

Tuber and turion dynamics in monoecious and dioecious hydrilla (*Hydrilla verticillata*)

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INTRODUCTION

Hydrilla is an invasive, nonindigenous submersed aquatic plant first discovered in the United States in the 1960s (Blackburn et al. 1969, Pieterse 1981). A native of Asia, the Pacific Islands, and New Zealand (Pieterse 1981, Cook and Lüönd 1982, Madiera et al. 2004), hydrilla exhibits aggressive growth, rapidly expanding to the surface (especially dioecious biotype) and forming a dense canopy. Limited light availability beneath the dense canopy results in competitive reduction of native vegetation and lower diversity (Sutton 1990, Barko et al. 1991). Additionally, excessive growth of hydrilla may degrade water quality and habitat for fish and other wildlife (Madsen 1997). Two distinct biotypes, monoecious and dioecious, exist in the United States (Spencer and Anderson 1986); monoecious hydrilla has both male and female flowers on the same plant, while the dioecious biotype produces male and female flowers on separate plants. Distribution of both biotypes includes the northern states of Maine, Wisconsin, and Washington; the Gulf and Atlantic coastal states; the western states of Arizona, Idaho, and California; the midwestern states of Tennessee, Arkansas (USGS 2010), Oklahoma (Gene Gilliland, Oklahoma Department of Wildlife Commission, pers. comm.), Indiana (Lembi 2006), Kentucky (<http://www.apms.org/apn/oct2008.pdf>), Kansas (<http://www.apms.org/apn/oct2009.pdf>), and recently the Ohio River from West Virginia to Indiana.

Monoecious hydrilla tends to be located in the northern states but has been found in recent years in many Tennessee Valley Authority (TVA) reservoirs, including Lake Guntersville in Alabama and Nickojack Reservoir in Tennessee. Dioecious hydrilla has always been considered an invasive plant of the south; however, this perception is changing because it has now been found in Idaho and Kentucky (Figure 1), suggesting it can endure more northern locations.

To better understand differences in the tuber dynamics between monoecious and dioecious hydrilla, an outdoor mesocosm study was conducted in Texas to compare differences between two biotypes under similar conditions. By understanding the tuber/turion dynamics of different hydrilla biotypes, implementation of management options may be better applied with more consistent control efficacy (Madsen and Owens 1998). This study examines differences in tuber/turion dynamics between monoecious and dioecious hydrilla.

METHODS

This study was conducted at the Lewisville Aquatic Ecosystem Research Facility (LAERF) in Lewisville, Texas (33°04'45"N, 96°57'30"W), in six 1845 L outdoor fiberglass tanks filled with alum-treated (to control phosphorus) Lewisville Lake water. Tanks were aerated using a regenerative blower and air stones to provide mixing and maintain oxygen saturation. We filled 384 containers, 5.5 L each, with heat-sterilized LAERF pond sediment (top 15 cm) amended with 1.4 g ammonium sulfate per container. Smart et al. (1995) found that LAERF pond sediments were fine-textured, generally consisting of equal parts clay, silt, and sand. In July 2006, each container in three tanks (32 containers per tank) was planted with three apical dioecious fragments (20 cm in length) collected from the LAERF ponds. Remaining tanks (three) were planted in a similar fashion with monoecious hydrilla shipped overnight from Lake Gaston, North Carolina-Virginia. A 30% shade cloth was suspended over tanks to moderate water temperatures. Although water temperature was not taken (data logger failure), average daily air temperatures were obtained from National Weather Service Forecast Office, Fort Worth, Texas (www.weather.gov/climate/index.php?wfo=fwd; Figure 2A).

Harvests were conducted every 6 weeks starting in October 2006, except for January through March 2007. Two containers from each tank (six per biotype) were collected per harvest date; biomass was divided into aboveground and belowground material (data not reported), and rhizome lengths were measured. Tubers and turions were collected from washed sediment and counted; it was noted if the tuber or turion had already spouted or was newly produced (attached to rhizome), and only unspouted tubers or turions were placed into germination containers (petri dishes) and distilled water. Unless they were collected during or after the start of winter (first freeze event), tubers and turions were exposed to cold treatments, approximately 10 days in a dark refrigerator at 4 C, to induce sprouting. New tubers were not counted for the November and December 2007 harvests because they were no longer attached to rhizomes.

Comparisons between the tuber and turion data for the two biotypes were made using a one-way ANOVA and the Tukey's test at a $p = 0.05$ level of significance (Statistix Analytical Software, Tallahassee, FL; Figure 2).

