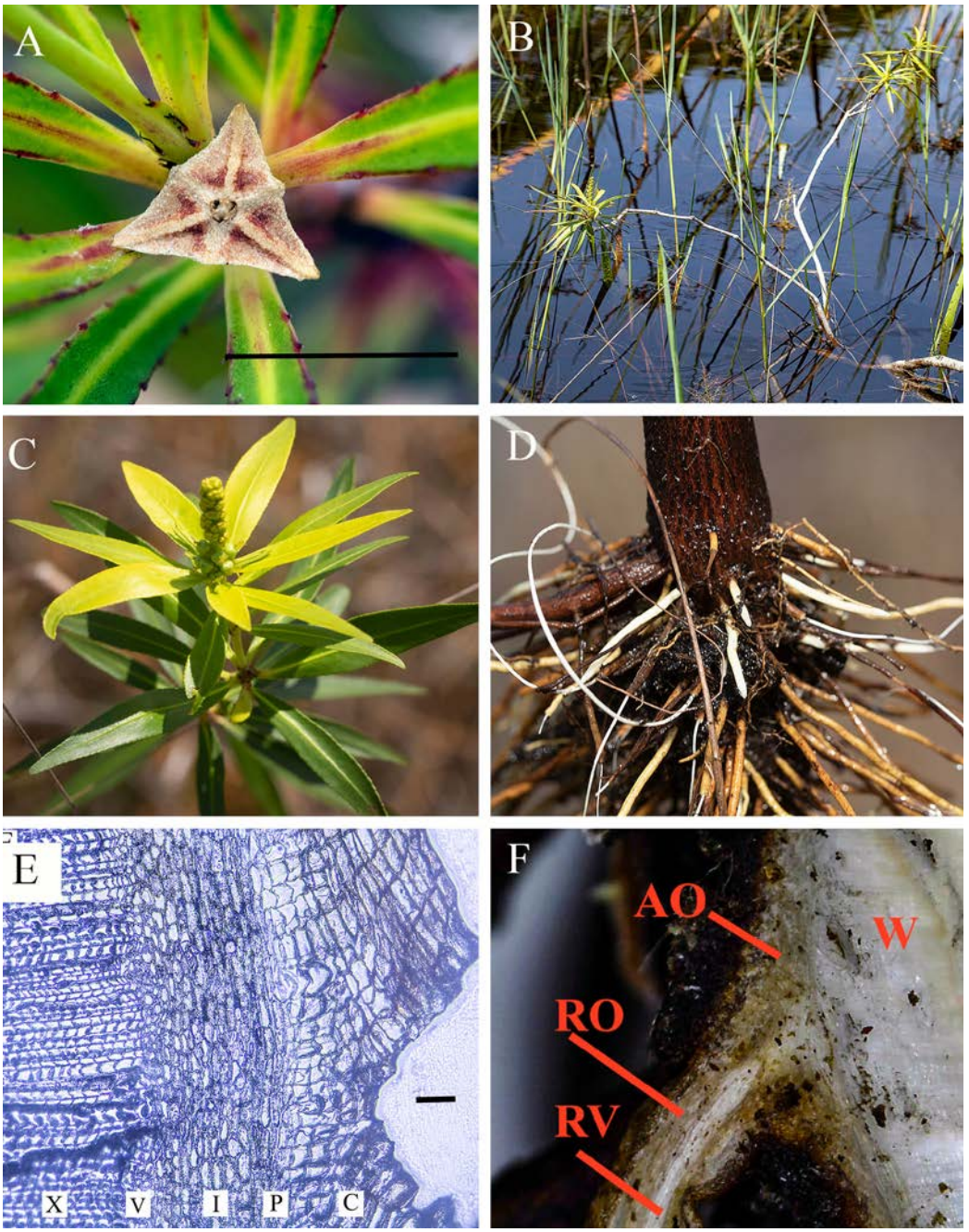

Fig. 1. *Stillingia aquatica*. **A.** Carpidiophore (aka gynobase). Scale bar = 6 mm. **B.** Habit. **C.** Leaf tuft, "bracts," subtending inflorescence. **D.** Submerged roots. **E.** Cross section of stem ca. 1.5 cm diam. just above water level. X=secondary xylem, V=vascular cambium, I=inner bark, P=phellogen (cork cambium), C=cork. Scale bar = 30 microns. **F.** Lateral root merging with stem base. The root vascular core (RV) enters the axis (W), whereas the root's aerenchymatous outer layer (RO) merges with the outer layer of the axis (AO).

total trapping time was 161 hours in sets of 4 or 5 slides left ca. 24 hours before examination except for removal due to impending rain.

Inflorescence bagging.—Inflorescences bagged in bud excluded flying insect visitors for multiple tests. Unless stated otherwise, bags were 1 mm mesh, 15 × 25.5 cm, with a basal drawstring, sold for agricultural pollinator/pest exclusion. Fruits reaching full size or nearly so containing hard seeds were regarded as successful fruitset even if still green in color. Bags tied at the base to stems did not exclude ants reliably unless sealed using stretched rubber tube in several tight loops around the bag-stem junction, or by wrapping the stem in soft fabric, placing the bag base over the fabric wrap and tightening two rings of copper wire indented into the fabric.

Self-compatibility assessment.—To test for self-pollination, inflorescences were bagged while entirely in bud. A preliminary test spanning April 2020, using ca. 30 fabric bags 7.5 × 10 cm at the Botanica, Pine Glades, and Hungryland sites simultaneously, was compromised by bag-induced damage, presumably mainly heat, to the tissues within. The experiment was repeated more favorably at the Botanica site with 10 larger 15 × 25.5 cm mesh bags. During this test, pollen-shedding staminate inflorescence regions were brushed against stigmas on the same plant by opening the bags when stigmas appeared fresh and moist, then reclosed immediately after the attempted artificial pollination. As a simultaneous check on wind pollination, two inflorescences were covered with wind-proof parchment bags. Likewise at the same place and dates, to sidestep bag-damage, three inflorescences were covered with mesh tents affixed to the ground until flooding in late May 2020. The components of this study were initiated on multiple days during the week of 13 Apr 2020, with final data taken and bags removed 22 Jun 2020.

Ant pollination assessment.—The possible necessity of ants for fruit initiation was checked at the Pine Glades site. Seventeen bags were sealed to the stem as described above to block ants while 12 more control inflorescences were covered with the same style bags tied only loosely and thus accessible to ants. The ant experiment was set up 26–27 May 2020 with the data collected 30 Jun 2020.

Inflorescence development.—The stages of inflorescence development were monitored using seven marked inflorescences in the Jones Creek Headwaters site recorded at intervals not exceeding 48 hours 22 Jul-22 Aug 2020. Additionally, to monitor hourly inflorescence changes, clusters of 10 plants at different sites were scored at different points in the day from morning through twilight for style status, presence of pollen on stigmas, pollen production, and nectar availability as wet (secreting) vs. dry glands.

Agamospermy testing.—Testing for agamospermy occurred multiple times using multiple approaches, primarily by removal of the staminate portions of inflorescences, "emasculation," while all flowers were in bud, then bagged. A preliminary test 10 May 2020–28 Jun 2020 occurred at the Botanica site with seven emasculated and bagged inflorescence buds. Damage from rising waters narrowed the results. A second test, post-flooding at the same site used a set of 10 emasculated inflorescence buds bagged, and 10 controls bagged without emasculation, all bags on separate plants. This second test ran 15–27 Jun 2020. A third and unconventional agamospermy check was at the Jones Creek Headwaters site, where 20 inflorescence buds were emasculated but not bagged. This test prevented damage from bagging but entailed the risk of false positives due to the exposed stigmas. To minimize self-pollination, all staminate flowers and buds were removed from the test plants, although cross-pollination from other plants in the population could not be prevented. At the same time 11 untreated buds of the same ages in the same population were marked as controls. This third test ran 2–22 Jul 2020. The intention for this test was that pervasive negative results would be evidence against agamospermy, whereas positive results would be regarded as ambiguous due to potential false positives.

