OBSERVATIONS ON ANTHESIS, FRUIT DEVELOPMENT, AND SEED DISPERSAL IN *GORDONIA LASIANTHUS* (THEACEAE)

Herrick H.K. Brown

Heritage Trust Program
South Carolina Department of Natural Resources
Columbia, South Carolina 29201, U.S.A. and
A.C. Moore Herbarium (USCH)
University of South Carolina
Columbia, South Carolina 29208, U.S.A.
herrick.brown@gmail.com

David S. Wethey

Department of Biological Sciences
University of South Carolina
Columbia, South Carolina 29208, U.S.A.
wethey@biol.sc.edu

ABSTRACT

The development of the flowers and fruits of loblolly bay (*Gordonia lasianthus*) is described in detail. Tests of meteorological conditions affecting the opening and closing of mature capsules reveals that seeds are typically released only when relative humidity falls below a critical threshold of 67%. Seedfall tests indicate that differences in the expressed aerodynamic pattern may account for variation in observed seedfall densities and affect horizontal displacement.

RESUMEN

Se describe en detalle el desarrollo de flores y frutos de (*Gordonia lasianthus*). Los test de las condiciones meteorológicas que afectan la apertura y cierre de las cápsulas maduras revelan que las semillas se liberan típicamente solo cuando la humedad relativa cae por debajo del umbral crítico del 67%. Los test de caída de semillas indican que las diferencias en el patrón aerodinámico expresado pueden contar en la variación de las densidades de semillas y afectar el desplazamiento horizontal.

INTRODUCTION

Background.—Common to Carolina bays, bayheads, and pocosins that accentuate the Southeastern Coastal Plain of the United States, *Gordonia lasianthus* (L.) Ellis, or loblolly bay, has enjoyed a long history of scrutiny. The first published description and illustration appeared in Plukenet's *Amaltheum Botanicum* (1705). Additional details regarding its taxonomic history, vernacular name, and first introduction to cultivation were summarized by Sargent and Faxon (1891). County-level range maps were published for the Carolinas by Radford et al. (1968), but these clearly reflect knowledge gaps that have since been filled by subsequent collections and observations (Forest Inventory and Analysis Database 2015; SERNEC Data Portal 2017). By compiling information from technical reports and herbarium specimens, Little (1977) produced a widely accepted range map spanning six southeastern states. More recently, occurrence data from the US Forest Service - Forest Inventory and Analysis (FIA) Program were used to produce a modeled extent which suggested a much smaller area where the species might be encountered (Ellenwood et al. 2015).

The biogeographic history of *G. lasianthus* remains uncertain, but one plausible scenario suggests that ancestral members of the tribe Gordonieae may have migrated from North America to Eastern Asia across the Bering land bridge prior to the Mid-Miocene (Li et al. 2013). Evidence for more recent changes in the area of occurrence is based on a 30-year comparison of FIA data, which indicated a non-significant northward and westward shift in recruitment of *G. lasianthus* potentially associated with climatological changes in available soil moisture (Fei et al. 2017). Gresham and Lipscomb (1985) gave a detailed account of the ecology of *G. lasianthus* including soil conditions, the timing of fruit development, release of seeds, and seed dispersal distance. While recruitment events and population migration can be extrapolated from occurrence data, some fundamental aspects of dispersal remain undefined such as the mechanisms involved in the release of seeds and seed flight time. Further details are presented here regarding the timing of phenological events with particular focus on meteorological conditions that affect the release of seeds, seedfall velocities, and seed dispersal

mechanisms. These properties are essential for evaluating proposed migration paths, understanding the current distribution, and modeling future distribution as influenced by a changing climate.

Phenology.—Details presented here, where not otherwise indicated, are based on the first author's personal observations primarily of a cultivated specimen growing at a private residence in Columbia, South Carolina. While the timing of phenological events may vary by latitude and location, these observations were generally consistent with a brief survey of herbarium specimen images (SERNEC Data Portal 2017) representing localities throughout the species' range and field observations in coastal South Carolina presented by Gresham and Lipscomb (1985). The first flush of new foliage for *G. lasianthus* begins about the last week of March, and by May young branches first emerge and continue to grow throughout the season. These are typically born on the 4th–6th most proximal leaf axils of new growth. In subsequent and distal axils, the elongated pedicels emerge from the main axis of new growth or from the newly emergent branches and are quite prominent; ranging 3.5–6 cm in length. The pedicels bear 3–4 leafy bracts and may appear to be additional vegetative branches. During this period leaves produced in the course of the last growing season may senesce and blush a conspicuous red hue in stark contrast to the dark green of those leaves retained and the lighter green of the fresh foliage. Throughout May, flower buds begin their development and transition from suggesting a small green pea to a cream-white sphere approximately 3 cm in diameter (Fig. 1). Anderson (1983) notes that aestivation is imbricate. The margins of the sepals and first (lower-most) petal are similarly ciliate. This characteristic is adequately depicted by Small (1933) and described in detail by Anderson (1983), but it appears to have been omitted in most early illustrations (e.g., Ellis 1770; Sargent & Faxon 1891) in which all petals are depicted as having entire margins. An illustration in *Curtis's Botanical Magazine* (Sims 1803), however, erred on the opposite extreme by depicting all petal margins as ciliate. Only the first petal bears a ciliate margin, and it remains bowl-shaped after anthesis (Fig. 2). The four more distal petals bear lacerate or crinkled margins and are only shallowly concave at anthesis. On the day prior to anthesis, the first petal, which almost completely envelops the other four, will begin to reflex and a small gap will appear between it and the next distal petal.

