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Effect of chilling duration on sprouting of *Hydrilla verticillata* subsp. *lithuanica* axillary turions

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ABSTRACT

Hydrilla (*Hydrilla verticillata*) is a highly invasive, submersed aquatic plant in the United States that includes three subspecies: *H. v. verticillata* primarily found in the southern United States, *H. v. peregrina* common in the mid-Atlantic to northern latitudes, and *H. v. lithuanica*, which was reported in Hartford County, CT, in 2016. This study aimed to determine whether a chilling period is necessary to break dormancy in *H. v. lithuanica* turions. Results showed no significant differences in sprouting in turions exposed to different chilling durations of 2, 4, 8, and 16 days at 4 °C until 4 days after removal from cold treatment. By the end of the study, turions chilled for ≥ 8 days exhibited significantly higher sprouting ($> 97\%$) compared to the nonchilled control (73%). Additionally, time to 50% sprouting was reduced in chilled turions (2.6 to 3.7 days) compared to nonchilled turions (6.9 to 10.9 days). These results indicate that *H. v. lithuanica* has a flexible dormancy strategy and high sprouting potential after brief chilling, warranting early season management and posing a risk to regions with variable winters.

Key words: cold stratification, Connecticut River, dormancy, hydrilla.

INTRODUCTION

Hydrilla verticillata (L.f.) Royle is a submersed aquatic plant widely recognized for its aggressive spread and ecological impact in freshwater systems across the United States (Langeland 1996). Since its introduction, hydrilla has become one of the most problematic aquatic invasive weeds because of its ability to form dense surface canopies, displace native vegetation, impede navigation, and alter nutrient and oxygen dynamics (Haller and Sutton 1975, Bradshaw et al. 2015, Gettys and Enloe 2016). Despite decades of research and active management, hydrilla continues to expand in distribution. Control efforts are often hindered because of its quick proliferation throughout the waterbody from drifting fragments, stoloniferous growth, and turions (Madsen and Smith 1999). In 2016, a previously unrecorded lineage in the United States, *H. v. lithuanica* (Tippery 2023), was confirmed in Hartford County, CT, and has since expanded throughout the lower portion of the Connecticut River and into at least 10 additional waterbodies across Connecticut and Massachusetts (Foley et al. 2024, J. Foley, pers. comm. 2025). This subspecies, colloquially referred to as "Connecticut River hydrilla" or officially as "northern hydrilla" (Tippery 2023), is genetically distinct from previously documented *H. v. peregrina* ("monoecious") and *H. v. verticillata* ("dioecious") subspecies in the United States, and little is known about its physiological traits or dormancy behavior (Tippery et al. 2020).

A key mechanism that contributes to the persistence and spread of *H. v. lithuanica* is the formation of axillary turions, which are compact vegetative propagules that detach from the parent plant, settle into the sediment, and allow the species to overwinter year to year. Plant propagule dormancy and sprouting are often regulated by environmental cues, especially low-temperature exposure (cold stratification) (Spencer and Ksander 2001, Sartain et al. 2024). However, no experimental data currently exist on whether cold stratification is necessary to break dormancy in this hydrilla subspecies.

The two subspecies previously present in the United States differ markedly in their turion dormancy and overwintering requirements. *Hydrilla. v. peregrina* ("monoecious hydrilla") axillary and subterranean turions require prolonged cold stratification to achieve germination (Sastroutomo 1980, Carter et al. 1987). This chilling requirement restricts the subspecies' distribution to regions with sufficiently cold winters and synchronizes sprouting with the onset of the growing season. Such predictability enables an optimal management period occurring after turion sprouting and prior to the formation of new turions (True-Meadows et al. 2016). In contrast, *H. v. verticillata* ("dioecious hydrilla") turions are unable to sprout at low temperatures, which limits the subspecies' geographic distribution to the southern United States. They also lack a strong chilling requirement, allowing them to sprout throughout the year in warmer climates (Steward and Van 1987). This trait supports perennial growth and often necessitates multiple management interventions (Netherland 1997, Maki and Galatowitsch 2008). These contrasting dormancy strategies underscore the importance of understanding turion physiology when evaluating invasion risk and control approaches.