RESULTS AND DISCUSSION

Seasonal growth

Dioecious hydrilla allocates growth principally to aboveground biomass during the summer months (Jun through

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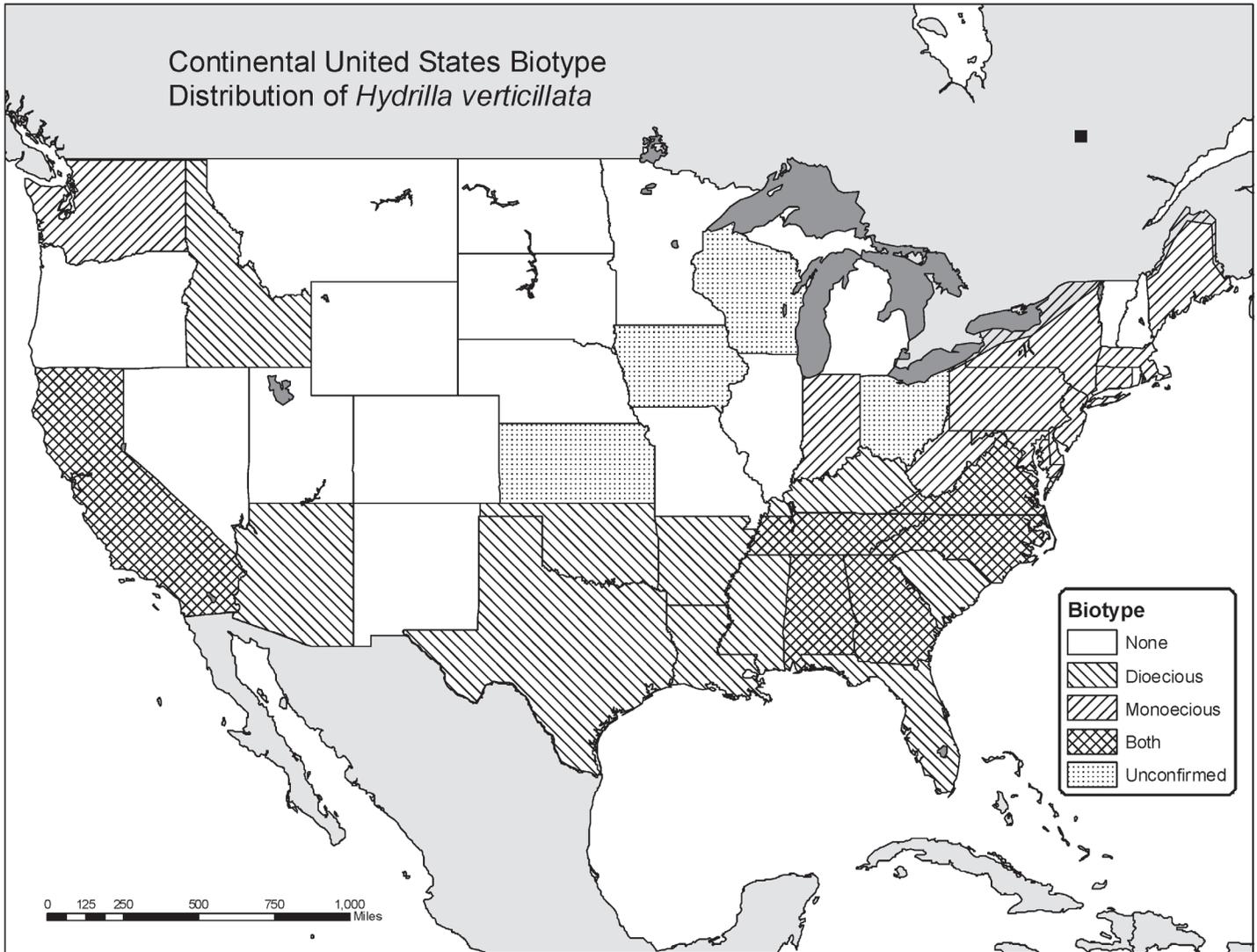


Figure 1. U.S. states with dioecious hydrilla infestations (Dioecious) and monoecious hydrilla infestations (Monoecious), states where both biotypes occur (Both), states with no hydrilla infestations (None), and states with hydrilla but the biotype has not been determined (Unconfirmed). Map created using ESRI Data and Map 9.3.1, Redlands, CA.