Anthesis.—Flowers are perfect with superior ovaries and begin to open about the first week of June. Anthesis may be delayed for several days during prolonged dry spells, but once initiated, the process occurs rapidly at daybreak and will last little more than 24 hrs. The androecium is adnate to the petal bases where the fused filaments form pronounced lobes that connect in a thick, fleshy ring bearing many anthers. The gynoecium consists of a single style approximately 1 cm long which terminates in a star-shaped stigma that is only slightly broader than the style. Nectaries are located at the junction of the staminal cup and the base of the style. A faintly pleasant fragrance is only detectable in close proximity to flowers. During the day-long pollination, flowers may be visited by a variety of insects including small beetles, ants, bees of the genus *Augochloropsis* or *Augochlorella* (Fig. 3), the occasional ruby-throated hummingbird (*Archilochus colubris*), and others including bumblebees, thrips, and flies (Gresham & Lipscomb 1985, 1990). The diversity of potential pollinators may be due to the over production of pollen and pseudopollen (Tsou 1997, 1998; Prince & Parks 2001) which is provided in such ample supply so as to placate pollen thieves. Other visitors appear to only seek the nectar. While short-lived, this limited window of opportunity is sufficient to ensure successful pollination.

As new flowers open the following morning, those from the previous day are shed. The entire corolla and its adnate androecium are forced into abscission by the contraction of the sepals toward the distal portion of the flower. This action not only sloughs off the fleshiest parts of the flower (an important first step toward removing excess moisture in a developing xerochastic fruit which must dry in order to open), but also leaves the sepals tightly clasping, and thus protecting, the young ovary.

Fruit Development.—Over the course of approximately two months, the ovary will continue to develop and reach a length of approximately 1.5 cm. By this time the fruit exceeds more than twice the length of the clasping sepals (Fig. 4). When fully matured, the ovate fruit is held erect on the pedicels and continues to ripen for another two months. By October (4–5 mos total), the fruit fades from green to brown, and the silvery-tinged hairs on its surface are readily apparent; however, the pedicels will remain green for several more weeks. When the fruit walls are adequately dehydrated, five lines of loculicidal dehiscence begin where the now-withered

Fɪɢ. 1. *Gordonia lasianthus.* Buds and flower at various stages of development.

Fɪɢ. 2. *Gordonia lasianthus.* **A.** A fully open flower. Note the ciliate margin and concave shape of the first petal (lowest pictured). Staminal lobes project from the base of petals. **B.** The same flower viewed from above. Note the star-shaped stigma.

style was attached and continue for about 80% of the fruit's length (Fig. 4). As part of this process, a fissure forms between the inner edges of the septa and the columella leaving each valve (each composed of 2 halves of adjacent carpels; i.e., the carpels are distally bifid) hinged only at the proximal end of the fruit. As the fruit continues to open, the outward (distal to the columella) movement of the valves effectively forces the removal of the tardily senescent sepals (Fig. 4). This results in an exposed zone of vascular bundle scars associated with the three lower whorls of floral parts. Assuming no ovules are aborted, four seeds are born in each of five locules (20 seeds total) and are paired on either side of each seam adjacent to the septum. Placentation is basal/central, and each seed bears a thin, membranous extension of tissue originating from the raphe (Tsou 1997, 1998) which forms a small "wing" toward the apical end of the fruit (Fig. 4).

Seed Dispersal.—Seedfall reaches its maximum from October to December, but may continue much later into March of the following year (Gresham & Lipscomb 1985, 1990). The wings, which are approximately 1.5–2 times the length of the seed, may carry seeds up to 1.5 times the height of the parent tree; however, the majority of seeds fall within a distance that is less than one-half the parent tree height (Gresham & Lipscomb 1985, 1990). Subsequent observations (present study) have revealed that the timing of dispersal events is carefully controlled by dry weather conditions, which trigger a dehiscence in the xerochastic fruits. It is important to note, however, that fruits may again close when the humidity is elevated.