Stigma receptivity.—The best indicator of stigma receptivity was direct observation of pollen tubes as described below. Stigma receptivity was tested secondarily as Makwana and Akarsh (2017) described using stigmatic immersion in 6% hydrogen peroxide in a shallow plastic container over transmitted light on a dissecting microscope. Continued bubble production was taken as a positive result. Cautions with this test are that it is not "tried and true" through widespread use, and that fractured and/or aged tissues give "positive" results. The test cannot be quantified, and it served only as backup to observing pollen tubes.

For a rapid test of stigma stickiness, chalk powder that glows under UV light (Global Innovations Network Lolo Crafts) was brushed onto stigmas, which were then freed of loose powder using a soft air blower for five seconds and swirled in water for five more seconds, then air dried. Examination using a head-mounted magnifier was under UV light.

Visualization of pollen tubes.—Pollen tubes extending from pollen grains into stigmas and styles were observed in order to check on self- and cross-compatibility, and to help pinpoint timing of stigma receptivity. Self- and cross-pollen were applied manually to pollen-free stigmas. That the stigmas were free of prior pollen was confirmed using a dissecting microscope where the large honey-colored grains are readily visible. Stigmas with too much prior pollen for hand-removal were rejected. To visualize pollen tubes, stigmas were fixed overnight in FAA (or killed by 30 minutes in boiling water), cleared 30 minutes in 88% lactic acid at 60 degrees C, and stained in lactophenol cotton blue for varied periods following Datta and Naug (1967) who used boiling. After initial viewing at 100× and 400×, many preparations were squashed by gentle pressure on the cover slips and re-examined. Due to frequent uncertainties in determining definitively the tips of the irregularly kinked tubes in the styles, data were confined to "growth" vs. "no growth" without measurements of tube lengths.

Inter-plant pollinator visits.—Wasps and bees are easily observed moving among inflorescences within and between individual plants. Photos served to confirm pollen loads.

Stem and root structure.—Stem and root sections were sectioned from green material on a sliding microtome mostly at 20 microns thickness. Microscope measurements were made at 100× and 400× using an ocular ruler calibrated with a stage micrometer.

RESULTS AND DISCUSSION

Vegetative structure.—Fertile individuals range in height from ca. 30 cm to about 2 m tall, with about 1 m commonplace. The basal stem diameter of fertile individuals is usually 1–2.5(5) cm. Each plant has usually 1–20(32) fertile branches with a terminal tuft of leaflets encircling the base of an inflorescence (Fig. 1C). These are referred to as "bracts" in the present paper. The leaf bases have small pointed caducous stipules. Broken tissues release milky sap.

Above the highwater stains near the stem base large conspicuous lenticels diminish in number toward the top of the main stem. That *Stillingia aquatica* is lenticellate in contrast with the absence of conspicuous lenticels on *Stillingia sylvatica* probably relates to submerged root aeration in the former.

A taproot the size of a carrot bears a thick brush of uniform white horizontal side roots (Fig. 1D). During inundation, adventitious roots emerge above the older roots. The side-roots have aerenchymatous channels ending at the junction with the vertical axis. The taproot and stem tissue are soft and free of aerenchyma. The stem wood has numerous closely spaced narrow uniseriate rays separating wedges of thin-walled xylary fibers having slitlike pits. The fibers in cross section usually measure 10–15 microns in diameter. The vessel elements are in well separated, disorganized radial rows or may be somewhat clustered. Mid-sized specimens have three or four growth rings, consistent with Harper (1901) encountering five or six rings on larger specimens.

The wood is exceptionally lightweight. Harper (1901) determined its specific gravity to be 0.20 g/cc dry. By comparison, balsa is 0.17 g/cc according to the CSGN Specific Gravity of Wood Table (http://www.csgnetwork.com/specificgravwdtable.html). Lightweight woods crop up convergently among unrelated woody species in seasonally inundated habitats. Solereder (1908) noticed this, highlighting *Leitneria floridana* Chapm. (Simaroubaceae) with specific gravity 0.207 g/cc (Harper 1901) matching *Stillingia aquatica*. (The name "corkwood" is applied to both species.) In seasonally inundated South American habitats Berry et al. (1999) citing prior authors separately came upon the same convergence. Berry and Wiedenhoeft (2004) added a subsequent euphorbiaceous example, *Micrandra inundata* P.E. Berry & A. Wiedenhoeft. Mennega (2005) commented on how (juvenile) wood of *S. aquatica* as a wetland species differs from wood of *S. lineata* (Lam.) Müll. Arg., a mostly upland Old World species. The main differences are that *S. aquatica* has xylary fibers with "extremely thin walls" (present measurements ca. 2–2.5 microns) and "preponderance of elongate vessel-ray pits," in addition to other minor distinctions. Thin-walled fibers are expected in woods of low density (Swensen & Enquist

2007). The *Stillingia aquatica* stem in transverse section (Fig. 1E) has a thick green inner bark containing chloroplasts. The aerenchymatous outer region of the side root merges with the basal extension of the stem inner bark (Fig. 1F).

Leaf Coloration.—The star-shaped leaf tufts, "bracts," subtending the inflorescence are generally conspicuous yellow green in contrast with the darker green leaves below them (Fig. 1C). They match the inflorescence color, suggesting a large false flower. The bracts and stem leaves can sometimes be reddish, which extended field observation revealed to be late-summer and autumn seasonal color. By January no red coloration remains in the study area. The yellow bracts show no noteworthy patterns under UV illumination. Colorful bracts are well known elsewhere in the Euphorbiaceae, most notably in *Euphorbia* and *Dalechampia*. *Stillingia aquatica* shares its habitat with *Rhynchospora latifolia* (Baldw. ex Elliott) W.W. Thomas (Cyperaceae), having its own showy white or partly white bracts about the same size and elevation as the *Stillingia* inflorescences. Alternative explanations for the yellowish bracts might be the pale color apparent in young foliage of many plants, and/or nutritional deficiency. Evidence against both of these possibilities, however, is that the yellow is associated closely with the inflorescences, and that the bracts do not turn green with time. Yellowish leaves below the inflorescence occur in additional *Stillingia* species.

Flowers.—The plants are monoecious, having erect spiciform much-condensed thyrses with (0)1–5(13) pistillate flowers basal to a "spike" of staminate cymules (Fig. 2A). The pistillate flowers consist of a trilobed ovary tipped with three exposed linear bow-shaped or curled stigmas diverging from a short style. Each pistillate flower is in the axil of a tiny bract equipped at the basal margins with large goblet-shaped nectar glands (Fig. 2B), which occur only in the inflorescence, and not on stem leaves. Extrafloral nectaries associated with flowers but absent on vegetative foliage are unusual, although true of the cyathia in *Euphorbia*. Yamasaki et al. (2013) described disk-shaped extrafloral nectaries on foliage leaves and on floral bracteoles in *Macaranga sinensis* (Baill.) Müll. Arg. (Euphorbiaceae) serving diverse floral visitors. As Rogers (1951) related, other species of *Stillingia* can have "2–3 cyathiform or scutelliform glands at base of blade." In his credible estimation, Rogers interpreted these vegetative foliar glands to be homologous with those limited to the inflorescence of *S. aquatica*.