The persistence of *H. v. lithuanica* in Connecticut suggests some degree of cold tolerance and turion dormancy, but it remains unclear whether this subspecies could persist in warmer latitudes or whether chilling is required for sprouting. Understanding the environmental conditions required for axillary turion sprouting in *H. v. lithuanica* is essential for predicting seasonal emergence patterns, assessing its invasion potential, and identifying optimal management

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windows (Netherland 1999). This study was conducted to determine the effect of chilling duration on *H. v. lithuanica* axillary turion dormancy and subsequent sprouting.

MATERIALS AND METHODS

Plant collection

Axillary turions were obtained in 2025 from a stock population of *H. v. lithuanica* originally collected from the Connecticut River in 2023 and maintained at the Center for Aquatic and Invasive Plants in Gainesville, FL (29.7273N; −82.4173W). The stock population was planted from turions and maintained in 0.6-m^3 fiberglass tanks under greenhouse conditions. Stock populations were planted in topsoil,[1] amended with 1 g L^{-1} of slow-release fertilizer[2] and capped with a thin layer of washed masonry sand to reduce nutrient leaching into the water column. Rotational submersed treatments of spinosad[3] and trichlorfon[4] were regularly applied to control generalist herbivores (Beets et al. 2025). Stock tanks were equipped with an aerator[5] with four aeration tubes and stones[6] distributed evenly throughout the tank and three water heaters[7] set to 22 °C, ensuring that turions did not experience conditions cold enough to break dormancy before the start of the study. Half of the collected turions were shipped to the Connecticut Agricultural Experiment Station's Office of Aquatic Invasive Species (41.3309N; −72.9195W) wrapped in a damp paper towel in a cooler with a hobo temperature logger and an icepack. Turions were in transit for two days (March 10 to 12, 2025) and kept in complete darkness with an average shipping temperature of 19.9 °C (4.2 °C std. dev). Due to elevated shipping temperatures (mean 19.9 °C), a few turions transported to Connecticut exhibited early signs of sprouting before the experiment began. Any turions showing early root development prior to placement in the 30 °C growth chamber were excluded from the study; this occurred only in the Connecticut trial. Prior to the start of the experiment in Connecticut, the shipped turions were stored in a dark environmental chamber set to 22 °C to mimic the stock tank environment.

Experimental design

The study was initiated on March 10, 2025, in Gainesville, FL, and on March 17, 2025, in New Haven, CT. The study was set up as a completely randomized design consisting of four treatments plus a nontreated control with four replications and three subreplicates per replicate. After collection, all turions except for the control group were placed in a plastic tub filled with unchlorinated well water and transferred to a completely dark growth chamber[8] set to 4 °C as a cold treatment (Sastroutomo 1980). At intervals of 0, 2, 4, 8, and 16 days, 12 turions were randomly chosen and removed from the cold treatment chamber and individually placed into three separate 30 or 60 mL vials (subreplicates) containing DI water and Smart and Barko solution (Smart and Barko 1985). The vials were then placed into a 600 mL beaker, which constituted an experimental unit. Beakers were then transferred to a second growth chamber[8] set to 30 °C, the temperature at which *H. v. lithuanica* turions have maximum sprouting (Howell et al. 2024). The growth chamber lighting was set to a 14 : 10 (light : dark) photoperiod with a light intensity of 180 to 200 μmol $m^{-2}s^{-1}$, measured with a light meter.[9] Temperature was monitored throughout the study using data loggers[10] placed on each shelf, and temperature standard errors were within 0.5 °C of target temperatures. Half of the Smart and Barko solution was replaced with fresh solution on day 8 to prevent algae growth.

Data collection

For chilled treatments, data were collected immediately after removal from the cold, dark growth chamber and at 1, 2, 4, 8, and 16 days after placement in the 30 °C chamber. For the nonchilled control, data collection began immediately after placement in the 30 °C growth chamber and followed the same timeline. At each time point, the number of branches and the presence or absence of root formation were recorded. Images of turions were captured using a scanner[11] at 1200 dots per inch resolution and saved as .tiff files. A ruler was included in each scan to provide scale. Turion lengths were measured in ImageJ[12] using Feret's diameter, which is defined as the longest distance between any two points along the selection boundary (Walton 1948). Measurements were taken by first adjusting the image contrast using the "Color Threshold Adjust" tool, followed by object detection using the "Analyze Particles" function.