Initial Observations.—In October 2015, field observations revealed noticeable movement in the valves of mature fruits following dehiscence in a cultivated specimen of *G. lasianthus* growing at a private residence in Columbia, South Carolina. The once-open capsules were completely closed during a precipitation event associated with an approaching cold front. It was assumed that relative humidity (RH) while raining was near 100%. After the skies cleared, cold dry air moved in accompanied by gusty winds. Four hours after the rain, the
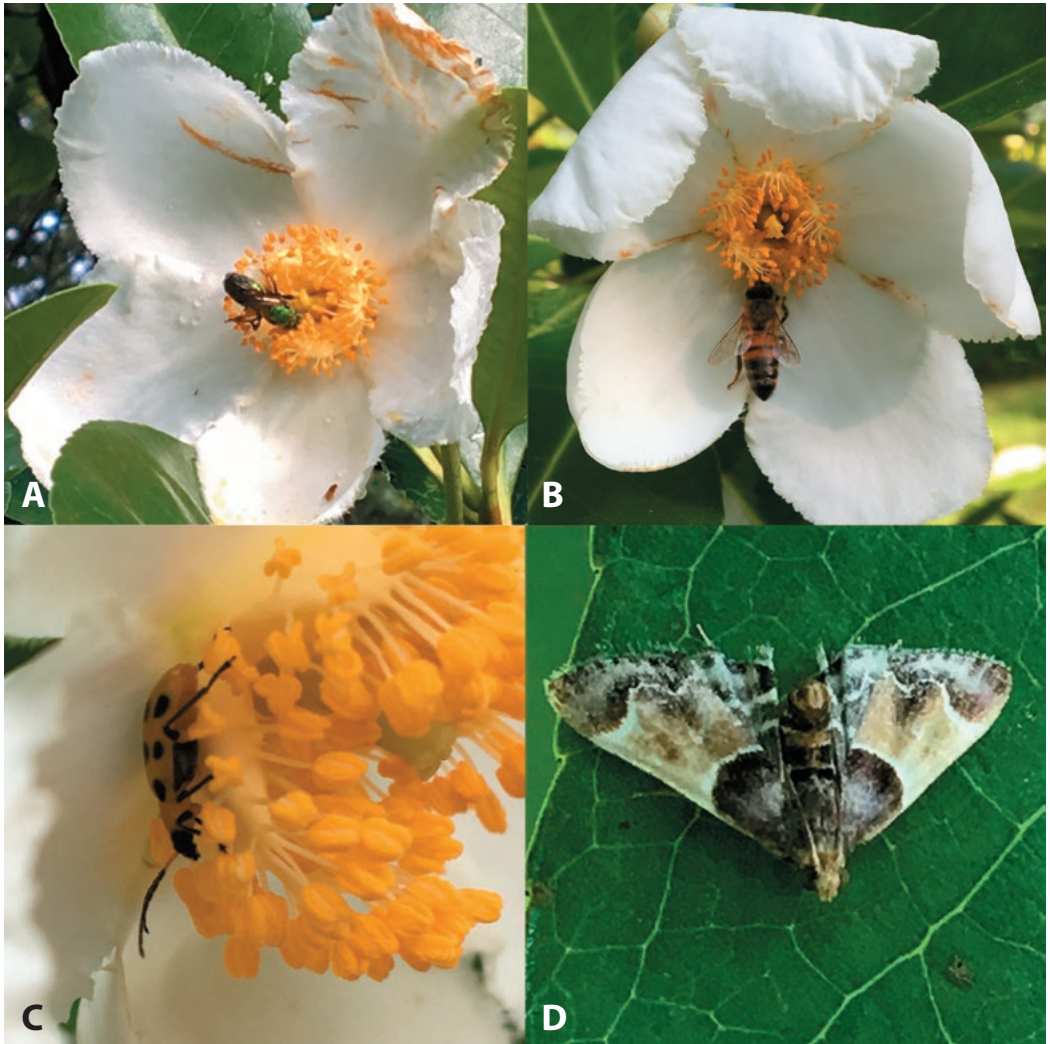
Fɪɢ. 3. *Gordonia lasianthus*. Pollinators, pollen thieves, and other visitors. **A.** Native bee, possibly (*Augochlorella* sp.); note the fruit fly on first (lowest) petal. **B.** Honeybee (*Apis* sp.). **C.** Spotted cucumber beetle (*Diabrotica undecimpunctata*). **D.** Meal moth (*Pyralis farinalis*).

capsules were again fully open and RH had dropped to near 40% (NOAA weather observations). This phenomenon suggested that wind-mediated dispersal events in *G. lasianthus* might only occur during periods of low RH.

