Short communication

A preliminary investigation of umbellate inflorescences in *Vallisneria americana* populations of Central Florida

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ABSTRACT

Vallisneria americana typically produces solitary pistillate inflorescences; however, unusual umbellate flowers have been observed in sub-tropical populations and are reported as rare. There are multiple hypotheses regarding the origin or cause of umbellate inflorescences—they may be relics of ancestral stocks surviving through asexual reproduction, heritable traits worthy of taxonomic recognition, or teratological specimens resulting from injury during flower formation. Through surveys of *Vallisneria* populations in four lakes in Central Florida, USA, we show these umbellate flowers are broadly distributed and we document their physical and reproductive traits, contrasted with solitary capsules (capsule number, capsule length and width, seed number, germination). Umbellate inflorescences were found frequently across space and time—capsules were found in three of four lakes, 40–80 % of the times flowering was observed. Umbellate inflorescences produced fewer seeds than solitary capsules, despite having 2–33 capsules per inflorescence. Seeds from umbellate capsules were viable, but germination occurred more slowly and at a lower percentage than seeds from solitary capsules. Nematodes were not detected within sampled inflorescences. Chironomid larvae were detected at a high rate (75–80 %) in umbellate capsules from two of three lakes but were not found on solitary capsules, suggesting they may be a possible cause for teratological growth. We conclude umbellate inflorescences are broadly distributed in Central Florida lakes and, while not sterile, they may have reproductive costs. Further study is needed to fully evaluate the cause of umbellate formation, population-level effects, and their range within *Vallisneria americana*.

1. Introduction

Vallisneria americana Michx. (Hydrocharitaceae) is a submerged aquatic macrophyte common in fresh and brackish waters across North America (hereafter *Vallisneria*). *Vallisneria* provides favored habitat for many animals while its structure and growth promote water quality (Korschgen and Green, 1988) and has thus received attention by scientists and managers for study, conservation, and restoration (Jarvis and Moore, 2008; McFarland and Shafer, 2008). A dioecious plant, *Vallisneria* reproduces both asexually through clonal expansion and sexually via water-facilitated pollination (epihydrophily). Pistillate flowers borne on long stalks that reach the water surface are pollinated by contact with free-floating staminate flowers that are released from an ovoid spathe at the base of male plants (McFarland and Shafer, 2008).

Pistillate flowers are predominantly solitary; however, unusual umbellate or spike-like inflorescences have been observed (Lowden, 1982; Les et al., 2008). The first mention of umbellate flowers characterized specimens from three distinct localities: Lake Miragoane (Haiti), Lake Peten Itza (Guatemala) and Biloxi (Mississippi, USA) (Lowden, 1982). With these three samples, Lowden (1982) described a diversity of inflorescence structures within umbellate material, ranging from 2 to 60 flowers on a single stalk. Some umbellate flowers had miniaturized floral size and reduced number of parts, with smaller flowers showing a change in sexual tendency from reduced stigmas and petal rudiments. In one case, an umbellate inflorescence had pistillate flowers as well as the floral parts of a male flower, suggesting a monoecious condition. Within North American populations, umbellate *Vallisneria* flowers are reported as relatively uncommon or rare, though there is minimal information

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about how they are distributed geographically or their local abundance (Lowden, 1982; Les et al., 2008; eFloras, 2021).