Above the pistillate flowers and separated by a short internode is a yellowish "spike" of tiny bracteate cymules of staminate flowers. Each staminate flower has an inconspicuous calyx and two exposed stamens. The staminate bracts have nectar glands matching those of the pistillate region and collectively far more numerous. Staminate maturation is initially acropetal, although eventually each bract at any given time subtends flowers of mixed maturity. Thus a mature staminate "spike" presents no vertical sequence of floral stages.

The inflorescences pass through three phases: first, the only open flowers are pistillate ("pistillate-only phase" hereafter), then comes a period where healthy stigmas and pollen-shedding staminate flowers overlap on the same inflorescence ("overlap phase" hereafter), and in the third phase the pistillate flowers have shed their stigmas, leaving the staminate flowers still shedding pollen ("staminate-only phase" hereafter) above maturing fruits.

Many-to-most inflorescences produce fruits. A minority have no discernable pistillate flowers at all, and often others develop pistillate flowers but fail to form fruits (Table 1). Seven marked inflorescences monitored at the Jones Creek site late Jul–late Aug 2020 revealed the durations of floral phases. The site was intermittently free of standing water during the observations. Three inflorescences formed fruits, and four had pistillate flowers fail to form fruits. The figures that follow are averages, although not all based on every inflorescence, given their divergent fates. They all produced open pistillate flowers before any staminate flowers opened, this pistillate-only phase being (4)6(8) days. The average overlap phase with stigmas and pollen-releasing staminate flowers overlapping in time was (2)4(5) days. The combined pistillate-only and overlap phase time was (8)10(11) days. The total time staminate flowers were active, the overlap phase plus staminate-only phase, was (18)20(22) days. One inflorescence formed its first stigmas 2 Jul 2020, and full-sized fruits by 25 Aug. The time from inflorescence bud opening to a brown drying fruit on another monitored plant was approximately 45 days.

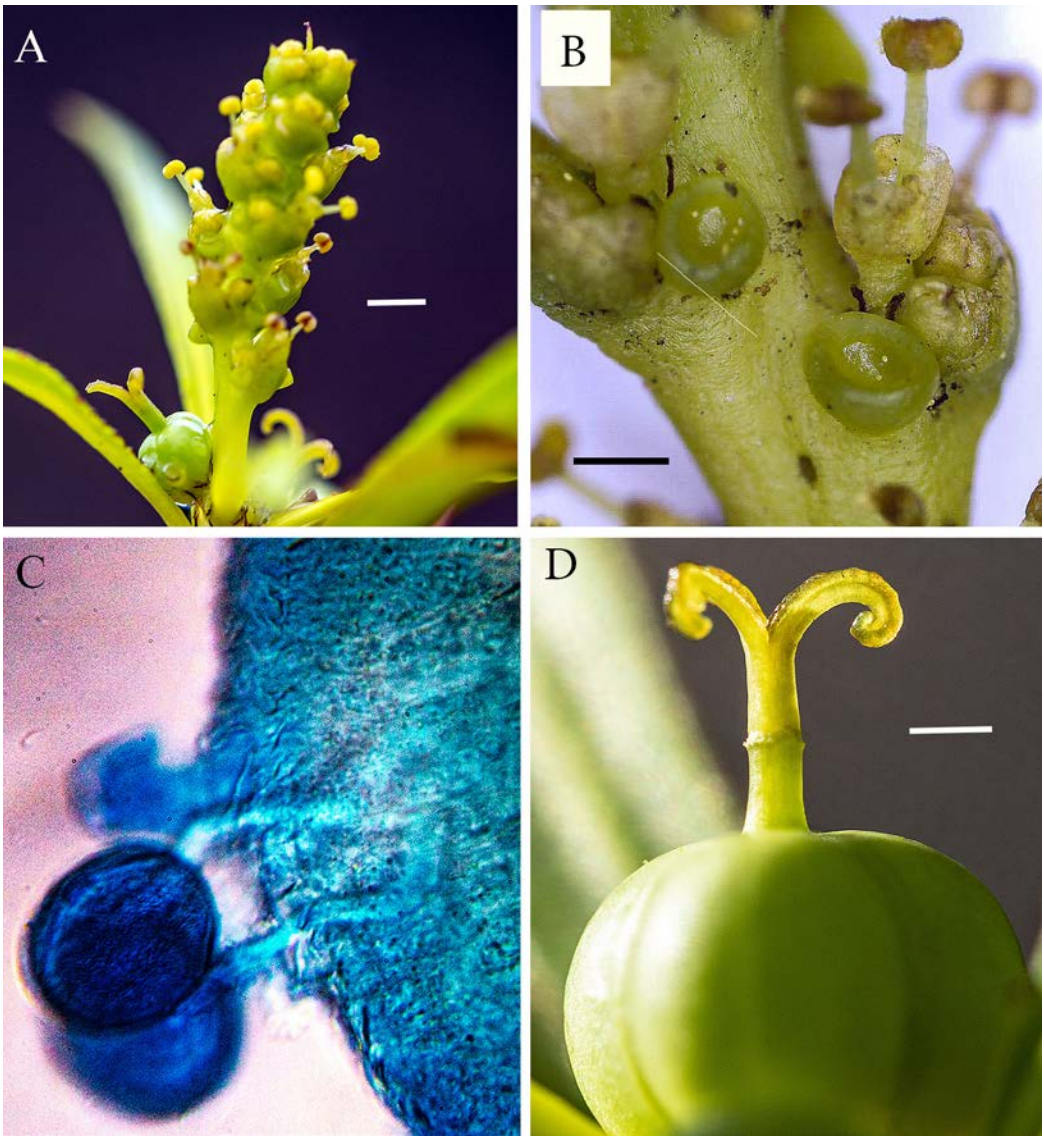

Fig. 2. *Stillingia aquatica.* **A.** Inflorescence. Scale bar = 4 mm. **B.** Nectar glands on bracts in inflorescence. Scale bar = 1 mm. **C.** Pollen grains germinating on stigmas. **D.** Abscission zone in style. Scale bar = 2 mm at same height as abscission zone.

Non-senesced green stigmas range in appearance from wet to glossy matte. Monitoring inflorescences in groups of 10 at different points in the day showed a peak of wet stigmas at mid-day with glossy matte becoming prevalent toward evening, although some wet stigmas may be encountered at any daylight hour. Similar patterns turn up in pollen and nectar availability, discussed below.

Pollination and breeding system.—As the inflorescence opens, the pistillate flowers experience their best odds of cross-pollination because in this pistillate-only phase no staminate flowers are open in the same inflorescence. A survey of 118 stigmas in the pistillate-only phase revealed the stigmas to bear pollen from

Table 1. Survey of inflorescence reproductive stages at three sites.