Aug) in Texas, rapidly elongating to the surface to maximize photosynthetic capabilities (Madsen and Owens 1998, Owens and Madsen 1998). During the fall months, hydrilla shuttles carbohydrates to belowground organs for winter storage. During the winter months, dioecious hydrilla does not become completely dormant, although growth slows and biomass decreases (Madsen and Owens 1998, Owens and Madsen 1998). This study finds that dioecious hydrilla biomass increases during the warmer, summer months, followed by decreasing biomass as temperatures drop and photoperiod decreases. However, vegetative biomass persisted during the winter months, indicating that dioecious hydrilla can behave as a perennial in Texas.

Monoecious hydrilla in Texas, however, exhibited the life cycle of an annual plant. During early spring through early fall (Mar through Oct), monoecious hydrilla produced new growth only from a portion of tubers and all turions produced the previous growing season, with no other overwin-

tering biomass (shoots or roots) observed. Note that Sutton et al. (1992) found that monoecious hydrilla grew as a perennial in south Florida, although shoot biomass was low. In the Potomac River, where the south Florida monoecious hydrilla originated, the hydrilla behaved as an annual with no observed aboveground biomass during the winter. In November 2006 and October 2007, monoecious hydrilla aboveground biomass began declining and had all but disappeared by December of both years.

Tuber number and size

Monoecious hydrilla produced approximately three times more tubers by October 2006 as did dioecious hydrilla (Figure 2B). The dioecious tuber number is low compared to monoecious hydrilla; however, it is similar in tuber number to other studies at LAERF conducted in similar-sized containers. Monoecious tuber production peaked in November.