Much of the discussion of umbellate *Vallisneria* inflorescences has been regarding its placement taxonomically. Lowden (1982) attributed umbellate material to two sub-species of *V. americana* based on staminodial conditions; the Haiti specimen had free staminodia and was thus attributed to *V. americana* var. *biwaensis*, while the Guatemala and Mississippi specimens had staminodia adnate to stylar bases and were placed in *V. americana* var. *americana*. In a later evaluation of *Vallisneria* (genus) systematics, Les et al. (2008) used morphological and molecular data to classify umbellate material found in Texas as most closely related to *Vallisneria neotropicalis,* which they characterized as a genetically distinct lineage that previously had been identified as a larger growth form of *Vallisneria americana*. Despite these classifications, all North American *Vallisneria* remains officially classified as *Vallisneria americana*, with *V. neotropicalis* considered a synonym (ITIS, 2021). Irrespective of taxonomic and identification discrepancies, umbellate flowers have now been reported in four (presently identified as) *Vallisneria americana* populations in tropical to sub-tropical regions in North America by these two primary sources. In addition, Flora of North America reports umbellate specimens from several populations in the southern United States (Florida, Mississippi, Alabama) (eFloras, 2021). No other mention of umbellate flowers within North American *Vallisneria* populations have been reported, to our knowledge, and many taxonomic keys report solitary pistillate flowers only (e.g., Godfrey and Wooten, 1979; Wunderlin and Hansen, 2011). Interestingly, the umbellate inflorescence has been found occasionally in other species of *Vallisneria*–in *V. triptera* and *V. annua* in tropical and sub-tropical regions of Australia (Jacobs and Frank, 1997) and in unspecified species in Asia (Les et al., 2008, L. Chen, personal communication).

In part because of their apparent rarity, Lowden (1982) considered the umbellate specimens he encountered to be abnormal and taxonomically insignificant. He hypothesized that *Vallisneria* plants with umbellate inflorescences may be "marginal ancestral stocks" having survived through asexual reproduction, regarding them as primitive specimens that may offer clues to the evolutionary path of *Vallisneria* species worldwide. This hypothesis implies that umbellate inflorescences are sterile; in this framework, the multi-flowered trait would not be heritable via sexual reproduction. Another hypothesis is that the umbellate inflorescence type is a heritable trait, and thus a characteristic worthy of taxonomic recognition within the *Vallisneria* genus. Les et al. (2008) acknowledges this possibility by including umbellate material in their phylogenetic analysis of *Vallisneria* (though they noted there was not enough consensus about *Vallisneria* systematics, nor enough available umbellate material to reach a conclusion). A third hypothesis is that umbellate inflorescences are malformations, teratological specimens that result from injury or exposure to pathogens or parasites during floral formation, as flower characteristics can change following apical damage (Gonzáles et al., 2016). The possible sources of injury are numerous, and may include stressful environmental conditions, toxicological exposures, damage from viruses and bacterium, injury from nematodes or insects, or interactions amongst many causes (Benner, 1988; Gonzáles et al., 2016).

While routinely monitoring *Vallisneria* patches across four lakes in Central Florida, we encountered umbellate inflorescences frequently across space and time, which we found surprising considering the present depiction of their rarity in the literature. Here, we describe our observations of umbellate inflorescences during monthly monitoring visits and the traits of the umbellate capsules we encountered. Additionally, we conducted a germination assay comparing seeds from umbellate and solitary capsules to assess seed sterility or other variations in seed germination. Finally, to investigate causes of teratological growth, we assessed capsules for the presence of nematodes and aquatic macroinvertebrates. With these efforts, we describe some of the defining characteristics of these inflorescence types in Florida populations of *Vallisneria,* and use these observations to inform the hypotheses

regarding the potential origin or cause of these specimens.

2. Methods

2.1. Lake monitoring

From May 2020–February 2021, we monitored four lakes in Central Florida, United States (Lakes Apopka, Hartridge, Jessamine, and Mariana) monthly (7 visits) to monitor the sexual reproduction of *Vallisneria americana* patches (30–60 m^2). Study locations were haphazardly chosen from a list of Central Florida lakes where *Vallisneria* was found during submerged aquatic vegetation surveys (Lakewatch, 2021). *Vallisneria* patches were monitored for the presence of female inflorescences, both solitary and umbellate capsules. If umbellate flowers or capsules were found, they were counted and harvested for further assessment alongside solitary capsules from the same patch. We averaged water quality data (pH, nitrogen, phosphorus, chlorophyll *a*, trophic state index, Secchi depth, turbidity, color) from 2020 for each lake using data compiled by the Florida Water Atlas (USF, 2021) to describe environmental conditions.