Reproductive Stages	Jones Creek 7/25/2020 % (85 inflorescences)	Hungryland 8/3/2020 % (n = 146)	C-18 Canal 8/3/2020 % (n = 62)
Stigmas open, staminate flowers all in bud (pistillate-only phase)	33%	11%	34%
Styles dehisced, staminate flowers in bud	0%	0.6%	0%
Stigmas healthy, staminate flowers releasing pollen (overlap phase)	19%	6%	6%
Stigmas senescing, staminate flowers releasing pollen	13%	0%	5%
Stigmas gone, fruit(s) expanding, staminate flowers releasing pollen (staminate-only phase in part)	6%	44%	35%
Pistillate flowers failed or absent, staminate flowers releasing pollen (staminate-only phase in part)	13%	15%	14%
Fruits only	16%	23%	5%

other plants or from separate inflorescences on the same plant before the overlap phase begins. An average of 0.60 grains/stigma, with up to 17 grains were observed during the pistillate-only phase. (And there were pollen clumps with the grains too numerous to count individually.) Not surprisingly, after the overlap phase begins, the numbers of grains per stigma jump to an average of 2.5 grains/stigma (n = 34). The increase is clearly due to the staminate flowers shedding pollen onto the stigmas below in the same inflorescence, this selfing probably enhanced by increased hymenopteran visitorship drawn to the staminate flowers.

Stigmas are receptive in both the pistillate-only and overlap phases. Hand-pollinated clean stigmas from both phases showed growth of cross- and self-pollen tubes (Fig. 2C). It was notably more difficult to induce pollen tube growth during the overlap phase than during the pistillate-only phase, not surprising since the aging stigmas in the overlap phase soon abscise. Hydrogen peroxide tests and stigma stickiness tests likewise suggested stigma receptivity at least early in the overlap phase.

That stigmas are receptive and often pollinated in the pistillate-only phase suggests that pollen tubes in potentially cross-pollinated pistillate flowers during that phase have a head start before staminate flowers increase the odds of self-pollination in the overlap phase.

The overlap phase no doubt provides reproductive assurance. During this phase young anthers and adjacent stigmas can be close together (Fig. 2A), the gap as narrow as 1 mm, probably allowing brief contact during physical disturbance. Movement of pollen from anthers to nearby stigmas is unavoidable with the help of gravity, wind, rain, and arthropods. In addition to pollen on stigmas, fallen grains cling to bracts and within the cups of the nectar glands.

Geitonogamy requires self-compatibility. Webster (2014) described self-incompatibility as rare in open-pollinated Euphorbiaceae, although known. Multiple tests using bagged inflorescences in the present study revealed *Stillingia aquatica* to be self-compatible and to self-pollinate. Despite excessive bag damage to the foliage and inflorescences in the first test, three of 21 bagged inflorescences yielded fruits. A second test included attempted artificial self-pollination. Seven of 10 bagged inflorescences produced fruits. During the same dates at the same site, one of three tented inflorescences formed fruits, as did one of two inflorescences in wind-proof parchment bags. The ant-proofing test described below with no attempt at artificial pollination added additional instances of self-pollination under bags. Alternative explanations for fruit production under mesh bags include agamospermy, pollen delivery by ants, or anemophily, all considered individually below. A cultivated individual at the author's home having no possibility of cross pollination 3.1 km from the nearest conspecifics produced fruits with an approximately even mix of healthy and failed seeds (see discussion of seeds below).

In addition to the selfing, abundant pollen-bearing flying insect visitors offer cross pollination. Given demonstrable selfing and insect pollen vectors observed with pollen loads, there must be a balance between geitonogamy and xenogamy. Several factors inevitably influence that balance, some of them constraining self-pollination, including the potential head start of cross-pollen during the pistillate-only phase. The subsequent short overlap phase ends abruptly when the styles break free along a sharp abscission zone, truncating pollen tube progress. The abscission zone swells, and the tissues on the two sides of the line differ in appearance (Fig. 2D).

A similar event occurs in *Spigelia* (Loganiaceae) which Erbar and Leins (2008) interpreted as prezygotic selection favoring faster-growing pollen tubes, with an advantage to the fittest tubes. In diverse plants authors have found tubes resulting from self-pollination sometimes to grow more slowly than those from cross-pollination (Goodwillie et al. 2005; Gibbs, 2014). Possible in *Stillingia aquatica* specifically is that the sharp cutoff ending the overlap phase favors tubes with the head start from the potentially cross-pollinated pistillate-only phase.

To continue with factors possibly constraining self-pollination, De Jong et al. (1993) and Ito and Kikuzawa (2003) described known and suspected general mechanisms for trees having mixed mating systems to compel floral visitors to depart and cross-pollinate. Such mechanisms include pistillate flowers placed toward bases of inflorescences, noting that arriving bees work upward. Also encouraging visitors to move from plant to plant are extended flowering periods featuring only limited rewards on individual plants.

Such general constraints apply to *Stillingia aquatica*. Its pistillate flowers are at the bases of the inflorescences. The flowering period is extended, year-round or nearly so in the study area. That numbers of inflorescences per *S. aquatica* individual are limited favors cross-visitation. A survey in the mixed-age Jones Creek Headwaters population gave the following inflorescence counts per plant: 1 inflorescence (10 plants), 2(10), 3(3), 5(1), 8(1), 9(2), 19(1), 22(1). At the even-aged and apparently young Hungryland site, ca. half (48) of the plants had only a single inflorescence. At the older mixed-age Botanica site the distribution was: 1 inflorescence (17 plants), 2(8), 3(9), 4(7), 5(4), 6(3), 7(1), 8(3), 9(1), 10+ (7 plants). In summary then, many plants have just 1–3 inflorescences, with not every inflorescence receptive and/or shedding pollen at a given moment (Table 1).

Contributing further to cross-pollination, the plants tend to be closely spaced (Fig. 3) sometimes with overlapping branches. The average center-to-center distance in Figure 3 is 138 cm, and a similar average in a separate survey of 54 individuals at the Hungryland site was 129 cm. Often an inflorescence is closer to a neighbor's flowers than it is to the most distant inflorescence on its own plant.

The large sticky grains usually in small numbers or sometimes in clumps are dispensed from clefts in the valvate anthers (Fig. 4A), with usually only a minority of the staminate flowers in an inflorescence open at once, limiting the pollen reward at any visit. Many anthers at any given moment are either pre-release, off-peak, or post-release. Cohorts of few-to-many unopened staminate flowers appear early in the morning followed by anther dehiscence later in the day as well as by additional staminate flowers breaking bud as the day progresses. The exposed pollen is unprotected from rain and wind.

Nectar is available in almost any *Stillingia* inflorescence but generally only from a minority of the nectaries, with substantial variation. Hourly inflorescence monitoring showed the following mean numbers (n=10 plants) of "wet" glands per inflorescence through the day: 9 am DST (1 wet gland), 11 am (16), 2 pm (30), 5 pm (9), and 6 pm (2). On occasion, however, with no obvious cue and not due to rain, an inflorescence may have an exceptionally high proportion of glands in the wet condition.

Ito and Kikuzawa (2003) discussed "nuisances" adapted to shorten pollinator visits. Perhaps germane to *Stillingia*, Villamil et al. (2020) studying *Turnera* (Turneraceae) related that, "ant patrolling…decreased pollinator foraging time and flower visit duration…increasing outcrossing 43 rates." Antagonistic actions between ants and wasps take place in *Croton suberosus* Kunth (Euphorbiaceae) (Narbona & Dirzo 2010).

