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WETLAND INVASIONS

Rare Production of Seeds by Invasive *Alternanthera philoxeroides* (Alligator Weed) in North America Observed in Terrestrial Populations

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Abstract

Fruiting in angiosperms is a complex process that is partially influenced by the external environment. In the case of invasive *Alternanthera philoxeroides*, introduction of this species to multiple global regions may have caused the failure of its sexual reproductive system due to genetic bottleneck and a propensity for clonal propagation. *Alternanthera philoxeroides* fruits rarely in its invaded ranges which raises questions regarding environmental stimuli that affect fruiting; we propose here that *A. philoxeroides* fruiting is partly caused by terrestrial conditions. Two instances of fruiting *A. philoxeroides* were observed in disparate locations in northern Mississippi, USA during 2022. Despite prolific fruiting in western Mississippi, no seeds germinated under any dormancy treatments at increasing durations. In both populations, fruiting was only observed in terrestrial forms of *A. philoxeroides*, even when nearby aquatic forms exhibited flowering but no fruiting. The exclusivity of fruiting to terrestrial *A. philoxeroides* seems to suggest drier conditions are an environmental trigger for *A. philoxeroides* fruiting. However, this process does not account for non-viability of seeds. Previous research suggests low genetic diversity can result in formation of nonviable seeds whether due to inbreeding depression or another unknown mechanism. We postulate that aquatic conditions present a barrier to *A. philoxeroides* fruiting and that if habitats transition from wet to dry, fruiting may be induced. However, environments are shifting and multiple *A. philoxeroides* haplotypes have been observed in the invaded range thus future work should assess the effects of terrestrial conditions on fruiting and seed viability in different *A. philoxeroides* haplotypes.

Keywords Aquatic Plant · Asexual Propagation · Environmental Stimulus · Fruit · Germination Trial · Sexual Reproduction

Background

Flowering and fruiting of angiosperms are complex processes that often involve significant input from the external environment (Du et al. 2020). While in some cases, the external stimuli that elicit fruiting events are well studied, in many plants these interactions remain unknown (Kapoor et al. 2022). While seeds are considered the primary unit of long distance dispersal, species that exhibit prolific clonal propagation often have complex dispersal strategies (Nathan 2006). Even though asexual propagation can improve the ability of plants to find suitable mates, there are several processes through which clonal propagation interferes with the sexual systems of plants (Barrett 2015). *Alternanthera philoxeroides* (Mart.) Griseb. (alligator weed), native to the Paraná River Valley of Argentina and Paraguay, exemplifies this conflict as an invasive aquatic plant that exhibits clonal propagation as its primary means of reproduction and dispersal in the invaded range (Tanveer et al. 2018). As is the case with other notable invasive aquatic plants, *A. philoxeroides* saw a major shift in its reproductive system due in part to the intense founder effect inherent in invasion (Barrett et al. 2008). Specifically, *A. philoxeroides* rarely fruits in its invaded range and viable seeds seem to not occur (Tanveer et al. 2018). Although *A. philoxeroides* readily flowers throughout the summer, flowers usually mature and dissociate from the spike without the development of fruit or seed (Julien et al. 1992; European and Mediterranean Plant Protection Organization 2016). As such, records of fruiting

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A. philoxeroides are highly sporadic and even when fruiting events are reported.

While the scarcity of fruiting, invasive *A. philoxeroides* is well cited in the literature, no biological mechanism has been proposed to explain this scarcity (Julien et al. 1995; Dugdale and Champion 2012; Tanveer et al. 2018). Flowering and fruiting can be strongly influenced by the external environment and these influences are often complex (Cho et al. 2017; Mendoza et al. 2017). Currently, there have been no efforts to determine environmental influence on *A. philoxeroides* fruiting, but *A. philoxeroides* exhibits two discrete growth forms: an aquatic growth form and a terrestrial growth form (Julien et al. 1992). The most notable difference between the aquatic and terrestrial growth form is the absence of a taproot in aquatic *A. philoxeroides* versus the presence of a taproot in terrestrial *A. philoxeroides* (Julien et al. 1992). However, our observations suggest that absence of fruiting in aquatic *A. philoxeroides* and production of fruit by terrestrial *A. philoxeroides* may also differentiate the two growth forms. The objectives of this paper are to report the first record of *A. philoxeroides* seed production in over 40 years and suggest terrestrial conditions may serve as the environmental stimulus for this phenomenon.