2.2. Traits comparison

In December 2020 and February 2021, we harvested umbellate capsules and adjacent (within a 5 m radius) solitary capsules from the same patch. We measured the wet weight of each capsule (including all capsule branches for umbellate inflorescences), then counted the number of capsule branches (ovules), the length and width of each capsule branch, and the total seeds per shoot. Site differences in capsule branches within umbellate inflorescences were assessed with a one-way ANOVA with site as a fixed factor (JMP Pro 15). Seed number and capsule weight were analyzed using a two-way ANOVA with site, capsule type (fixed factors) and their interaction. For capsule length and width, we ran the same model, but capsule type was separated into solitary, dominant umbellate, and side umbellate capsules (3 capsule types; Fig. 1). Post-hoc analysis was conducted using Tukey HSD.

2.3. Germination study

On October 30, 2019, we collected both umbellate and solitary capsules from a single 10 m^2 patch at Lake Apopka, Florida. In February 2020, we removed and pooled seeds from 5 of both umbellate and solitary capsules and counted four replicates of 50 seeds for each capsule-type. Experimental units were plastic containers with clear tops (15 cm × 15 cm by 4.5 cm deep), filled 1.5 cm deep with a 50:50 mixture of potting soil and sand and flooded with tap water. Containers were randomly assigned a location on a greenhouse bench, and seeds were evenly distributed across the assigned container on February 20, 2020. New germinations were monitored approximately 1–2 times weekly for 11 months, until January 22, 2021. Mean germination time (MGT) was calculated using the equation:

$$MGT = \Sigma(nT)/N$$

where n are the newly germinated seeds at time T; T is the number of days from the initiation of the germination test; and N is the total number of germinated seeds. For percent germination, we conducted a two-way ANOVA which included capsule type and time (fixed factors) and their interaction, conducting Tukey HSD for post-hoc analysis. To analyze MGT, we conducted a one-way ANOVA with capsule type (solitary or umbellate) as the fixed factor and used a Student's *t*-test for post-hoc analysis.