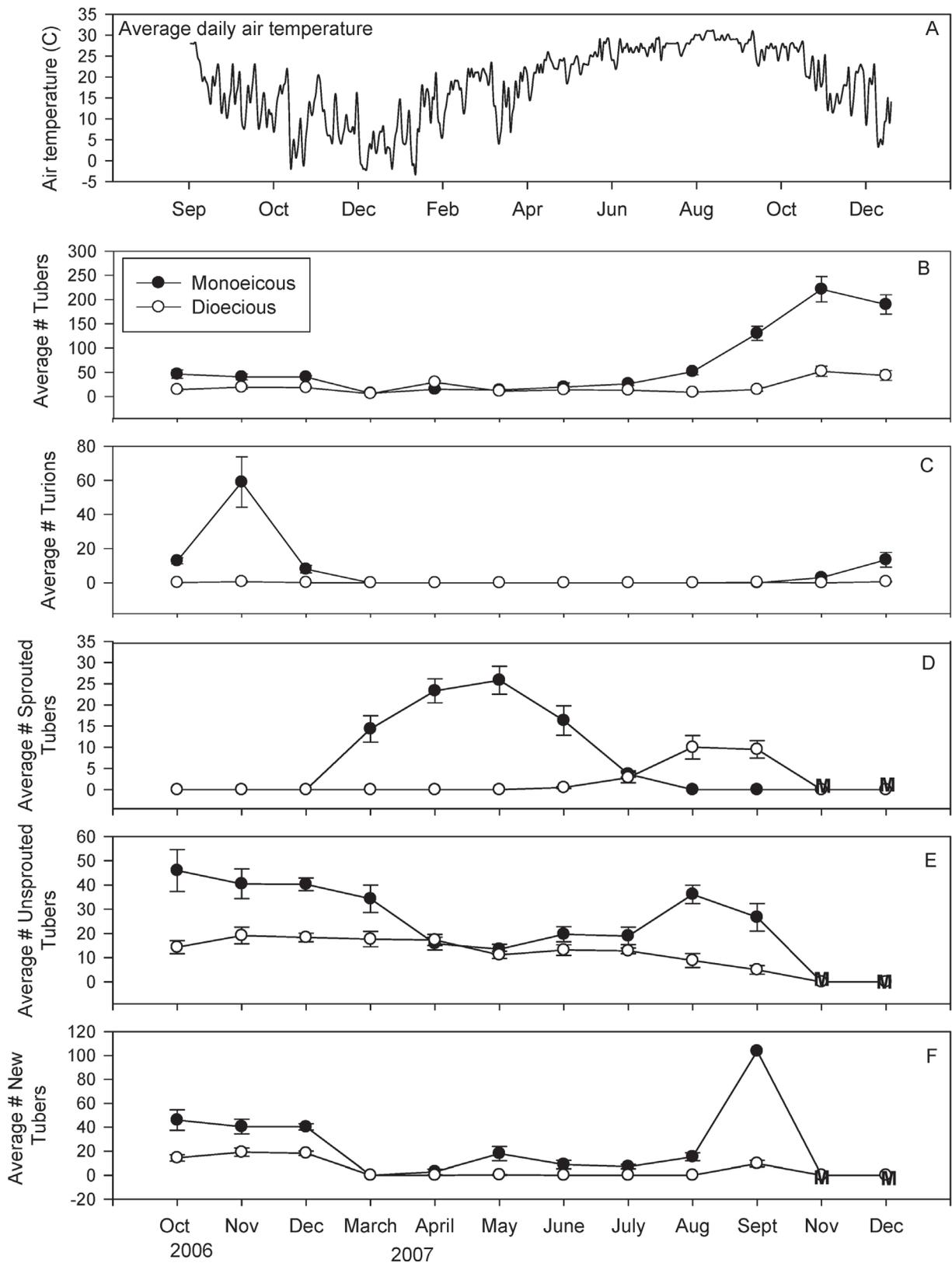


Figure 2. (A) Daily air temperature (C) from October 2006 to December 2007. Comparison between monoecious and dioecious hydrilla tubers and turions (containers) for (B) average # tubers collected ($F = 38.09, p = 0.0000$), (C) Average # turions collected ($F = 13.93, p = 0.0000$), (D) average # sprouted tubers ($F = 24.54, p = 0.0000$), (E) average # unsprouted tubers ($F = 14.65, p = 0.0000$), and (F) average # new tubers ($F = 33.53, p = 0.0000$). M (missing) indicates that new tuber numbers were not counted due to uncertainty in age of tuber (unattached to rhizome). Sprouting was not determined. Bars indicated Standard Error, and # indicates number

Those tubers began sprouting in March 2007 (Figure 2D), and soon thereafter (April 2007) new tubers began to form (attached to rhizomes; Figure 2F). Early sprouting of monoecious hydrilla tubers was reported by Spencer et al. (2000) in northern California (Davis), where sprouting occurred as early as February. Harlan et al. (1985) found that monoecious tubers in three North Carolina lakes began to sprout in March and continued sprouting through August. Van (1989) suggested that monoecious tuber production in early summer would guarantee survival in northern climates, which may explain the more northerly range of the monoecious hydrilla biotype in the United States. Madiera et al. (2004) found that monoecious hydrilla introduced into the Mid-Atlantic States in the 1980s was of Korean origin. The Korean peninsula is located between Japan (east) and China (west), along the northern border of China. Monoecious hydrilla in the United States originally dispersed from the Mid-Atlantic states northward into New England, although recent locations in the TVA system of reservoirs suggest that monoecious hydrilla can establish in reservoirs with warmer water temperatures. Also note that the point of entry for monoecious hydrilla (Mid-Atlantic) into the United States was approximately 800+ miles north of the point of entry for dioecious hydrilla in Florida. Maybe the reason that monoecious hydrilla currently has a more northerly distribution is related to proximity and dispersal from the original US entry point.

No dioecious tubers had sprouted and no new tubers were being produced during the early summer timeframe (May and June, Figures 1D-F). By July 2007, few monoecious tubers were observed sprouting, but dioecious tubers began sprouting and continued into September 2007 (Figure 1D).

In this study, monoecious hydrilla produced new tubers throughout most of the growing season, increasing production in September 2007, probably in response to shortening days and/or declining temperatures (Figure 1A and 1F). Spencer and Anderson (1986), and Van (1989) state that monoecious hydrilla produced new tubers after a 28-day exposure to a 10-hour photoperiod and after a 56-day exposure to a 16-hour photoperiod. Dioecious hydrilla initiated tuber production starting in September (Figure 1A and 1F). McFarland and Barko (1990) reported that dioecious hydrilla tuber production increased under shorter days. Thakore et al. (1997) suggested that a minimum of 20 to 38 short days is necessary for tuber production by dioecious hydrilla.

In October, monoecious rhizome length averaged 8.3 cm (S.E. 0.76) and dioecious averaged 14.3 cm (S.E. 0.67); in November, monoecious averaged 3.83 cm (S.E. 1.25) and dioecious averaged 14.83 cm (S.E. 0.83); and by December, monoecious rhizomes were not present and dioecious rhizomes averaged 11.83 cm (S.E. 0.70). Overall, monoecious hydrilla rhizomes were significantly shorter than dioecious hydrilla rhizomes. Harlan et al. (1985) found that 93 to 100% of monoecious tubers in three North Carolina lakes were located in the upper 12 cm of sediment. Netherland (1997) found that dioecious rhizomes can penetrate sediments up to 30 cm.