Ants as pollinators?—Ants scurry up and down the inflorescences and consume nectar from the glands (Fig. 4B). Their frequent abundance, lively activity, and nectar consumption raise the question of roles beyond

Fig. 3. Map of *Stillingia* cluster within the Botanica site 7/21/2020. Each letter represents an inflorescence. B unopened buds only, P pistillate flowers only, S- stamens only with no developing pistillate flowers, S staminate and pistillate flowers or developing fruits, L inflorescence senescing, F fruits only.

possibly shortening pollinator visits. Ants fed by extrafloral nectaries traditionally suggest a symbiotic defensive function, which is possible in *Stillingia* for ants and conceivably for wasps, noting that several herbivorous insects are observed on the inflorescences. These include thrips, broad-headed bugs (Alydidae), ebony bugs (*Corimelaena* sp.), and bush katydids (*Scudderia* sp.). Cottony cushion scale (*Icerya purchasi*) is sometimes severe. Miller and Miller (2005) suggested *S. sylvatica* to be apparently ant-pollinated. Delnevo et al. (2020), however, described effective ant pollination as rare and usually limited to dry or to cold habitats. Dutton and Frederickson (2012) regarded ants as ineffective pollinators, due largely to pollen-toxic antibiotic secretions, not characteristic of wasps and bees. Narbona and Dirzo (2010) dismissed ants as significant pollinators of *Croton suberosus*, allowing, however, for their contribution to geitonogamy.

That ants aid geitonogamy in *S. aquatica* is likely. Faegri and Van der Pijl's (1979) general comments on this topic are, "ants crawling around in flowers and inflorescences may cause auto- or geitonogamy and this will occur wherever they discover an available source of nectar or pollen." In the Euphorbiaceae, Raju and Ezradanam (2002) attributed ants with effecting geitonogamy in *Jatropha curcas* L. Ants helping pollen from anther to stigma seems unavoidable in *S. aquatica* recalling that the separation may be as close as 1 mm. Any *Stillingia* inflorescence may host several ants at once, and pollen sticks visibly to them (Fig. 4C). Pollen grains sticking within the goblet-shaped nectar glands guarantee automatic contact with any ant or wasp pushing its face into the concavity (Fig. 4D). The nectar may add "glue" to the already-sticky pollen.

Whether or not ants add to self-pollination, they are not critical for fruitset. Of 14 ant-excluded inflorescences, five inflorescences produced a total of seven fruits. Of 12 bagged but ant-accessible controls in the same population at the same dates, six inflorescences produced seven fruits, essentially the same outcome as ant-exclusion.

***Wind Pollination?*—**In favor of wind pollination, the plants are the tallest emergents in open marshes where the graminoid species are mainly wind-pollinated. The anthers and large stigmas are fully exposed.

Fig. 4. *Stillingia aquatica* and floral visitors. **A.** Pollen releasing from anther cleft. Width of anther ca. 1 mm. **B.** Ant feeding at nectar gland in inflorescence. **C.** Ant with *S. aquatica* pollen (marked). **D.** Nectar gland with pollen grains in the cup. **E.** *Melissodes communis*. **F.** *Polistes dorsalis*.

Unlikely for wind-pollination, however, the pollen is sticky and large (fresh grains averaging 82.5 × 46.5 microns, n = 10). One of two inflorescences enclosed in wind-proof parchment bags produced fruit. Pollen-trapping experiments totaling 161 hours yielded just four *Stillingia* pollen grains and, separately, one complete *Stillingia* anther. Moreover, the agamospermy test where staminate flowers near pistillate flowers were removed while the stigmas were left uncovered produced only one fruit out of 18 inflorescences. (A second fruit formed where the stigmas turned out to be adjacent to an overlooked staminate flower.) These results collectively indicate wind pollination to be negligible or nearly so, although wind probably aids within-inflorescence geitonogamy by means of physical disturbance.

Flying visitors.—Flying hymenopterans are commonplace on *Stillinga aquatica* inflorescences, often with multiple visitors active within a clump of *Stillingia* simultaneously. Floral features suggesting entomophily include the general yellow coloration of the inflorescence and its subtending bracts, productive nectar glands among the flowers, and large sticky pollen grains. Floral fragrance is detectable on rare occasions. Bees and wasps photographed and identified were honeybees, sweat bees (*Agapostemon splendens*), crabronid wasps (*Cerceris* sp.), long-horned bees (*Melissodes communis* Fig. 4E), the paper wasp *Mischocyttarus mexicanus,* and mixed species of *Polistes* paper wasps including *P. bellicosus, P. dorsalis* (Fig. 4F), *P. fuscatus*, *P. major,* and additional unidentified wasps. *Stillingia* pollen grains clinging to wasps are visible in photographs (Fig. 5A). Numerous field outings revealed the balance of flying hymenopteran visitors to shift from mixed bees and wasps in the dry season to wasps essentially exclusively during the summer and autumn flooded months. The sole observed possible exception to exclusive summer wasp visitation was a honeybee captured by a green lynx spider (*Peucetia viridans*) on a *Stillingia* leaf. The plant was adjacent to the dry shore. Green lynx spiders, among general insect prey, "favor" *Polistes* wasps according to Weems (2001) citing prior work.

The main *S. aquatica* visitors are *Polistes* wasps. Narbona and Dirzo (2010) in *Croton suberosus* (Euphorbiaceae) found *Polistes* to be the chief pollinator and to defend the plants from herbivores. Referring to *Croton,* Webster (1994) discerned *Polistes* to be more important for pollination than for defense. Within *Asclepias* (Apocynaceae), Hallett et al. (2017) found *Polistes* wasps to equal bumblebees in pollen transfer.

The inflorescences are frequent perches for varied arthropods not suspected as pollinators except maybe by aiding within-inflorescence geitonogamy and perhaps influencing pollinator behavior. Non-hymenopteran floral visitors include the herbivores listed above, ambush bugs (*Phymata* sp.), and frequent spiders.

Agamospermy?—Fruitset by bagged inflorescences necessitates consideration of agamospermy. In a preliminary agamospermy test two emasculated bagged inflorescences failed to develop fruits, while six were ruined by rising water. In the second agamospermy test, none of 10 emasculated bagged inflorescences produced fruits. The fruit-production results for 10 non-emasculated bagged control inflorescences at the same place and dates were 0, 0, 0, 1, 1, 2, 2, 4, and two inflorescences dead. An additional 10 unbagged control inflorescences in the same population during nearly the same dates (14–27 Jun 2020) generated fruits as follows: 1, 2, 4, 2, 6, 0, 3, 2, 3, and 1.

The third agamospermy check using unbagged inflorescences with all inflorescences on the test plants (but not every plant in the population) emasculated resulted in 18 inflorescences with no fruits, and two with one fruit each. Of these two cases, one inflorescence sprouted staminate flowers from an overlooked bud adjacent to the fruit-making pistillate flower. The other fruit probably originated by cross-pollination, although an isolated instance of agamospermy cannot be ruled out. A tagged, but otherwise, untreated control had five inflorescences collectively responsible for nine fruits, and six fruitless inflorescences. The three tests collectively suggest agamospermy to be absent or negligible.

That unbagged emasculated inflorescences experienced almost no pollination during the wasp-only wet season is consistent with Narbona and Dirzo's (2010) observation of strong wasp preference for staminate flowers, even though both flower types in the *Croton suberosus* they studied, and in *S. aquatica*, offer nectar. They speculatively attributed the difference to higher nectar availability and to visual attraction in the staminate flowers. Both of these factors apply in *S. aquatica*.