2.4. Nematode and chironomid assay

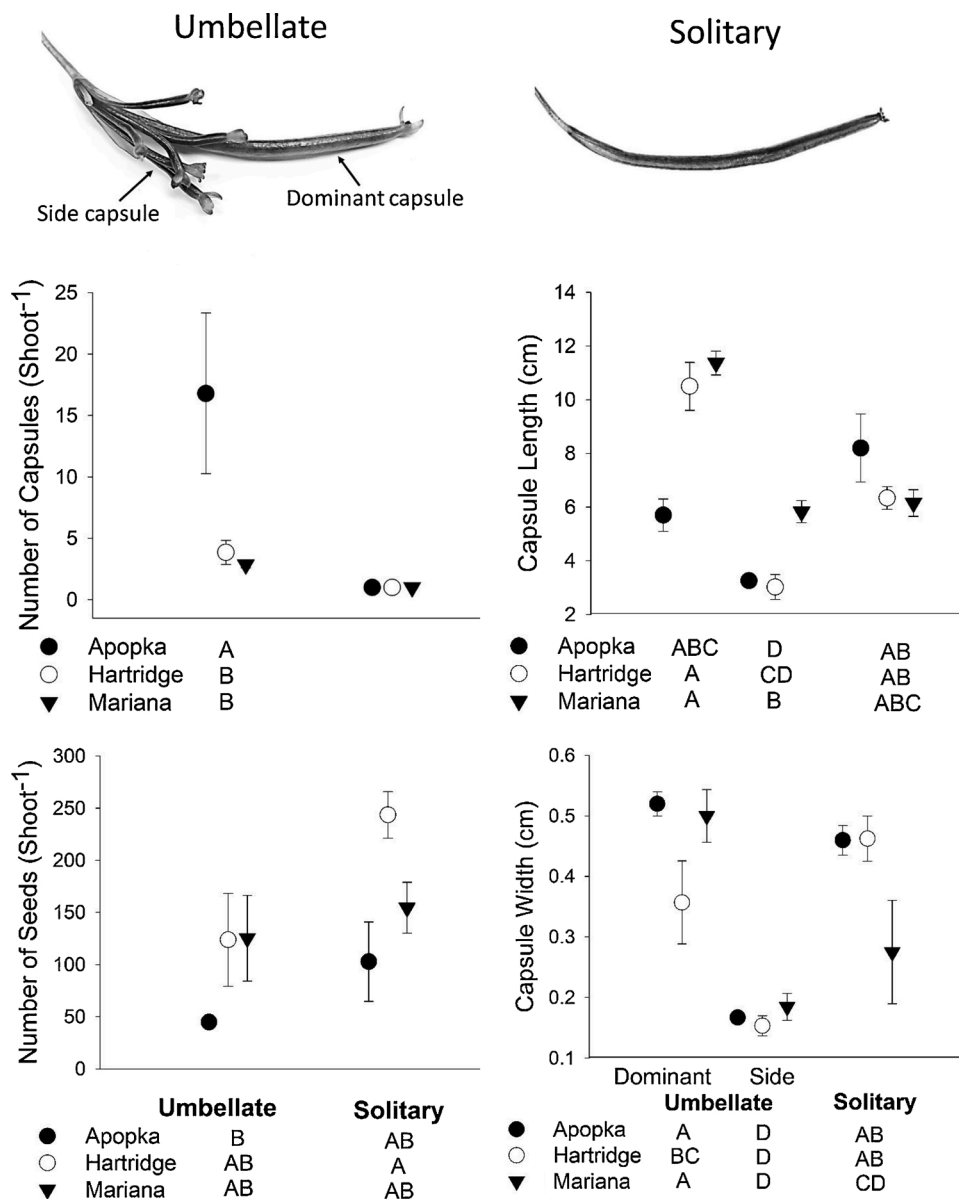In September and October 2020, we collected umbellate and solitary

Fig. 1. Number of capsules per shoot, number of seeds per shoot, and capsule length and width in umbellate and solitary capsules collected at Lake Apopka (n = 5 umbellate, n = 5 solitary), Lake Hartridge (n = 7 umbellate, n = 8 solitary), and Lake Mariana (n = 7 umbellate, n = 4 solitary) in Central Florida, USA. Letters under graphs indicate significant differences between means (Tukey HSD post hoc comparisons.) Solitary capsules were excluded from the number of capsules analysis because their value was always one, violating model assumptions.

capsules for nematode assessment (Table S1). We stored capsules in water at 4 °C until they were transported to the University of Florida nematode assay lab for analysis. Each capsule's tissue was assessed for the presence of nematodes with two methods; tissue was fine sectioned and analyzed under a microscope; capsule tissue was macerated, incubated in water for 2 days, and scanned for nematodes. In February 2021, we collected umbellate and solitary capsules for a qualitative assessment of chironomid presence (Table S1). We agitated the base of each collected capsule and assessed for the presence of chironomid larvae.

3. Results

3.1. Lake monitoring

At Apopka, we observed female inflorescences during 5 of 7 visits, and found umbellate inflorescences 2 times (40 % occurrence; Table S1). At Mariana, we observed female inflorescences 5 times, and umbellate inflorescences 4 times (80 % occurrence). At Hartridge, we observed female inflorescences 7 times, and umbellate inflorescences 3 times (43 % occurrence). At Jessamine, we observed female inflorescences 5 times and umbellate inflorescences 0 times (0 % occurrence). When umbellate

inflorescences were found, we typically encountered 1–5 umbellate inflorescences amongst patches with solitary capsules several orders of magnitude greater in density. However, at one visit to Apopka, we observed >50 umbellate inflorescences within a single ~3 m² patch (Fig. S1), approximately 1/3 of the total inflorescences present.