MATERIAL AND METHODS

Meteorological Conditions Affecting Release of Seeds

Testing RH.—To test the effects of RH on the expansion and contraction of the valves, we collected five recently dehisced fruits from the same cultivated specimen initially observed. While the pedicels were beginning to turn brown, they retained some green color and therefore also retained some residual moisture. We designed small humidity chambers from plastic deli food containers into which we placed two small dishes. In one dish
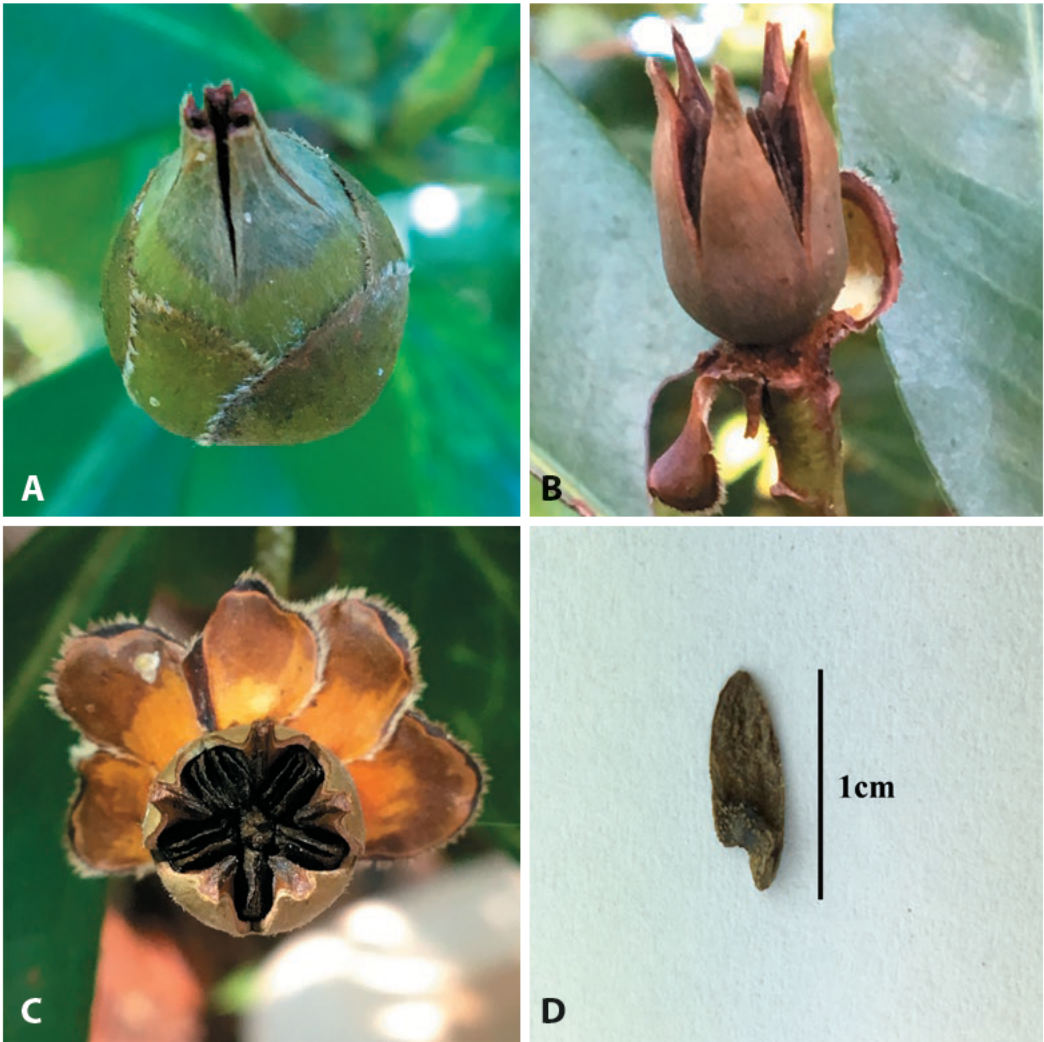
Fig. 4. *Gordonia lasianthus.* **A.** A mature fruit now exceeding the sepals which remain clasping as fissures begin forming along lines of dehiscence. **B.** Mature fruit showing the release of tardily senescent sepals. Note the pedicel is still green. **C.** Viewed from above, the seeds (wings up) are neatly arranged four in each locule. **D.** A seed enlarged approximately 4× as it would appear in a capsule with its wing up.

we placed a small amount of saturated salt solution, and in the other dish a small amount of deionized water. We used a rubber flask stopper as a stand for each capsule by placing the pedicel through the hole in the stopper, which enabled us to maintain the upright orientation of the fruit. The chambers were first covered with plastic wrap before the lids were affixed in an effort to ensure a sufficient seal.

To control humidity, we selected a variety of salt solutions that would maintain specific RH levels to approximate our field observations (Table 1). Fruits were exposed to each humidity chamber for a 24-hour period, after which time they were removed. Before transferring to a different RH treatment, the maximum distance between non-adjacent valve apices was recorded. In an effort to account for any variation in the ability of the fruits to expand or contract at different rates, we varied the progression between RH treatments by moving fruits into the chamber with the next highest RH initially and then reversed this process.

Table 1. Saturated salt solutions and expected relative humidity.

Salt	%RH	Mean Apeture (% Open)
KNO_3	95	48
KCl	85	61
NaCl	75	73
NH_4NO_3	67	76
MgCl	33	92

For each fruit we expressed the degree to which it was open (aperture) at varying RH as a percentage. This was calculated for each fruit by dividing the maximum distance recorded between non-adjacent valve apices under each RH treatment by the maximum distance recorded between non-adjacent valve apices during the entire trial. We then calculated the mean aperture for all fruits at each RH.