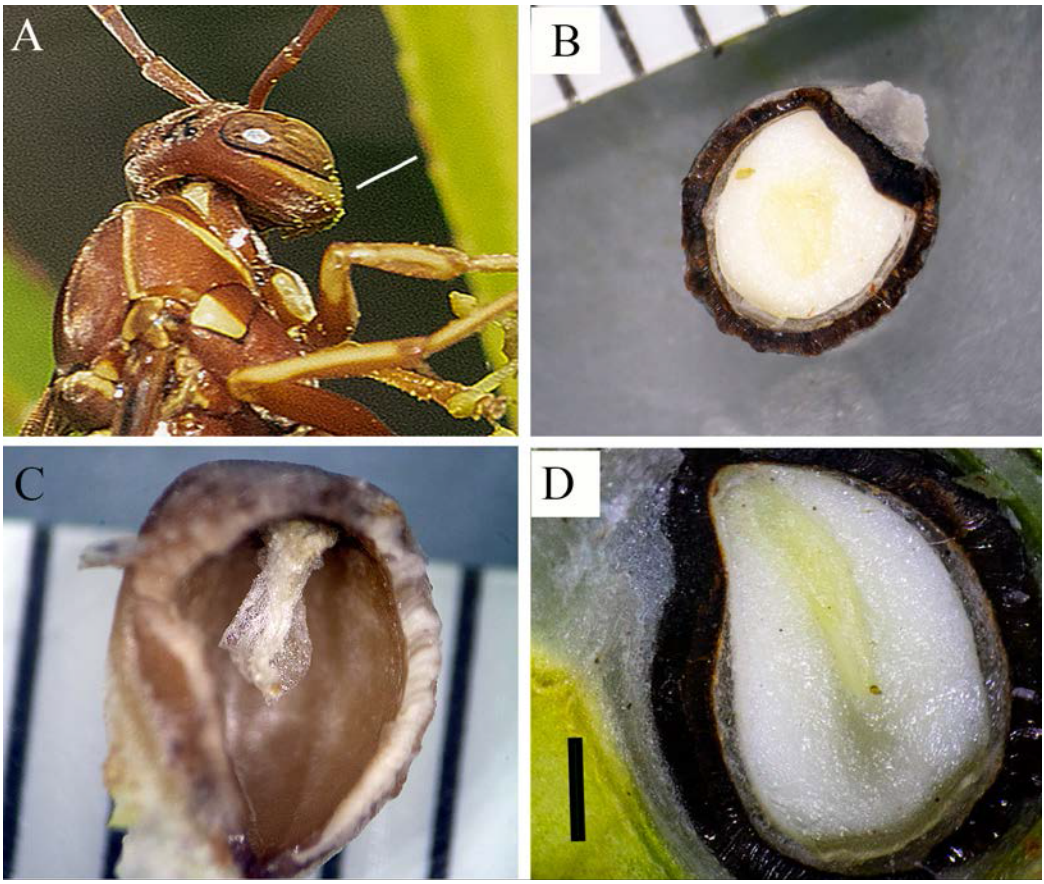

Fig. 5. *Stillingia aquatica* pollen and seeds. **A.** *Stillingia aquatica* pollen on wasp face (marked with line). Pollen is also on antenna and legs. **B.** Seed, with caruncle at upper right. Ruler marks = 1 mm. **C.** Nonviable seed. Ruler units = 1 mm. **D.** Healthy seed with embryo. Scale bar = 1 mm.

Dispersal.—*Stillingia aquatica* overall produces abundant fruits, even if a fraction of the inflorescences fail to make fruits. A survey of fruit-bearing inflorescences at the Hungryland site 7 Jul 2020 gave the following frequencies of enlarged green or brown fruits per inflorescence 1 fruit/inflorescence (50 inflorescences), 2(26), 3(22), 4(3) and 5(2). The largest number of fruits/inflorescence encountered in the entire study was 13, on an exceptionally fecund individual in the Cypress Creek population also with two clusters of 10 fruits.

The septicidal capsules usually break apart on the plant, releasing their seeds encased within a segment of the capsule. (Some authors refer to the fruits as schizocarps.) *Stillingia sylvatica* has explosive discharge according to Stamp and Lucas (1990). *Stillingia. aquatica* seeds are gray, hard-coated, and coarsely rugose. The caruncle (Fig. 5B) is partly embedded within a groove in the testa. Upon wetting it enlarges and becomes gelatinous. Caruncles (elaiosomes) generally attract ant distributors. On 24 Jun 2020, I observed an ant engaged with the caruncle of a *Stillingia* seed on wet mud. Bianchini and Pacini (1996) found the similar but larger seeds of *Ricinus communis* L. (Euphorbiaceae) to hydrate via the caruncle.

The seeds are highly heterogeneous in form, coat, and size. In a set of 40 seeds collected from different plants at different sites in Jul 2020, about half (21) were deformed and/or markedly undersized. The seed photo for *S. sylvatica* in Wunderlin et al. (2020) suggests heterogeneity for that species, too. Rogers (1951) reasonably

attributed such variation to introgression between *S. sylvestris* and *S. aquatica*. Hybridization, however, is unlikely as the main cause of the pronounced seed sterility described below, since the plants in the study area have no morphological appearance of introgression with *S. sylvatica,* and no populations of that species are known within the study area.

Normal-looking enlarged fruits from *S. aquatica* contain high percentages of obviously nonviable seeds (Fig. 5C). With the notable exceptions discussed below, most samplings of enlarged normal-looking fruits at different sites reveal roughly half of the seeds to be nonviable. Healthy seeds (Fig. 5D) have white mealy endosperm and robust uniform embryos in contrast with nonviable seeds being hollow and/or with the contents blackened. Percentages of healthy seeds from different sites are in Figure 6. At the author's home a cultivated individual with no possibility of outside pollination, 3.1 km from the nearest *Stillingia,* at this time of this writing 6 Sep 2020 held five full-sized fruits. Those fruits contained eight healthy seeds (53%) and seven nonviable ones reflecting the ratios at most field sites.

The varied seed success rates in enlarged fruits are not likely a simple difference in pollination rate, since many of the failed seeds contain aborted embryos which would require pollination in the absence of agamospermy. The variability may in part reflect differential cross- vs. self-pollination rates, where selfing and consequent inbreeding depression are more prevalent where flying cross-pollinators are comparatively sparse.

The two populations with the high seed success rates (Jones Creek 86%, Pine Glades 85%) (Fig. 6) differ jointly from all the other populations by being in small depression ponds embedded in diversified woody habitats as opposed to expansive marshes, pine savanna, or cypress swamp. Because the Pine Glades and Jones Creek populations had exceptionally high healthy seed percentages, they were resampled approximately three weeks after the initial sampling. The resampling at both sites 18 Sep 2020 gave 83.3 % (25/30) healthy seeds in both cases, echoing the original results. Except for the unique Cypress Creek site, all the lower-success populations are large open marshes or marshy pine savanna. The Cypress Creek population is a small cluster of shaded individuals in a bald cypress swamp. It may be that the two particularly successful populations owe their comparatively high healthy seed production to proximity to diversified woodland habitat favored by paper wasps.

According to a literature review concerning foraging behavior by different *Polistes* species in Silva-Filho et al. (2020), *Polistes* wasps are strong and fast fliers variably capable of covering long distances. The large-bodied Brazilian wasp they studied, *Polistes lanio lanio*, returned to the nest from a release point 2050 m with a foraging area of 13.2 square km. *Polistes simillimus* has a reported forage area of 7.2 square km. Such abilities demonstrate how stillingias in expansive flooded marshes could receive visitation. Yet on the other hand, the recorded effective ranges of various other *Polistes* species point to foraging activity mainly near nesting habitats. Effective ranges Silva-Filho et al. (2020) reported from prior literature are: *Polistes versicolor* (200 m, with maximum of 850 m), *P. gallicus* 300–400 m (recorded as return distances, sometimes extending > 600 m), and *P. canadensis canadensis* (50–250 m). Thus, although specific data are needed, in a general sense *Polistes* paper wasps appear to combine potentially broad foraging regions with tethering to their nesting habitats.