Statistical analysis

Data were analyzed in RStudio using the *drc* and *ggplot2* packages (Ritz et al. 2015, Wickham 2016, R Core Team 2022). Sprouting was defined as either $\geq 25\%$ elongation or the formation of adventitious roots. Percent sprouting was calculated as the number of subreplicates that sprouted divided by the total number of subreplicates. Percent sprouting and percent root development data were arcsine-square-root transformed to improve normality according to a Shapiro-Wilkes test. Two-way ANOVAs were used to assess the effects of trial location and chilling duration on percent sprouting, branching, and root formation. Differences between treatments were determined by Tukey's HSD test ($\alpha = 0.05$), and back-transformed results are presented for clarity. Additionally, percent sprouting data were fit to a two-parameter log-logistic model to estimate the time required to reach 50% and 90% sprouting:

$$f(x) = \frac{1}{1 + \exp\{b[\log(x) - \log(e)]\}} \qquad [1]$$

RESULTS AND DISCUSSION

There was no significant interaction between chilling duration and site (Florida vs. Connecticut; $P > 0.05$); therefore, data were pooled across sites for analysis. There were no differences in branching between the chilling durations at any posttreatment time period ($P > 0.05$), except for a marginal difference 8 days after chilling (DAC) ($P = 0.036$). At the end of 16 DAC, mean branch counts per treatment ranged between 1.118 and 2.125 (Table 1). There were differences in percent of turions with roots on day 4 ($P = 0.0003$) and day 8 ($P = 0.0121$) with the 16 day chilling group exhibiting more root development in comparison to

Table 1. Branching of turions by chilling duration.

Chilling duration	Days After Transfer to 30 °C					
	0	1	2	4	8	16
Day	Mean number of branches[1]					
0	0a	0.042a	0.083a	0.125a	0.958ab	1.25a
2	0.083a	0.208a	0.208a	0.25a	0.667b	1.188a
4	0.042a	0.083a	0.208a	0.333a	1.354ab	1.375a
8	0a	0a	0.125a	0.667a	1.875a	2.125a
16	0a	0a	0.083a	0.792a	1.458ab	1.875a

[1] Means sharing the same letters within each column are not different according to Tukey's HSD test ($a = 0.05$).

Table 2. Percent turions with roots by chilling duration.

Chilling duration	Days After Transfer to 30 °C					
	0	1	2	4	8	16
Day	Percent turions with roots[1]					
0	0a	4a	4a	12c	42b	58a
2	0a	10a	10a	52ab	60ab	65a
4	0a	0a	0a	21bc	71ab	71a
8	0a	0a	4a	58a	83ab	83a
16	0a	4a	4a	62a	92a	92a

[1] Means sharing the same letters within each column are not different according to Tukey's HSD test ($a = 0.05$).

the control group (Table 2). No differences in sprouting were observed among chilling durations until 4 DAC ($P < 0.0001$). However, from 4 DAC onward, a clear effect of chilling duration was observed. By 16 DAC, turions chilled for 8 ($P = 0.001$) or 16 days ($P = 0.01$) exhibited greater sprouting rates (> 97%) compared to the nonchilled control group (73%) (Table 3).

Time to 50% sprouting (T_{50}) decreased with increasing chilling duration, from 8.9 ± 2 DAC in nonchilled turions to 3.15 ± 0.55 DAC for turions chilled eight or more days. Similarly, estimated time to 90% sprouting (T_{90}) was reduced from 33.7 ± 19.9 DAC in the nonchilled group to just 4.9 ± 1.1 DAC in the 16-day chilling treatment. Additionally, the confidence interval for the T_{50} and T_{90} decreased with increased chilling duration, signifying that variability in sprouting decreases after longer exposure to cool conditions. This indicates an earlier and more synchronized emergence response following chilling, similar to monoecious hydrilla (Carter et al. 1987). Alternatively, although nonchilled turions still sprout, the sprouting process is more sporadic and delayed. This means that management timing may be easier to plan and estimate in colder regions. However, if this subspecies invades warmer systems, management timing will be more complicated because the turions may sprout sporadically throughout the year, requiring multiple management events, similar to that of perennial *Potamogeton crispus* (Turnage et al. 2018).

Root formation followed a similar trajectory, with significantly higher rooting percentages in chilled turions. By 16 DAC, 92% of turions chilled for 16 days had formed roots, compared to 58.3% in the nonchilled group (Table 2). Root development appeared to be an early indicator of dormancy break, as chilling duration correlated positively with both earlier and more frequent rooting. Although there were no significant changes in branch count between treatment groups at 16 DAC, turions chilled for 8 (mean = 2.13) and 16 days (mean = 1.87) had slightly higher branching than the control (mean = 1.25) (Table 1). This suggests that chilling not only initiates sprouting but may enhance early vegetative vigor, potentially increasing establishment success in the field.