Methods

Site Descriptions

The first population of *A. philoxeroides* in this study was observed at Muscadine Farms Wildlife Management Area (WMA) in Washington County, Mississippi, USA (33.2078° N, 90.9640° W; Fig. 1) on 30 June 2022. This population is in the Mississippi Delta which is the region of northwestern Mississippi in the Mississippi River Alluvial Valley. Muscadine Farms WMA is a publicly-managed land unit primarily managed for migratory waterfowl habitat. The WMA consists of 90 leveed pools covering approximately 809 ha that are seeded with desirable forage and flooded during fall, winter, and spring in an effort to support migratory waterfowl habitat. Many pools support dense stands of *A. philoxeroides* cohabited by *Persicaria* sp. (L.) Mill. and *Ludwigia* sp. L. The pool supporting the population used in this study was flooded in early October 2021 and drained in late April 2022. *Alternanthera philoxeroides* was fruiting prolifically at this site and all plants were growing in a terrestrial environment.

Another population was observed in a spillway on the south side of Columbus Lake in Lowndes County, Mississippi, USA (33.5243° N, 88.4624° W; Fig. 1) on 26 July 2022. This system is connected to the greater Tennessee-Tombigbee Waterway in the Black Belt Prairie region of eastern Mississippi. This spillway has an area of roughly 0.1 ha and is periodically to semi-permanently flooded with considerable drained periods. In 2022, the spillway was flooded from January to June, after which it remained nearly completely drained through September. This spillway has a dense population of *A. philoxeroides* that covers roughly ninety percent of the spillway. The *A. philoxeroides* population in this system is densest in the channel with the margins of the population encroaching on upland habitat directly adjacent to the spillway. While flowering *A. philoxeroides* was dense throughout the spillway, fruiting plants were sparse and were only observed on the upland margin of the system where plants were subjected to prolonged terrestrial conditions. Cohabitants of this system include *Hydrolea uniflora* Raf., *Persicaria* sp. (L.) Mill., *Pontederia crassipes* Mart., *Salvinia molesta* D.S.Mitch, and *Azolla filiculoides* Lam.

Plant Material

The *A. philoxeroides* population at Muscadine Farms WMA exhibited widespread flowering and fruiting on 30 June and 1 July, 2022. Vouchers that exhibited both flowering and fruiting *A. philoxeroides* were collected on 30 June and 1 July, 2022 (Schmid 14 MISSA037070; Schmid 15 MISSA037071; Figs. 2 & 3; supplementary file 1). Fruits were harvested via collection of entire infructescence. Fruit stock was stored in a dark, dry environment at room temperature for up to 14 days after collection. At Columbus Lake spillway, the *A. philoxeroides* population exhibited widespread flowering with the only fruiting exhibited in individuals growing on the upland margins of the spillway. A voucher specimen that exhibited fruiting was collected from this population on 26 July, 2022 (Schmid 19 MISSA037072; Fig. 4; supplementary file 1). Insufficient fruits were collected from the Columbus Lake spillway population to test seed viability.

Germination Trials

Seeds were subjected to two factors that may affect dormancy and thus germination: dormancy environment and duration. After two weeks of dark, dry storage at room temperature (22 °C), fruits were randomly assigned to one of four environments: a reference that underwent no dormancy treatment, a room temperature (22 °C) dry substrate (filter paper) treatment, a cold (7 °C) dry substrate treatment, and a cold wet substrate treatment. Within each environment, seeds were subjected to four dormancy durations: one, two, four, and eight weeks. After the specified treatment duration, three pseudo replicates of fifty fruits were placed in a petri dish lined with wet filter paper to stimulate seed germination. Germination was attempted on reference group immediately. Petri dishes were housed in a growth chamber