While general trends were evident in the data recorded from humidity chamber experiments, we sought to document the time required for capsules to open or close. In preparation for documenting the opening of capsules, fruits were exposed to 95% RH (using the same methods described above) for 24 hrs. Closed fruits were removed from the humidity chamber, and the distance between apices of valves was recorded. Fruits were then placed under a fume hood, which provided a steady stream of airflow at low "ambient" RH. Time-lapsed video of the fruits was recorded with a JVC GZ-HM860 HD Everio Camcorder at a rate of one frame every 80 s for approximately 4 hrs (when played back, the video was 2400× speed). We used 1 cm graph paper as a backdrop so that we could measure the movement of the valves on video playback.

To record the time required for fruits to close, we removed them from the fume hood, recorded the distance between the apices of the valves, and misted them lightly with deionized water. The moistened fruits were then placed under an inverted 10 gal aquarium that also covered a dish of water. A folded paper towel was allowed to wick water from the dish and effectively functioned as an evaporative radiator. Video was recorded using the same equipment and settings as before.

Seedfall Velocity and Dispersal Mechanisms

Seed Dispersal.—Dispersal distance is the result of interactions between the seedfall velocity and the aerodynamics (mechanism) of the seed or diaspore and other factors including horizontal wind speed and direction (Augspurger & Franson 1993). To better understand how these interactions might impact dispersal distance, we carefully removed twenty seeds using forceps from several mature fruits of a herbarium specimen: U.S.A. South Carolina. Sumter Co.: Electronic Weapons Range, about 7.5 mi SE of Wedgefield, 4 Apr 2002, *Nelson 23418* (USCH). Prior to taking measurements, each seed was placed in a glass vial along with a printed, paper label with the assigned number (1–20).

Seed Weights.—We used an electro balance (Cahn C-27) to weigh seeds from *Nelson 23418* to the nearest μg. For comparison, we also weighed seeds collected from a cultivated specimen in Columbia, South Carolina to determine if fresh material might be heavier due to potentially higher residual moisture content. Additionally, we recorded the weights of freshly collected and one-year-old, dry capsules from the same cultivated specimen.

Seed Wing Area and Wing-loading.—We used a Canon EOS 5D Mark II (21.1 megapixel) camera with Canon 50mm f/2.5 EF compact macro lens to capture high-quality close-up images of seeds with a scale bar. We then calculated the total surface area (seed plus the wing) for each seed using ImageJ (Rasband 1997). We calculated wing-loading (WL) in Pascals as the gravitational acceleration (9.81 ms^{-2}) times the seed weight (wt) in kg divided by the area (a) in m^2 of the wing.

$$WL = 9.81 \times \left(\frac{wt}{a}\right)$$

Seedfall Velocity.—In order to calculate seedfall velocities in still air, we recorded video at 150 frames s^{-1} with a JVC GZ-HM860 HD Everio Camcorder to capture the paths of seeds that were dropped from a height of approximately 2 m. The viewing area included a vertically oriented, metric measuring tape and a standardized

label that identified the seed number and repetition. Each seed was subjected to a minimum of three repetitions (seeds exhibiting inconsistent behavior were subjected to additional repetitions). Seeds were manually dropped approximately 1 dm in front of the measuring tape using forceps and an outstretched arm while standing on a stepladder. Since the seeds were originally collected in 2002 (about 13 yrs prior to the present study) and then dried for preparation as a voucher, they were handled only with forceps in order to avoid any potential transfer of moisture (which might otherwise affect seed weight and wing loading). In order to capture the maximum velocity of falling seeds, the camera was focused between 55 cm and 95 cm above the floor, which encompassed the point at which the seed had fallen 1.25 m to 1.55 m. Playback at normal speed produced slow motion videos which allowed for the identification of the first frame (FF) when the seed had entered the viewing area. Since the capture frame rate was 150 frames s^{-1}, every 10 frames equal $\frac{1}{15}$ s. Therefore, once the FF was identified, we recorded the vertical position relative to the tape measure and then advanced the video 10 frames before recording the next (lower) vertical position. This process was repeated until the seed was no longer visible in the viewing area.

Seed Dispersal Mechanisms.—Aerodynamic patterns were characterized based on the orientation and position of the wing during frame by frame advancement of the same videos used to calculate seedfall velocity.

Analysis.—We used a type III last-wise ANCOVA available in the car package in R (Fox & Weisberg 2011) to compare the effects of wing-loading and aerodynamic properties on seed velocities. This included a preliminary test for equal slopes followed by a test of the adjusted means.

RESULTS

Effects of RH on Seed Capsule Opening.—Initial observations suggested that an RH of approximately 40% would induce valves to open. However, humidity chamber tests revealed that most fruits were sufficiently open (mean aperture of 76%) to release seeds when RH was as high as 67% (Table 1).