The sprouting behavior of *H. v. lithuanica* aligns with previous findings in related aquatic macrophytes. For instance, Howell et al. (2024) found that *H. v. lithuanica* turions chilled for 72 h reached 50% sprouting within 3.1 days after warming, closely matching our T_{50} values for two- to four-day chilling treatments. These results are also consistent with studies on Eurasian species such as *P. crispus* and *Myriophyllum oguraense*, which show sprouting proportional to chilling duration (Sastroutomo 1981, Kadono 1988).

Compared to *H. v. peregrina*, whose distribution overlaps with that of *H. v. lithuanica* and fails to sprout without chilling (Carter et al. 1987), *H. v. lithuanica* exhibited greater plasticity, with 73% of nonchilled turions successfully sprouting. This indicates a reduced chilling requirement and may support its establishment in regions with variable winter conditions. Conversely, its robust sprouting, characterized by greater branching, rooting, and elongation, following short chilling periods suggests cold adaptation and increased potential for synchronized emergence in northern climates.

These physiological traits may enable *H. v. lithuanica* to expand into both colder and milder regions, occupying broader ecological niches unavailable to other U.S. subspecies. Beets et al. (2025) reported that *H. v. lithuanica* produces 2.3 times more turions per plant than *H. v. peregrina* and 61.5 times more than *H. v. verticillata*, further amplifying its invasive potential. Given that a majority of these turions can sprout without chilling, this lineage poses a high risk of range expansion, particularly if introduced into southern waterbodies.

From a management perspective, these findings suggest that management interventions should be planned for execution following seasonal increases in water temperature when chilled turions are breaking dormancy. However, this phenological event likely varies across systems and regions. Root development and branching metrics may serve as useful proxies for identifying when turions have sprouted for optimal treatment timing.

Additional research further examining environmental triggers will be essential to understand how this lineage responds to overwintering conditions in both native and introduced ranges. Rybicki et al. (2001) demonstrated that environmental factors such as light penetration, sediment conditions, and nutrient availability strongly influence establishment. Thus, even with this subspecies' high turion production, site-specific conditions may determine whether *H. v. lithuanica* successfully establishes. Field monitoring of turion sprouting and propagule bank dynamics across systems would therefore provide critical context for translating laboratory phenology into applied management recommendations.

Chilling and light may be acting in combination to cue sprouting. For example, *P. crispus* turion germination is

Table 3. Percent turions sprouted by chilling duration and log logistic model parameters.

	Days After Transfer to 30 °C						Model Parameters[1]		
Chilling duration	0	1	2	4	8	16	b	T_{50}	T_{90}
Days	% sprouted[2]						Days after chilling[3]		
0	0a	1a	1a	7c	61c	73b	−1.7	8.9 ± 2.0	33.7 ± 19.9
2	0a	3a	6a	58ab	76bc	92ab	−1.4	4.7 ± 1.1	21.6 ± 12.5
4	0a	0a	3a	50bc	88abc	88ab	−2.0	4.5 ± 0.9	13.4 ± 6.7
8	0a	0a	5a	80ab	98ab	98ab	−3.8	3.2 ± 0.5	5.8 ± 1.7
16	0a	1a	4a	88a	99a	100a	−4.6	3.0 ± 0.4	4.9 ± 1.1

[1] Values are derived from a two-parameter log logistic model with b as the slope, T_{50} as the estimated time in days to 50% sprouting, and T_{90} as the estimated time in days to 90% sprouting.

[2] Means sharing the same letters within each column are not different according to Tukey's HSD test ($a = 0.05$).

[3] 95% confidence interval.

inhibited in darkness, and factors such as water depth, substrate type, and buoyancy have been shown to influence germination success (Jian et al. 2003, Xie et al. 2014). To confirm whether chilling alone is sufficient, experiments will be replicated under dark conditions, which will also help clarify sprouting capacity across varying light availability.