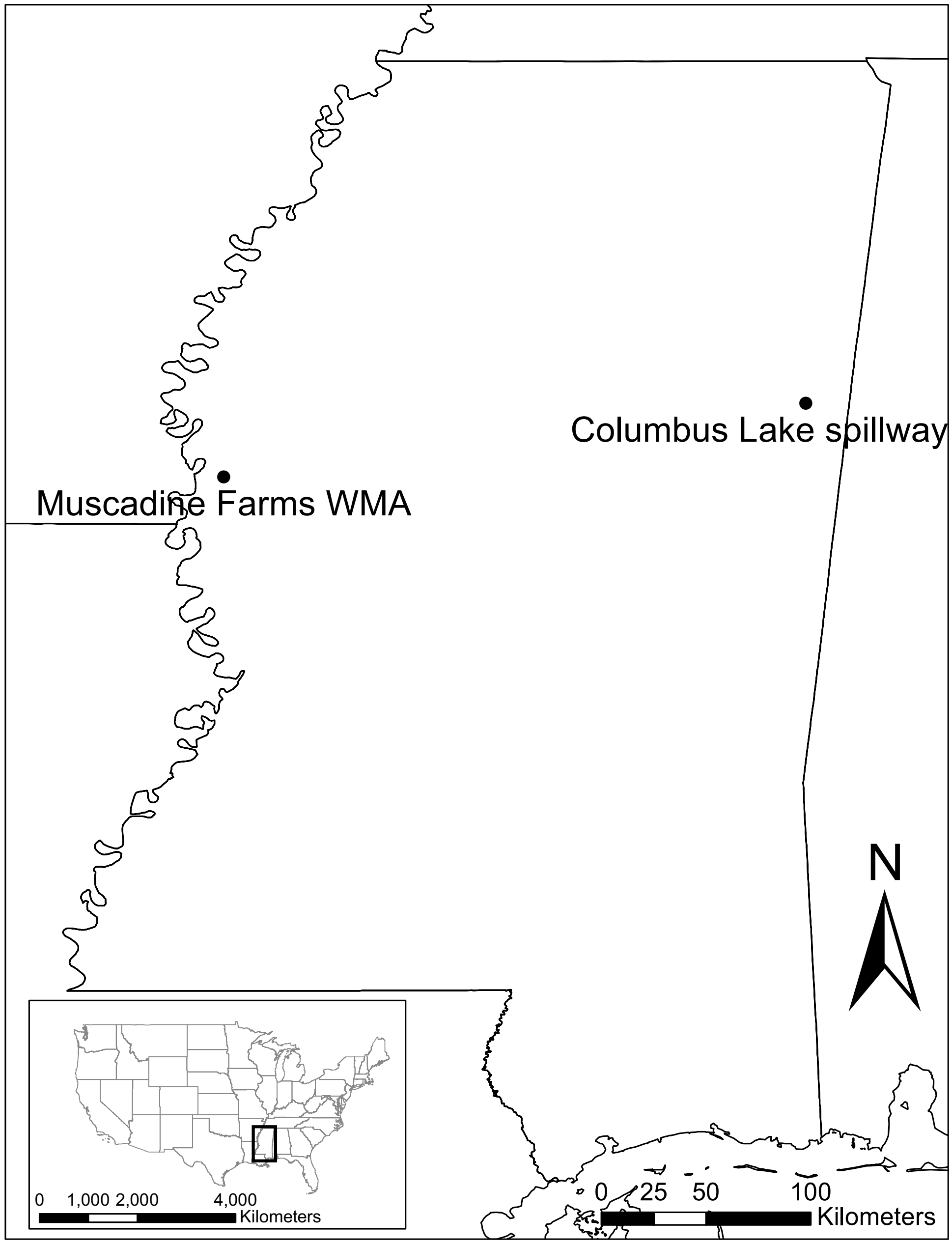

Fig. 1 Map of the two alligator weed populations that exhibited fruiting observed in northern Mississippi USA. Distance between the two populations is roughly 475 km

set to 25 °C with a 16 h. photoperiod and monitored daily for seed germination.

Results and Discussion

Plants from Muscadine Farms WMA population exhibited fruits at varying degrees of maturation, from immature green fruits to mature brown fruits (Fig. 5). Fruits were achenes adnate to the dry, papery corolla which readily disassociated from the calyx, suggestive of fruits at maturity (Fig. 5). Achenes were cordate and 3–5 mm wide with a persistent stigma (Fig. 5). Each fruit housed one seed which was flat, roughly 1 mm in diameter, and had a wrinkled seed coat (Fig. 5). Vouchers taken from Muscadine Farms WMA exhibited taproots in addition to infructescences (Schmid 14 MISSA037070; Schmid 15 MISSA037071; Figs. 2 & 3) whereas the voucher from Columbus Lake spillway did not have a taproot (Schmid 19 MISSA037072; Fig. 4) despite its terrestrial habitat. The population at Muscadine Farms WMA consisted of plants that appeared shorter and with sparse foliage compared to other populations of aquatic *A. philoxeroides* growing in northern Mississippi at the same time of year (Schmid, pers. obs.). Regardless of treatment, all attempts at germination failed. Petri dishes were housed in germination conditions for at least 1.5 weeks