Fresh weights of tubers were also measured in October, November, and December 2006. Tubers produced by monoecious hydrilla (0.1 to 0.15 g) exhibited significantly lower (by

a factor of two) biomass than dioecious tubers (0.2 to 0.3 g). Sutton et al. (1992) found that monoecious tubers weighed approximately 32% less than dioecious tubers. Spencer et al. (1987) suggested that propagule size may provide a survival advantage: the larger the propagule, the better chance of sprouting and survival. The smaller monoecious tubers are produced on shorter stolons closer to the sediment surface but in larger numbers, which could represent a difference in survival strategies between monoecious and dioecious hydrilla (Spencer and Anderson 1986, Spencer et al. 1987).

Tuber sprouting

Sprouting studies were conducted for most harvests. Approximately 70 to 100% of monoecious hydrilla tubers sprouted, whereas 10 to 90% of dioecious hydrilla tubers sprouted. Monoecious tubers tended to sprout sooner (perhaps indicative of smaller size), generally within the first week, while dioecious tubers took as many as several weeks (6 weeks) to sprout. Coupled with greater numbers, monoecious tuber production may be geared toward high numbers of shorter-lived propagules. Spencer et al. (1987) also hypothesized that smaller monoecious tubers may not contain sufficient starch reserves to remain as long-lived as dioecious tubers. Van and Steward (1990) found that monoecious tubers survived in undisturbed sediments for approximately 4 years, while Nall and Schardt (1978) indicated that dioecious tubers could remain viable for up to 10 years in hydrosol. Several studies (Basiouny et al. 1978, Carter et al. 1987, Kojima and Izawa 1989), indicated that short periods of low temperature broke tuber dormancy; however, time periods (0 to 42 d) suggest inconsistency of results.

Turions

Turions in this study were formed solely in the fall months by both biotypes, starting in October of 2006 and 2007 (Figure 1A). In November 2006, approximately 60 turions (average) were collected per monoecious container, while less than one turion per container was found on dioecious hydrilla (Figure 1A and 1C). In addition to turions collected from plants and containers, large numbers were recovered from the bottom of monoecious tanks during the winter months for both years. The December 2007 turion count was 3-fold smaller than that of 2006 (Figure 1C). Pieterse et al. (1984) suggested that turion formation could be increased due to low availability of nitrogen and phosphorus. Interestingly, both axillary and terminal turions were observed on monoecious hydrilla as well as double turions produced at same location of stem (Owens, pers. observ.). Terminal and double turions have not been reported (to our knowledge) for monoecious hydrilla in literature. Further research on monoecious hydrilla turion production is warranted, especially due to the potential for large quantities to be produced.

CONCLUSIONS

Based on this study, dioecious hydrilla exhibited a perennial life cycle while monoecious hydrilla behaved as an annual plant. Additionally, monoecious hydrilla produced three

times more tubers than dioecious hydrilla and exhibited significantly greater turion formation.

Due to different tuber/turion dynamics (production and sprouting), reliable control methods could prove very different between the two biotypes. While many herbicides have been shown to effectively control both biotypes, application timing has not been extensively studied based on life cycle differences. Poovey and Getsinger (2010) found that endothall was effective in reducing biomass (>85%) for both biotypes (monoecious and dioecious). They suggest, however, that because monoecious tubers sprout in spring and early summer, that early use of endothall could be an effective application treatment for monoecious hydrilla. They further suggest that treatment of sprouted dioecious tubers could be more difficult because sprouting is more random. Grodowitz et al. (2010) found that survival of the hydrilla leaf-mining fly (*Hydrellia pakistanae*) was reduced in tank studies when the flies were introduced to monoecious hydrilla as compared to the dioecious biotype. Additionally, establishment of the *Hydrellia* fly on Lake Gaston, North Carolina-Virginia, was ineffective due to complete winter dieback of the monoecious hydrilla. Poovey and Kay (1998) found that a properly timed drawdown (summer) could suppress monoecious hydrilla growth and tuber/turion production. This study found that monoecious hydrilla produces copious quantities of turions (axil and terminal); thus, interrupting this cycle could reduce one method of hydrilla survival. By understanding the tuber/turion dynamics of hydrilla, whether dioecious or monoecious biotype, implementation of management options may be better applied with more consistent control efficacy.

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