To further understand the cold stratification requirements of *H. v. lithuanica*, this study should be replicated with subterranean turions. The lower production of subterranean turions, compared to monoecious and dioecious hydrilla, observed by Beets et al. (2025) may indicate a shift in reproductive and dispersal strategy that relies more heavily on axillary turions. Monoecious axillary turions are generally smaller than subterranean turions and therefore contain less carbohydrate storage, resulting in shorter viability of about 1 yr compared to approximately 4 yr for subterranean turions (Spencer et al. 1987; Van and Steward 1990). If *H. v. lithuanica* depends primarily on axillary turions, the longevity of its propagule bank may be reduced, though further studies are needed to evaluate turion longevity in this subspecies. Another important avenue for investigation is turion formation. Both monoecious and dioecious hydrilla produce turions under shorter photoperiods (Van 1989), but characterizing the timing of turion production in *H. v. lithuanica* is critical for informing management. Overall, there is a strong need for additional research on phenological differences to refine our understanding of subspecies-specific ecological niches and invasion potential under varying climates and environments. Our finding that *H. v. lithuanica* sprouts proportionally with increased chilling yet retains the ability to sprout without chilling suggests that it represents an intermediate form between monoecious and dioecious hydrilla, underscoring its unique plasticity and the importance of continued comparative study.

SOURCES OF MATERIALS

[1] Scotts Premium Topsoil, Scotts Miracle-Gro Company, 14111 Scottslawn Road, Marysville, OH 43041.

[2] Osmocote Slow Release Fertilizer, Osmocote Garden, P.O. Box 8819, Bloomington, IN 47407.

[3] Entrust SC Naturalyte Spinosad, Corteva Agriscience, 9330 Zionsville Road, Indianapolis, IN 46268.

[4] Dylox 420 SL, Bayer AG, 51368 Leverkusen, Germany.

[5] Top Fin Air 100 Aquarium Air Pump, Top Fin Shop, 2674 Brannon Avenue, Jacksonville, Fl 32244.

[6] Aquascape 2 Outlet Aeration Kit, Aquascape Construction, 901 Aqualand Way, Saint Charles, IL 60174.

[7] Bulk Reef Supply 600 Watt titanium fish tank heater, Bulk Reef Supply, 6325 Sandburg Road Ste 200, Golden Valley, MN 55427.

[8] E-36VL and E-22L, Percival Scientific, 505 Research Dr., Perry, IA 50220.

[9] Li-Cor 250A, Li-Cor Environmental, 4421 Superior St., P.O. Box 4425, Lincoln, NE 68504.

[10] HOBO, 470 MacArthur Boulevard, Bourne, MA 02532; Elitech RC-5, Elitech Technology, Inc., 2528 Qume Dr., Ste 2, San Jose, CA 95131.

[11] LaserJet 100 color MFP, M76w, HP Inc., 1501 Page Mill Road, Palo Alto, CA 94304; Epson Expression 10000 XL, Epson America, Inc., 3131 Katella Avenue, Los Alamitos, CA 90720.

[12] ImageJ, 441 E. Renfro St., Burleson, TX 76028.

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LITERATURE CITED

Beets J, Foley KJ, Sperry BP, Howell AW, Richardson RJ. 2025. Growth patterns of three *Hydrilla verticillata* biotypes in the United States. Aquat. Bot. 201:103924.

Bradshaw EL, Allen MS, Netherland M. 2015. Spatial and temporal occurrence of hypoxia influences fish habitat quality in dense *Hydrilla verticillata*. J. Freshw. Ecol. 30:491–502.

Carter V, Rybicki N, Schulman C. 1987. Effect of salinity and temperature on germination of monoecious hydrilla propagules. J. Aquat. Plant Manage. 25:54–57.

Foley JR IV, Stebbins SE, Doherty R, Tippery NP, Bugbee GJ. 2024. Northern hydrilla (*Hydrilla verticillata* ssp. *lithuanica*): Discovery and establishment outside the Connecticut River. Invasive Plant Sci. Manage. 17:55–59.

Gettys LA, Enloe SF. 2016. Hydrilla: Florida's worst submersed weed. SS-AGR-400/AG404. EDIS. 2016(3):7.

Haller WT, Sutton DL. 1975. Community structure and competition between hydrilla and vallisneria. J. Aquat. Plant Manage. 13:48–50.

Howell AW, Foley KJ, Sperry BP, Richardson RJ. 2024. The role of temperature on clade C turion sprouting and growth [poster]. Aquatic Plant Management Society Conference, St. Petersburg, FL.

Jian Y, Li B, Wang J, Chen J. 2003. Control of turion germination in *Potamogeton crispus*. Aquat. Bot. 75:59–69.