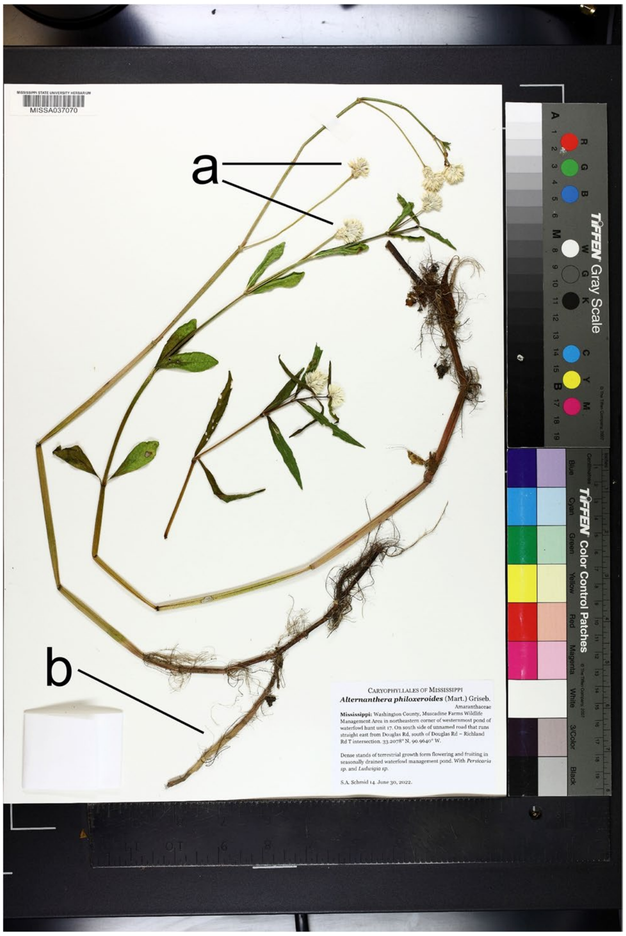

Fig. 2 Voucher specimen Schmid 14 MISSA037070 of alligator weed collected from Muscadine Farms WMA on 30 June 2022. a) infructescences; b) taproot

Fig. 3 Voucher specimen Schmid 15 MISSA037071 of alligator weed collected from Muscadine Farms WMA on 1 July 2022. a) infructescences; b) taproots

and monitored approximately daily for germination. After roughly 1.5 weeks, petri dishes typically grew slime mold plasmodia at which point germination was considered failed yet monitoring continued. Although seeds in this study were subjected to dormancy, seeds from the native range readily germinated with no dormancy, suggesting that failure to germinate was not due to procedural error (Sosa et al. 2003).

The prolific fruiting of *A. philoxeroides* at Muscadine Farms WMA was quite unique of invasive *A. philoxeroides* as fruiting events in the introduced range are often cited as very rare or nonexistent (Lui-qing et al. 2007; Clements et al. 2014; Tanveer et al. 2018). Although North American *A. philoxeroides* has been observed in fruit previously, no prior records provide an ecological mechanism for the rare production of seeds in *A. philoxeroides*'s invaded range (Vogt et al. 1992; Lui-qing et al. 2007). Draining of pools at Muscadine Farms WMA likely induced the transition of the *A. philoxeroides* population from an aquatic growth form to a terrestrial growth form as evidenced by the taproots present in voucher specimens (Schmid 14 MISSA037070; Schmid 15 MISSA037071; Figs. 2 & 3; Julien et al. 1992). Terrestrial *A. philoxeroides* produces less shoot biomass and shorter stems with less leaf area than aquatic populations (Julien et al. 1992). These findings seem consistent with the terrestrial population observed at Muscadine Farms WMA. It is possible that this rare fruiting event occurring in a terrestrial *A. philoxeroides* population is noncoincidental. The thesis that fruit production is exclusive to the terrestrial forms of *A. philoxeroides* seems to be supported by the fruiting of *A. philoxeroides* on the upland margins of the Columbus Lake spillway and matches previous observations of fruit production by terrestrial *A. philoxeroides* in the Sunflower River floodplain (Ervin, pers. obs.). If true, this hypothesis may provide insight into selective pressures in the native range of *A. philoxeroides* in South America. *A. philoxeroides* is native to the Paraná River which is subject to substantial, seasonal variation in hydrology with distinct wet and dry seasons which has shown to substantially affect plant community composition of the riparian zone (Kita and Souza 2003; Roberto et al. 2009).