Under drying conditions, timelapse video analysis showed that the valves had ceased their outward (opening) movement at 180 frames or 4 hrs. By contrast, however, when misted and exposed to humid conditions, the fruits closed after 70 frames or 1.55 hrs. Thus, fruit closure was attained in less than half the time it takes to fully open.

Seed Weights.—We found no significant difference in the weights of fresh or dried seeds. Mean dry seed weight was 2.972e-6 kg (n = 20, min 1.450e-6 kg, max 3.521e-6 kg, SE 0.103e-6 kg,), and the mean weight of fresh and dried capsules was 0.65967 g. Gresham and Lipscomb (1985) apparently in error reported a much heavier mean seed weight of 0.69 g (SE 0.03 g) which is consistent with the weight of a capsule, however they also provided an estimate of approximately 292,000 (SE 15,000) seeds per kilogram. The later estimate equates to a seed weight of about 3.4247e-6 kg, which is similar to our recorded mean and within the range of weights we recorded.

Wing Area and Wing-Loading.—Mean seed wing area was 19.25e-6 m^2 (SE 0.53e-6 m^2), and mean wing-loading was 1.5151 kg/ms^{-2} (SE 0.0417 kg/ms^{-2}).

Seed Dispersal Mechanism.—Morphologically the seeds of *G. lasianthus* are autogyros (Augspurger 1986) and by design during descent should rotate around a vertical axis roughly centered on the heavy end of the diaspore (where the actual embryo is located opposite the wing). However, we observed three different aerodynamic patterns, with some seeds exhibiting more than one kind of pattern on subsequent repetitions. The following aerodynamic patterns were observed:

Autogyration sensu Augspurger (1986), or rotation around a vertical axis like the samara produced by species of *Acer*.

Autorotation sensu Vogel (1981), or rotation around a horizontal axis like the samara produced by *Ailanthus altissima*.

Barochory, or simple gravitational dispersal lacking a readily apparent aerodynamic pattern.

TABLE 2. Mean velocities for seeds exhibiting different aerodynamic patterns.

Aerodynamic Pattern	Mean Velocity (ms^{-1})	SE	SD
Autogyration	0.983976	0.01137598	0.1203921
Autorotation	1.419054	0.01691064	0.06764256
Barochory	4.113542	0.07266432	0.2055257

Analysis.—When testing for interaction between wing-loading and aerodynamic types, the type III last-wise ANCOVA initially revealed that the slopes were equal (p = 0.4565, DF = 2, F = 0.82). A second test found significant differences among the adjusted means (p = 2.2e-16, DF = 2, F = 1316.21). We therefore concluded that there was no effect from wing-loading relative to observed velocities. However, the effects of aerodynamic properties were very strong, with seeds exhibiting gyration or rotation falling at significantly slower velocities than those exhibiting simple barochory (Table 2).

DISCUSSION

Anemochory is considered a derived character state which may arise in certain climates lacking other dispersal agents (Van der Pijl 1982). Effectively the morphology of the diaspore (i.e., the seed in *G. lasianthus*), through interactions with the air, serves to slow the rate of descent and maximize horizontal displacement (Van der Pijl 1982; Augspurger 1986; Augspurger & Franson 1987; Matlack 1987). Timing the release of seeds to coincide with optimal conditions for dispersal can be a critical first step toward ensuring successful recruitment. For example, diaspores of the common dandelion (*Taraxacum officinale*) are only released when wind velocities exceed a threshold (Van der Pijl 1982), thus ensuring that seeds will be carried some distance from the parent plant. In *G. lasianthus* however, the maturation of fruits coincides with a seasonal decline in precipitation, and capsules typically open when RH < 67%. Air turbulence is still required to move supple, fruit-bearing branches and shake seeds out of the open capsules (Gresham & Lipscomb 1985, 1990). Thus, multiple meteorological conditions must be met before maximum dispersal distances can be achieved. Van der Pijl (1982) refers to these complexities as "Polychory and Attendant Phenomena." In this context, dispersal is characterized not only by its spatial elements but also on a temporal scale. Such interactions may suggest a tradeoff between optimal conditions for dispersal and the seasonal availability of habitat suitable for seedling establishment.

Being rid of excess weight from atmospheric moisture when dry, wing-loading on seeds exhibiting autogyration or autorotation is reduced which permits slower fall velocities and allows more time for horizontal displacement (Augspurger 1986; Augspurger & Franson 1987; Matlack 1987; Thomson & Neal 1989). Conversely, during precipitation events or when RH exceeds a critical threshold, wind-dispersed seeds are more likely to absorb excess moisture which negatively impacts dispersal potential (Augspurger & Franson 1987; Matlack 1987). Given that the fruits of *G. lasianthus* close when RH exceeds a critical threshold of 67%, it is unlikely that moistened seeds would be shed in a natural setting. The fruits, therefore, serve as an important mechanism for preventing the release of seeds when weather conditions would limit dispersal potential and diminish the chances of successful seedling establishment.