Lake Jessamine water quality was superior to the other lakes – it had the lowest nitrogen, phosphorus, chlorophyll-a, turbidity, trophic state index, and color and the highest Secchi depth. Lake Apopka's water quality was the poorest, with the highest nutrients, and lowest visibility (Table S2).

3.2. Traits comparison

Umbellate capsules from Apopka had more capsule branches than umbellate capsules from Hartridge and Mariana ($F_{2,2} = 5.1$, $p = 0.02$; Fig. 1). There was a significant capsule type*site interaction for both length ($F_{4,4} = 3.3$, $p = 0.01$) and width ($F_{4,4} = 7.2$, $p < 0.001$; Fig. 1). Dominant capsules were longer and wider than side capsules from the same site (Fig. 1). Umbellate capsules had fewer seeds (total seeds across all capsule branches from one shoot) than solitary capsules ($F_{1,29} = 7.2$, $p = 0.01$), and seed number differed by site ($F_{2,29} = 3.8$, $p = 0.03$).

Within umbellate capsules, dominant capsules had more seeds than side capsules (T = 4.5, p < 0.001; dominant: avg 81 ± 17 seeds; side: avg 4 ± 2 seeds). There were no significant differences in capsule weight by site ($F_{2,2} = 1.4$, p = 0.3) or capsule type ($F_{1,1} = 0.9$, p = 0.4).

3.3. Germination study

Percent germination was significantly different by capsule type (Fig. 2; $F_{1,1} = 267.4$, p < 0.001), with germination 16 % greater in seeds from solitary capsules compared with umbellate. Percent germination was different across time periods ($F_{36,36} = 59.5$, p < 0.001), but there was not a significant capsule type*time interaction ($F_{36,36} = 1.2$, p = 0.20). Mean germination time was significantly different by capsule type ($F_{1,1} = 28.9$, p = 0.002), with seeds from solitary capsules germinating in 39 fewer days on average than seeds from umbellate capsules.

3.4. Nematode and chironomid assay

No nematodes were detected in any of the assessed umbellate or solitary capsules. Chironomid larvae were detected at the base of 3/4 umbellate capsules, but 0/4 solitary capsules harvested from Hartridge (Fig. S2). Chironomid larvae were not detected in the umbellate and solitary capsule harvested from Mariana. Chironomid larvae were detected in 4/5 umbellate capsules, but 0/5 solitary capsules harvested from Apopka.

4. Discussion

The literature describes umbellate inflorescences in *Vallisneria americana* to be aberrant and rare, however "rarity" (which can be defined in different ways, such as a limited geographical range and/or low abundance (Gaston, 1994)) for these inflorescence forms is poorly defined. We encountered umbellate material frequently across space and time in our survey of four haphazardly chosen *Vallisneria* populations in Central Florida lakes, suggesting umbellate forms are broadly distributed in this area. However, umbellate inflorescences were typically (though not always) locally rare (i.e., low in density relative to solitary inflorescences at the patch scale). Umbellate inflorescences were present in three out of four surveyed lakes and, at those locations, were observed 40–80 % of the times that flowering occurred. In addition to the umbellate inflorescences documented in our regular monitoring, we have incidentally observed umbellate inflorescences in *Vallisneria* populations in numerous other Florida lakes (e.g., Lake Maggiore, Lake Eloise; S. Gorham, personal observation) as well as in nursery stock (E. Latimer, personal communication) and in Florida herbarium records.

Lowden (1982) suggested that the rare umbellate inflorescences they

Fig. 2. Cumulative percent germination (mean ± standard error) of seeds from umbellate and solitary inflorescences collected at Lake Apopka in October 2019. Mean germination time is the average days to germination ± SE.

encountered were ancestral stock, primitive forms that had persisted over time via effective asexual reproduction. However, the frequency of umbellate inflorescences in Central Florida makes this hypothesis less likely. In addition, seeds from umbellate capsules are not sterile, suggesting the umbellate inflorescence characteristic has the potential to be a heritable trait. However, to determine heritability, further study is needed to evaluate if seeds from umbellate capsules can produce plants that have this trait (e.g., quantitative genetic experiments investigating parent and offspring trait expression), or if the umbellate form is maintained by the same individual over multiple growing seasons.