Fig. 4 Voucher specimen Schmid 19 MISSA037072 of alligator weed collected from the Columbus Lake spillway on 26 July 2022. a) infructescences

While terrestrially-induced fruiting has not been investigated in Amaranthaceae, there is previous evidence of Southeast Asian trees (namely Dipterocarpaceae) masting as a response to periodic droughts and monsoons caused by El Niño Southern Oscillation (Williamson and Ickes 2002; Fredriksson et al. 2006). Research in southern Mexico also found strong environmental influence on fruiting (Cortés-Flores et al. 2019). At the community level, herbaceous plants exhibited fruiting timing that maximized dry season seed dispersal (Cortés-Flores et al. 2019). In addition to clues into the native ecology of *A. philoxeroides*, this could provide a framework for inducing seed production under laboratory conditions. Further investigation into the stimuli that induce fruiting and seed production in *A. philoxeroides* is required to better determine current and future potential for spread of invasive *A. philoxeroides* through sexual reproduction. Regardless of the stimuli responsible for *A. philoxeroides* fruiting, fruits being produced in disparate locations in Mississippi suggest that *A. philoxeroides* fruiting is not an isolated incident.

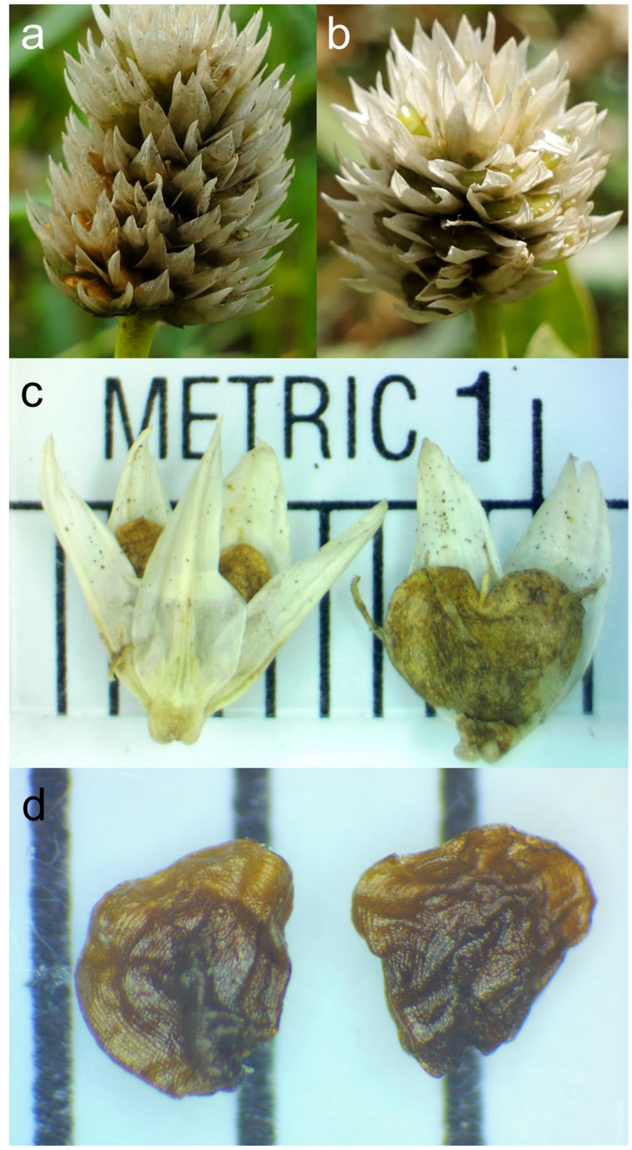

Fig. 5 Images of alligator weed fruits and seeds from Muscadine Farms WMA population. a) mature infructescence with brown exocarp; b) immature infructescence with green exocarp; c) individual fruits with intact (left) and dissected (right) corolla (graduations = 1 mm); d) individual seeds (graduations = 1 mm)