Germination in *G. lasianthus* apparently requires contact with mineral soil (Gresham & Lipscomb 1985, 1990) which suggests that seedling viability increases proportionately with dispersal distance. However, nearly all seeds fall within a distance equal to the parent tree height (Gresham & Lipscomb 1985, 1990). The observed variation in the aerodynamic properties of different seeds and the associated differences in fall velocities may explain some of the variation in seedfall density reported by Gresham & Lipscomb (1985). However, other factors such as the general columnar growth form of source trees (Gresham & Lipscomb 1985, 1990), climate dynamics, and ecological variation across the species' range may all contribute to differences in the dispersal distance. Dispersal potential can also be functionally limited, suggesting the reduced likelihood of encountering favorable environments beyond those more proximal to the source tree (Van der Pijl 1982; Augspurger & Kitajima 1992).

Fɪɢ. 5. *Gordonia lasianthus.* National Champion Jacksonville Arboretum, Jacksonville, Florida (Duval County), U.S.A. The recorded height is 117 ft, though LiDAR data and personal estimates suggest it may actually be less than 100 ft tall.

TABLE 3. FIA survey plot data (n = 10,537) show mean Actual Tree Height (ACTUALHT) equates to a size equivalent to 30 years of age. ACTUALHT is defined as total height of the tree including any missing portion, which if available is measured and if not is estimated.

Mean ACTUALHT (m)	Min	Max	SD
12.2	1.5	33.5	5.3

Consistent with "pioneer vegetation" (Van der Pijl 1982), recruitment rates in *G. lasianthus* evidently increase on disturbed sites (Gresham & Lipscomb 1985, 1990). Mature trees resprout vigorously following fire (Gresham & Lipscomb 1985; Matlaga et al. 2010) or mechanical damage, and will flower on the new growth (pers. obs.). Low grade, surface fires may provide sufficient clearing of leaf litter and expose the soil surface, thereby increasing the chances for recruitment proximal to source trees. Prolonged dry conditions have been suggested to facilitate invasion into new sites along the edges of bay heads (Landman & Menges 1999).

Pond pine (*Pinus serotina*), which also produces an anemochorous, winged seed, shares several autecological similarities with *G. lasianthus* including increased seedling establishment following fire and the ability to sprout if top-killed (Gresham & Lipscomb 1985). The two species are often found in close association with each other in seasonally wet depressions that occur in the fire-dominated landscape of longleaf pine (*Pinus palustris*) savannas. FIA survey plot data support this relationship across all states in which *G. lasianthus* is found, except in Mississippi where *P. serotina* is not known to occur, and comparison of the mapped and modeled ranges (Little Jr. 1971, 1977; Ellenwood et al. 2015) show a high degree of overlap.

In the absence of fire or other environmental disturbance, protected sites support some of the largest specimens (State and National Champions) of *G. lasianthus* (Fig. 5). These habitats may include bay heads in Florida (Stalter et al. 1980; Landman & Menges 1999; Matlaga et al. 2010), the interiors of pocosins and Carolina bays (Gresham & Lipscomb 1985, 1990), and hardwood drainages in the Sandhills of South Carolina (pers. obs.). Given denser canopy cover, these sites may have reduced herbaceous diversity, and recruitment of *G. lasianthus* is likely to be low due to lack of suitable conditions for germination.

While overwhelmingly *G. lasianthus* appears to be well-adapted to colonizing recently disturbed habitats, the limited dispersal potential of its seeds restricts recruitment opportunities to localities proximal to the source tree. Therefore, increases in population density and regular migration likely depend on recurrent, natural disturbances such as fire which can sustain early successional habitats in the vicinity of source trees. If optimal conditions for recruitment are constant, the population migration rate can be calculated. Assuming that the majority of seeds fall within 2 times the parent tree height (Gresham & Lipscomb 1990) and the mean height of trees recorded in FIA data (Table 3) equates to individuals approaching 30 yrs of age (Gresham & Lipscomb 1985), we estimate that a population would take upwards of 1200 years to migrate 1 km. Thus, any noticeable changes in population distributions or range-wide shifts are likely to occur on a millennial scale. When confronted with an accelerated rate of climate change, conservation strategies need to be adaptable and should consider challenges a species may encounter when dispersal rates and distances fall short of suitable environmental conditions.

REFERENCES

ANDERSON, L.C. 1983. Trichomes and stomata of *Gordonia lasianthus* (Theaceae). Sida 10:103–113.

AUGSPURGER, C.K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. Amer. J. Bot. 73:353–363.

Augspurger, C.K. & S.E. Franson. 1987. Wind dispersal of artificial fruits varying in mass, area, and morphology. Ecology 68:27–42.

Augspurger, C.K. & S.E. Franson. 1993. Consequences for seed distributions of intra-crop variation in wing-loading of wind- dispersed species. Vegetatio 107/108:121–132.