Kadono Y. 1988. Germination of the turion of *Myriophyllum oguraense* Miki. Aquat. Bot. 31:355–360.

Langeland KA. 1996. *Hydrilla verticillata* (LF) Royle (Hydrocharitaceae), "the perfect aquatic weed." Castanea 61:293–304.

Madsen JD, Smith DH. 1999. Vegetative spread of dioecious hydrilla colonies in experimental ponds. J. Aquat. Plant Manage. 37:25–29.

Maki KC, Galatowitsch SM. 2008. Cold tolerance of the axillary turions of two biotypes of hydrilla and northern watermilfoil. J. Aquat. Plant Manage. 46:42–50.

Netherland MD. 1997. Turion ecology of hydrilla. J. Aquat. Plant Manage. 35:1–10.

Netherland MD. 1999. Management impacts on the quiescence and sprouting of subterranean turions of dioecious hydrilla (*Hydrilla verticillata* (LF) Royle). Dissertation. University of Florida, Gainesville, FL.

R Core Team. 2022. R: A language and environment for statistical computing, version 4.4.2. Vienna: R Foundation for Statistical Computing.

Ritz C, Baty F, Streibig JC, Gerhard D. 2015. Dose-response analysis using R. PLOS ONE. 10(12):e0146021.

Rybicki NB, McFarland DG, Ruhl HA, Reel JT, Barko JW. 2001. Investigations of the availability and survival of submersed aquatic vegetation propagules in the tidal Potomac River. Estuaries 24:407–417.

Sartain BT, Harms NE, Coomes AB. 2024. Influence of shade and cold stratification on germination success of vegetative propagules from multiple *Butomus umbellatus* genotypes. Aquat. Bot. 193:103774.

Sastroutomo SS. 1980. Dormancy and germination in axillary turions of *Hydrilla verticillata*. Bot. Mag. Tokyo. 93:265–273.

Sastroutomo SS. 1981. Turion formation, dormancy and germination of curly pondweed, *Potamogeton crispus* L. Aquat. Bot. 10:161–173.

Smart RM, Barko JW. 1985. Laboratory culture of submersed freshwater macrophytes on natural sediments. Aquat. Bot. 21:251–263.

Spencer DF, Anderson LW, Ames MD, Ryan FJ. 1987. Variation in *Hydrilla verticillata* (L.f.) Royle propagule weight. J. Aquat. Plant Manage. 25:11–14.

Spencer DF, Ksander GG. 2001. Field evaluation of degree-day based equations for predicting sprouting of hydrilla (*Hydrilla verticillata*) turions and tubers. J. Freshw. Ecol. 16:479–486.

Steward KK, Van TK. 1987. Comparative studies of monoecious and dioecious hydrilla (*Hydrilla verticillata*) biotypes. Weed Sci. 35:204–210.

Tippery NP. 2023. Subspecies classification of hydrilla (*Hydrilla verticillata*, Hydrocharitaceae). J. Bot. Res. Inst. Tex. 17:401–412.

Tippery NP, Bugbee GJ, Stebbins SE. 2020. Evidence for a genetically distinct strain of introduced hydrilla (*Hydrilla verticillata*, Hydrocharitaceae) in North America. J. Aquat. Plant Manage. 58:1–6.

True-Meadows S, Haug EJ, Richardson RJ. 2016. Monoecious hydrilla—A review of the literature. J. Aquat. Plant Manage. 54:1–11.

Turnage G, Madsen JD, Wersal RM. 2018. Phenology of curlyleaf pondweed (*Potamogeton crispus* L.) in the southeastern United States: A two-year mesocosm study. J. Aquat. Plant Manage. 56:35–38.

Van TK. 1989. Differential responses to photoperiods in monoecious and dioecious hydrilla. Weed Sci. 37:552–556.

Van TK, Steward KK. 1990. Longevity of monoecious hydrilla propagules. J. Aquat. Plant Manage. 28:74–76.

Walton W. 1948. Feret's statistical diameter as a measure of particle size. Nature 162(4113):329–330.

Wickham H. 2016. ggplot2: elegant graphics for data analysis. R package version 3.5.1. https://CRAN.R-project.org/package = ggplot2.

Xie D, Yu D, Xia C, You W. 2014. Stay dormant or escape sprouting? Turion buoyancy and sprouting abilities of the submerged macrophyte *Potamogeton crispus* L. Hydrobiologia 726:43–51.