The failure of all attempts to germinate *A. philoxeroides* seeds seem to suggest that seeds at the Muscadine Farms WMA population were nonviable. Additionally, seeds harvested from this population looked thin and sunken with wrinkled seed coats (Fig. 5). When compared to the viable seeds of the congener *A. sessilis* (L.) R.Br. ex DC., the thin and wrinkled appearance of the Muscadine Farms WMA *A. philoxeroides* population may indicate mal-development of the cotyledons which would likely render the seeds nonviable (Government of Canada CFIA 2014). While there do not seem to be available photos of viable *A. philoxeroides* seeds, fruits of *A. philoxeroides* from its native range that reportedly housed viable seeds appeared much fatter, which suggests much more developed seeds (Sosa 2022, pers. comm.). *A. philoxeroides*'s production of strictly nonviable seeds seems to be a phenomenon unique to its invaded range as viable seeds were readily observed and successfully germinated in its native, South American range (Sosa et al. 2003).

Like many other invasive species, the founder effect has subjected *A. philoxeroides* to an immense loss of genetic diversity in its invaded range (Xu et al. 2003; Roman and Darling 2007). This dramatic reduction in genetic diversity can cause the collapse of sexually reproductive systems in invasive species as many out-breeding adaptations fail to produce viable embryos when genetic diversity is critically low (Barrett et al. 2008). While the proximate biological mechanism that induces production of non-viable seeds often remains unknown, low genetic diversity is often considered the ultimate cause for seed non-viability (Kittelson and Maron 2000; Ghazoul and Satake 2009). This is consistent with the current understanding of *A. philoxeroides* genetics, as the prolific clonal propagation in the invaded range produces populations with very low genetic diversity (Xu et al. 2003). In North America, however, there are at least six distinct haplotypes that have been identified with multiple co-occurring throughout the southeastern United States (Williams et al. 2020).

Alternatively, polyploidy has caused the breakdown of some sexually reproductive strategies by inhibiting normal seed production (Comai 2005). Since all known haplotypes of *A. philoxeroides* in North America are hexaploid, this could explain why no viable seeds have been discovered in North America (Williams et al. 2020). Comparatively, readily germinating seeds from the native range have been collected from plants reported as tetraploid (Sosa 2022, pers. comm.). Genotype investigations that compare viable and non-viable seed producing *A. philoxeroides* may determine the mechanism preventing viable seeds in the invaded range. Regardless of the cause of seed non-viability, if viable seed production is inhibited by both an environmental and a biological mechanism, then a suitable, terrestrial habitat with the appropriate haplotypes present may provide the conditions necessary to produce viable *A. philoxeroides* seeds. In summary, the production of nonviable seeds in terrestrial environments may provide evidence of an environmental impediment to sexual reproduction in North American *A. philoxeroides*. While prior research suggests that *A. philoxeroides* exclusively disperses via stem fragments, seeds are the primary method for long distance dispersal in plants (Nathan 2006). Further investigation into *A. philoxeroides* fruiting and seed development should be conducted to better describe the factors that promote and inhibit this species' seed production and viability. Specifically, induced fruiting under laboratory conditions will be critical to better describe the relationship between environmental stimuli and *A. philoxeroides* fruiting.

Conclusion

Observations from this study provide the first records of fruiting *A. philoxeroides* in the United States in over 40 years. Despite these two observations occurring in disparate locations, both fruiting events occurred under terrestrial conditions. This seems to suggest terrestrial conditions as a putative environmental stimulus for *A. philoxeroides* seed production. While numerous seeds were collected from eastern Mississippi and germination was attempted, no germination occurred and seeds appeared to be non-viable. If the observed fruiting populations are capable of fruiting but incapable of producing viable seeds, there may be a genetic mechanism preventing seed viability.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s13157-023-01662-x.

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Data Availability Data used in the preparation of this article will be made available by the corresponding author upon reasonable request.

Declarations

Competing Interests The authors declare no competing interests were operative in the preparation of this article.

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