Augspurger, C.K. & K. Kitajima. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. Ecology 73:1270–1284.

Ellenwood, J.R., F.J. Krist Jr., & S.A. Romero. 2015. National individual tree species atlas. U.S. Forest Service, Forest Health Protection, Forest Health Technology Enterprise Team, Fort Collins, Colorado, U.S.A.

Ellis, J. 1770. A copy of a letter from John Ellis, Esq; F.R.S. to Dr. Linnaeus, F.R.S. &c. Philos. Trans. Roy. Soc. London 60:518–523.

Fei, S., J.M. Desprez, K.M. Potter, I. Jo, J.A. Knott, & C.M. Oswalt. 2017. Divergence of species responses to climate change. Sci. Adv. 3:1–9.

Forest Inventory And Analysis Database. 2015. U.S. Department of Agriculture, Forest Service, Northern Research Station, St. Paul, Minnesota, U.S.A. Accessed 14 Feb 2015.

Fox, J. & S. Weisberg. 2011. An R companion to applied regression. Sage, Thousand Oaks, California, U.S.A.

Gresham, C.A. & D.J. Lipscomb. 1985. Selected ecological characteristics of *Gordonia lasianthus* in coastal South Carolina. Bull. Torrey Bot. Club 112:53–58.

Gresham, C.A. & D.J. Lipscomb. 1990. *Gordonia lasianthus* (L.) Ellis, loblolly-bay. In: R.M. Burns & B.H. Honkala, eds. Silvics of North America. Vol. 2. Hardwoods Agriculture Handbook 654. USDA Forest Service, Washington, D.C., U.S.A. Pp. 365–369.

Landman, G.B. & E.S. Menges. 1999. Dynamics of woody bayhead invasion into seasonal ponds in South Central Florida. Castanea 64:130–137.

Li, M.M., J.H. Li, P. Del Tredici, J. Corajod, & C.X. Fu. 2013. Phylogenetics and biogeography of Theaceae based on sequences of plastid genes. J. Syst. Evol. 51:396–404.

Little Jr., E.L. 1971. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. U.S. Dep. Agric. Misc. Publ. 1146:9.

Little Jr., E.L. 1977. Atlas of United States trees. Vol. 4. Minor eastern hardwoods. U.S. Dep. Agric. Misc. Publ. 1342:17.

Matlack, G.R. 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant species. Amer. J. Bot. 74:1150–1160.

Matlaga, D.P., P.F. Q.-Ascendo, E.S. Menges, & R. Pickert. 2010. Fire mediated edge effects in bayhead tree islands. J. Veg. Sci. 21:190–200.

Plukenet, L. 1705. Amaltheum Botanicum. Pubished by the author, London, U.K.

Prince, L.M. & C.R. Parks. 2001. Phylogenetic relationships of Theaceae inferred from chloroplast DNA sequence. Amer. J. Bot. 88:2309–2320.

Radford, A.E., H.E. Ahles, & C.R. Bell. 1968. Manual of the vascular flora of the Carolinas. The University of North Carolina Press, Chapel Hill, North Carolina, U.S.A.

Rasband, W.S. 1997. ImageJ. U.S. National Institutes of Health, Bethesda, Maryland, U.S.A.

Sargent, C.S. & C.E. Faxon. 1891. The silva of North America: A description of the trees which grow naturally in North America exclusive of Mexico. Houghton, Mifflin, and Company, Boston, New York, U.S.A.

sernec data portal. 2017. http//:sernecportal.org/portal/index.php. Accessed 27 Nov 2017.

Sims, J., Ed. 1803. *Gordonia lasianthus*. Smooth *Gordonia*, or Loblolly Bay. Curtis's Bot. Mag. 18. Academic Press [etc.], London, U.K.

Small, J.K. 1933. Manual of the southeastern flora: Being descriptions of the seed plants growing naturally in Florida, Alabama, Mississippi, eastern Louisiana, Tennessee, North Carolina, South Carolina, and Georgia. University of North Carolina Press, Chapel Hill, North Carolina, U.S.A.

Stalter, R., A. Laessle, & P. Bielling. 1980. Some ecological observations of a *Gordonia lasianthus* Bayhead, Hughes Island, Florida. Castanea 45:233–235.

Thomson, J.D. & P.R. Neal. 1989. Wind dispersal of tree seeds & fruits. Amer. Biol. Teacher. 51:482–486.

Tsou, C.H. 1997. Embryology of the Theaceae-anther and ovule development of *Camellia, Franklinia,* and *Schima*. Amer. J. Bot. 84:369–381.

Tsou, C.H. 1998. Early floral development of Camellioideae (Theaceae). Amer. J. Bot. 85:1531–1547.

Van Der Pijl, L. 1982. Principles of dispersal in higher plants. 3rd ed. Springer, Berlin, Germany.

Vogel, S. 1981. Life in moving fluids: The physical biology of flow. Willard Grant Press, Boston, Massachusetts, U.S.A.