If inbreeding via selfing contributes meaningfully to seed failure, different inbred parents having different genotypes would likely vary in percentages of healthy vs. aborted seeds. Consistent with that possibility, a survey 13 Sep 2020 of 10 plants at the Botanica SE site gave the following distribution of seed failures per 15 seeds from five three-seeded fruits per plant: 0 failures/15 seeds, 3/15, 4/15, 4/15, 5/15, 6/15, 7/15, 8/15, 8/15, 8/15. This wide distribution deviates substantially from an expected average of 5.3 failed seeds per plant if evenly distributed (χ^2 $p < 0.05$). Potential explanations for post-pollination embryo failure exist apart from inbreeding depression. Sun and Hauser (2005) demonstrated root stress from salinity to cause embryo abortion, hinting that in *Stillingia* anoxia stress from submerged roots could matter. Additional possible causes of embryo failure include ovule competition, suppression of selfed ovules, and resource limitations (Bawa et al. 1989; Charlesworth 1989; Wiens et al. 1989; Goodwillie et al. 2005). Also possible are various maternal effects (see e.g., Kärkkäinen et al. 1999; Meyer et al. 2014).

The distribution of nonviable seeds is also non-random with respect to the three-seeded fruits. The seed

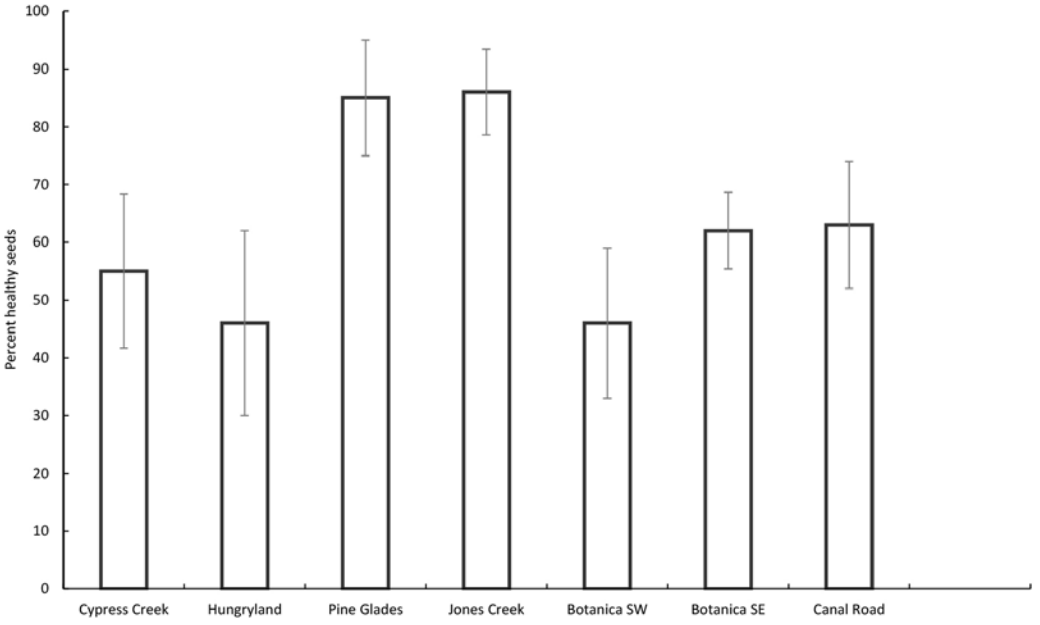

Fig. 6. Percentages of healthy *S. aquatica* seeds at seven different populations. Error bars = 95% confidence intervals.

trios tend toward "all or nothing," with a deficit of fruits having a mix of healthy and nonviable seeds (n = 411 seeds in trios from 137 fruits, χ^2 p = < 0.05).

Insect seed predation appears to be minimal with a curious exception. A dissected seed from the Hungryland site contained a larva resembling (to an unschooled eye) the moth larva (*Cydia deshaisiana* Lucas) within Mexican jumping "beans." The "jumping beans" are the septicidal capsule segments from *Sebastiania pavoniana* (Müll. Arg.) Müll. Arg., a co-member of the tribe Hippomaneae with *Stillingia*. The fruits are similar. The moth is neither exclusive to *S. pavoniana* nor reported within or near Florida. This isolated informal observation is emphatically not put forth as an identification of the larva in *S. aquatica*, merely as an oddity that others may encounter and decipher.

That viable *S. aquatica* seeds occupy the depression marsh seedbank is demonstrated by seedlings rising uncrowded in wet mud during the low-water season, and in wet mud exposed fleetingly by weather fluctuations in the summer rainy season. It is not clear if germination requires exposure to air, or if it can occur underwater. At the Jones Creek site during the summer of 2020 relatively dry spells freed the site of standing water intermittently. Seedlings ca. 10–20 cm tall were apparent on the freshly exposed mud. That none smaller than ca. 10 cm could be found suggested germination while still submerged, if only shallowly. Seedlings can withstand immersion, and early in life they become tall and spindly with a single leaf tuft held above the highwater line. All efforts to germinate the seeds have failed to date, including planting in pots with the caruncle intact, planting with the caruncle removed, physical scarification, and placement for several weeks between moist paper towels. In general, seeds in seasonally flooded seedbanks have diverse species-specific germination requirements, may lie dormant for long periods, and respond to varied cues (Ge at al. 2012).

Avenues for further research.—The lightweight wood associated with seasonally submerged conditions invites anatomical and physiological investigation, especially with respect to woody wetland plants. Aeration of seasonally submerged roots is a topic still poorly understood, with limited published data suggesting xylem-mediated gas exchange, and/or a "closed system" involving photosynthetic outer stem tissues. *Stillinga* offers an attractive case study with the advantage of easy cultivation and large-diameter, aerenchymatous, shallow

roots easily accessed. Also of interest would be quantified tests on the apparent but unproven attractive role of the yellow bracts. Additional points for further investigation include the molecular genetics of the mixed breeding system, pinning down relative contributions of self-pollination vs. xenogamy perhaps in relation to habitat. The roles of ants in the reproductive cycle warrant further research. The literature on *Polistes* and other wasps as pollinators is thin, with *Stillingia* an unexplored example. Beyond a glimpse in Rogers (1951), chromosome counts for *S. sylvatica* and *S. aquatica* are absent. Given the odd distributions of *Stillingia* species, a full molecular phylogeny of the genus will be welcome when it happens.

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REFERENCES

Bawa, K., K. Ganeshaiah, S. Hedge, & R. Shaanker. 1989. Embryo and seed abortion in plants. Nature 342:625.

Berry, P., R. Miller, & A. Wiedenhoeft. 1999. A new lightweight-wooded species of *Anaxagorea* (Annonaceae) from flooded black-water shrublands in southern Venezuela. Syst. Bot. 24:506–511.

Berry, P. & A. Wiedenhoeft. 2004. *Micrandra inundata* (Euphorbiaceae), a new species with unusual wood anatomy from black-water river banks in southern Venezuela. Syst. Bot. 29:125–133.

Bianchini, M. & E. Pacini. 1996. The caruncle of *Ricinus communis* L. (castor bean): its development and role in seed dehydration, rehydration, and germination. Int. J. Pl. Sci. 157:40–48.

Charlesworth, D. 1989. Why do plants produce so many more ovules than seeds? Nature 338:21–22.

Datta, P.C. & A. Naug. 1967 (published online 2009). Staining pollen tubes in the style; cotton blue *versus* carmine for general use. Stain Technol. 42:81–85.