Umbellate flowers in *Vallisneria* may not be a heritable trait worthy of taxonomic recognition, but instead may occur because of injury to the apical meristem during flower formation. Possible indications of malformation such as irregular and asymmetric umbellate inflorescence forms, fused capsule tissue, and excess or exaggerated growth in some of the capsules we encountered led us to consider injury as a possible cause of umbellate inflorescence formation (Fig. S3; Wise and Abrahamson, 2008). In plants with terminal inflorescences, as in the pistillate flowers of *Vallisneria*, apex removal can result in excessive branching and the production of greater numbers of inflorescences (Benner, 1988). For example, this phenomenon has been demonstrated in *Potamogeton richardsonii*, where clipping of apical meristems led to increased branching and flowers (Sheldon, 1986). Apical damage can result from a multitude of factors, including a pathogen attack, physical breakage by wind or currents, frost or desiccation (in terrestrial species), or herbivory (Benner, 1988). The timing and the manner of injury can produce variable wounding responses (Benner, 1988; Spirko and Rossi, 2015), which could explain the variability in umbellate inflorescence traits we found both within and across sites.

Chironomid larvae were found at a high rate in umbellate flowers collected at two lakes, suggesting injury from herbivores is a possible cause for the formation of umbellate inflorescences (though we did not always find chironomids, indicating other sources of injury, such as mechanical clipping, are also possible). We do not know if the chironomid larvae found in umbellate inflorescences were the cause of injury, or simply attracted to the more complex structure that the dense cluster of capsules provided. Chironomids (*Endotribelos* sp. and *Polypedilum illinoense* sp.) have been found to form tunnels in the leaves of *Vallisneria* (Harms and Grodowitz, 2010), suggesting they could have contributed to apical damage via tunneling behavior. However, Harms and Grodowitz (2010) noted that chironomids may not directly feed on *Vallisneria*, and instead may primarily use it as a substrate for feeding on epiphyton or algae. We investigated the presence of just two possible biological sources of injury to flower formation (chironomids and nematodes), but many other sources of injury, both biological and physical, are possible drivers of umbellate formation.

Umbellate flowers may also develop in response to environmental conditions. Aquatic plants display high levels of phenotypic plasticity along environmental gradients, particularly in leaf shape and floral characteristics (Caruso, 2006). We observed umbellate material in three out of four lakes – lakes with elevated nutrients and reduced water clarity compared with the lake (Jessamine) where umbellate inflorescences were not found (Table S2); and we observed the most in Apopka, the highest nutrient lake. Umbellate flowers may form in response to elevated nutrients, or perhaps the elevated nutrient environment led to the increased presence of (or *Vallisneria's* susceptibility to) umbellate-causing stressors. Chironomids (possible stressors) are known to proliferate in nutrient-rich water and have become a nuisance in many Central Florida waterbodies following eutrophication (Beck and Beck, 1969). Manipulative studies and more widespread surveys of *Vallisneria* populations are needed to fully evaluate these hypotheses.