Delnevo, N., E.J. van Etten, N. Clemente, L. Fogu, E. Pavarani, M. Byrne, & W. Stock. 2020. Pollen adaptation to ant pollination: a case study from the Proteaceae. Ann. Bot. (Oxford). 126:377–386.

Dutton, E.M. & M.E. Frederickson. 2012. Why ant pollination is rare: new evidence and implications of the antibiotic hypothesis. Arthropod-Pl. Interact. 6:561–569.

Erbar, C. & P. Leins. 2008. Secondary pollen presentation and a curious rupture of the style in *Spigelia* (Spigeliaceae, Gentianales). Pl. Biol. 1:389–402.

Esser, H.-J. 2012. The tribe Hippomaneae in Brazil. Rodriguésia 63:209–225. [Main reference to *Stillingia* p. 215.]

Faegri, K. & L. Van Der Pijl. 1979. The principles of pollination ecology. Revised. Ed. 244 p. Pergamon. Oxford, U.K.

Ge, X., J. Liu, & R. Wang. 2012 (2013). Effects of flooding on the germination of seed banks in the Nansi Lake wetlands, China. J. Freshwater Ecol. 28:225–237.

Gibbs, P.E. 2014. Late-acting self-incompatibility: the pariah breeding system in flowering plants. New Phytologist 203:717—734.

Goodwillie, C., S. Kalisz, & C. Eckert. 2005. The evolutionary enigma of mixed mating systems in plants: occurrence, theoretical explanations, and empirical evidence. Annual Rev. Ecol. Evol. Syst. 36:47–79.

Hallett, A., R. Mitchell, E. Chamberlain, & J. Karron. 2017. Pollination success following loss of a frequent pollinator: the role of compensatory visitation by other effective pollinators. AOB Plants. Published online. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC5544916/.

Harper, R. 1901. On a collection of plants made in Georgia in the summer of 1900. Bull. Torrey Bot. Club. 28:454–484.

Huft, M. 2016. *Stillingia*. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico. 19+ vols. New York and Oxford. Vol. 12:233–234.

Ito, E. & K. Kikuzawa. 2003. Reduction of geitonogamy: flower abscission for departure of pollinators. Ecol. Res. (Tokyo) 18:177–183.

Jong, de T., N. Waser, & P. Klinkhamer. 1993. Geitonogamy: the neglected side of selfing. Tree 8:321–325.

Kärkkäinen, K., O. Savolainen, & V. Koski. 1999. Why do plants abort so many developing seeds: bad offspring or bad maternal genotypes? Evol. Ecol. 13:305–317.

Li, S., B. Chen, X. Huang, X. Chang, T. Tu, & D. Zhang. 2017. *Stillingia*: A newly recorded genus of Euphorbiaceae from China. Phytotaxa 296:187.

Makwana, M. & P. Akarsh. 2017. Stigma receptivity test in diverse species of tomato. Int. J. Agric. Sci. Res. 7:1–8.

Mennega, A. 2005. Wood anatomy of subfamily Euphorbioideae; a comparison with subfamilies Crotonoideae and Acalyphoideae and the implications for the circumscription of the Euphorbiaceae. IAWA Bull. 26:1–68. [*S. aquatica* 43, 44.]

Meyer, K., L. Soldaat, H. Auge, & H. Thulke. 2014. Adaptive and selective seed abortion reveals complex conditional decision making in plants. Amer. Naturalist 183:376–383.

Miller, J. & K. Miller. 2005. Forest plants of the Southeast and their wildlife uses. Univ. Georgia Press, Athens, Georgia, U.S.A.

Narbona, E. & R. Dirzo. 2010. A reassessment of the function of floral nectar in *Croton suberosus* (Euphorbiaceae): A reward for plant defenders and pollinators. Amer. J. Bot. 97:672–679.

Raju, A. & V. Ezradanam. 2002. Pollination ecology and fruiting behaviour in a monoecious species, *Jatropha curcas* L. (Euphorbiaceae). Curr. Sci. 83:1395–1398.

Rogers, D.J. 1951. A revision of *Stillingia* in the New World. Ann. Missouri Bot. Gard. 38:207–259.

Silva-Filho, R., B.P. Brüger, and 10 additional authors. 2020. Flight distance and return capacity of *Polistes lanio lanio*. Florida Entomol. 103:38–40.

Solereder, H. 1908. Systematic anatomy of the Dicotyledons: A handbook for laboratories of pure and applied botany. Vol. 1. Introduction, Polypetalae, Gamopetalae. Translated from the original 1899 edition by L.A. Boodle and F.E. Fritsch and revised by D.H. Scott. Clarendon Press, Oxford, UK. Vol. 2. Monochlamydeae, Addenda, Concluding remarks. Translated from the original 1899 edition by L.A. Boodle and F.E. Fritsch and revised by D.H. Scott. Clarendon Press, Oxford, UK.

Stamp, N. & J. Lucas. 1990. Spatial patterns and dispersal distances of explosively dispersing plants in Florida sandhill vegetation. J. Ecol. 78:589–600.

Sun, K., Y. Cui, & B. Hauser. 2005. Environmental stress alters genes expression and induces ovule abortion: reactive oxygen species appear as ovules commit to abort. Planta 222:632–642.

Swenson, N. & B. Enquist. 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. Amer. J. Bot. 94:451–459.

Villamil, N., K. Boege, & G. Stone. 2020. BioRxiv preprint. Ant guards influence the mating system of their plant hosts by altering pollinator behaviour. bioRxiv preprint doi: https://doi.org/10.1101/2020.02.11.943431.

Webster, G. 1967. The genera of Euphorbiaceae in the southeastern United States. J. Arnold Arbor. 48:303–361.

Webster, G. 1994. Classification of the Euphorbiaceae. Ann. Missouri Bot. Gard. 81:3–32.

Webster, G. 2014. Euphorbiaceae. In: K. Kubitzki, ed. The families and genera of flowering plants. Flowering plants. Eudicots. Malpighiales. Springer, Berlin and Heidelberg, Germany. Pp. 51–216.

Weems, H. 2001 (revised 2014). Green lynx spider. Florida Div. Pl. Industry Entomol. Circ.181. Accessed online 8/20/2020. http://entnemdept.ufl.edu/creatures/BENEFICIAL/green_lynx_spider.htm

Wiens, D., E. King, D. Nickrent, C. Calvin, & L. Vivrette. 1989. Reply to Bawa et al.: Embryo and seed abortion in plants. Nature 342:626.

Wiens, D., L. Allphin, D. Mansfield, & G. Thackray. 2002. Developmental failure and loss of reproductive capacity as a factor in extinction: a nine-year study of *Dedeckera eurekensis* (Polygonaceae). Aliso 21:55–63.

Wunderlin, R.P., B.F. Hansen, A.R. Franck, & F.B. Essig. 2020. Atlas of Florida plants (http://florida.plantatlas.usf.edu/). [S. M. Landry & K. N. Campbell (application development), USF Water Institute.] Institute for Systematic Botany, Univ. S. Florida, Tampa, U.S.A. Accessed 24 Sep 2020.

Wurdack, K., P. Hoffmann, & M. Chase. 2005. Molecular phylogenetic analysis of uniovulate Euphorbiaceae (Euphorbiaceae sensu stricto) using plastid RBCL and TRNL-F DNA sequences. Amer. J. Bot. 92:1397–1420. [*Stillingia* discussed, 1412]

Yamasaki, E., A. Kawakita, & S. Sakai. 2013. Modified leaves with disk-shaped nectaries of *Macaranga sinensis* (Euphorbiaceae) provide reward for pollinators. Amer. J. Bot. 100:628–632.