Our research indicates that the umbellate inflorescence type comes with potential reproductive costs; umbellate capsules produce fewer seeds, and those seeds have reduced germination compared with seeds from solitary capsules (we describe reproductive costs with the assumption that umbellate capsules are derived from *V. americana*,
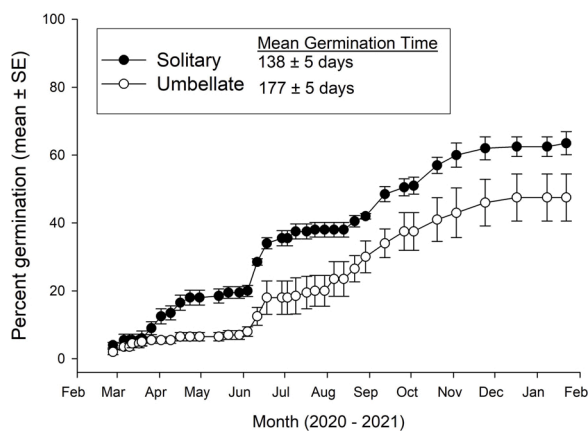
however this may not be the case, as discussed below). This lower reproductive performance is likely due to allocation of carbohydrates to production of additional capsules rather than healthy seeds (Aguirre et al., 2018). The reproductive deficiencies may also be explained by disruptions to pollination caused by the umbellate form. Female flowers must open at the water surface in order to be pollinated effectively by water-borne male flowers (McFarland and Shafer, 2008); in an umbellate growth form, variation in pedicel length may leave some flowers submerged, eliminating the opportunity for pollination. Furthermore, when the peduncle coils soon after pollination is initiated (McFarland and Shafer, 2008), some flowers in the umbellate form may be retracted prior to pollination. Conversely, umbellate flowers that effectively reach the surface for pollination have the potential to provide a reproductive benefit by increasing pollination chances, which may be important in *Vallisneria* where fertilization is frequently limited by environmental factors (McFarland and Shafer, 2008). For example, umbellate flowers may increase the surface area or time at the water surface for pistillate flowers to encounter male flowers (Fig. S4). We did not find consistent evidence for this hypothesis, though the large seed number found in one umbellate capsule from Lake Mariana (339 seeds compared with an average of 154 seeds in solitary capsules from that site) suggests these benefits may be occasionally realized.

Here, we describe the umbellate *Vallisneria* as abnormal populations of Florida *Vallisneria americana* (syn. *Vallisneria neotropicalis*) in order to remain consistent with the Integrated Taxonomic Information System which formally recognizes all North American *Vallisneria* as *V. americana* (IT IS, 2021; see introduction). However, given the unique characteristics in inflorescence and capsule traits (described here and in Lowden, 1982), there is a possibility for umbellate *Vallisneria* to be a separate species, or perhaps the result of hybridization between *V. americana* and another unknown species, or interbreeding between *V. americana* and the subtropical subpopulation of *V. americana* (syn. *V. neotropicalis*). Hybridization could be another possible explanation for the lower seed production and germination rate we observed (Padgett et al., 2002). Molecular genetic studies of the umbellate *Vallisneria* populations compared with adjacent populations of *Vallisneria* with single inflorescences are needed to conclusively identify the taxonomic status of these populations. In addition, the morphology of the umbellate inflorescence has only been described based on two populations in Lowden (1982). More detailed inflorescence schemes using specimens from a wider range of locations would help describe potential taxonomic and/or morphologic diversions.

Vallisneria is a widespread and important species for providing habitat and maintaining water quality in water bodies, and seeds play an important role in the spread and maintenance of these populations (Korschgen and Green, 1988; McFarland and Shafer, 2008; Jarvis and Moore, 2008). Thus, the umbellate inflorescence, which we show can lead to reduced seed production and seed quality, is important to document and investigate across its full range, in order to fully understand the causes and possible implications for its reproductive deficiencies. Our preliminary investigation cannot conclude whether umbellate inflorescences in *Vallisneria* are relics of ancestral stocks, heritable traits worthy of taxonomic recognition, or teratological specimens resulting from injury; however, we highlight their prevalence in Central Florida, and suggest greater attention be paid to each of these hypotheses in future investigations.

CRediT authorship contribution statement

Christine B. Rohal: Conceptualization, Investigation, Writing - original draft. **Laura K. Reynolds:** Conceptualization, Writing - review & editing, Methodology, Supervision, Funding acquisition, Project administration. **Carrie R. Adams:** Conceptualization, Writing - review & editing, Methodology, Supervision, Funding acquisition, Project administration. **Charles W. Martin:** Conceptualization, Writing - review & editing, Funding acquisition, Project administration. **Siobhan B. Gorham:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquabot.2021.103436.

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