Monoecious hydrilla—A review of the literature

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ABSTRACT

Hydrilla verticillata is a submersed aquatic weed that has become one of most expensive and difficult to manage in the United States. It disrupts water flow, interferes with recreation, displaces native vegetation, and can negatively impact nonplant species. There are two biotypes of hydrilla found in the United States—a triploid dioecious and a triploid monoecious biotype. The monoecious biotype is typically found from North Carolina northward and is rapidly spreading, whereas dioecious hydrilla is common further south and is not currently demonstrating significant range expansion. Monoecious hydrilla behaves as a herbaceous perennial with shoots senescing over winter and repopulation occurring through prolific turions. This is in contrast to dioecious hydrilla, which has more persistent stems and root crowns, but produces fewer turions. Monoecious hydrilla turions also sprout at a far greater rate under cooler temperatures than dioecious hydrilla. Differences in biology between the two U.S. biotypes have been reported in genetic profiles, with monoecious biotypes, possibly originating from hybridization between two distinct dioecious biotypes. Cryptic speciation of hydrilla biotypes is an interesting consideration that has recently been suggested, and additional research is needed on hydrilla genetic diversity worldwide to determine if this has occurred. The body of research focusing strictly on the monoecious biotype is much smaller than that of the dioecious, as reflected in the literature. Many publications on hydrilla make no mention of biotype; therefore only an educated guess can be made based on study locations to decipher biotype. Thus, as monoecious hydrilla continues to spread and now presents a distinct threat to glacial lakes, additional research focused on this biotype is needed. The impact of latitudinal climate changes on monoecious growth and competition with native plants has not been well documented. The native-species spectrum of northern U.S. lakes is different than in traditional monoecious areas. Research needs to evaluate the ecological impact of hydrilla invasion as well as best management techniques for removing monoecious hydrilla from these plant communities. In addition, although seed production of monoecious hydrilla has been reported, it is poorly understood *in situ*. Seed production, viability, and potential dispersal also represent areas that have not been adequately documented.

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SPECIES OVERVIEW

The submersed aquatic monocotyledonous angiosperm *Hydrilla verticillata* (L.f.) Royle is an aggressive, opportunistic, nuisance species in the Hydrocharitaceae family that has spread from its native Asia to every continent except Antarctica (Pieterse 1981, Cook and Luond 1982). Taxonomic classification for Hydrilla along with other genera of Hydrocharitaceae is shown below (USDA 2013), with the genus *Najas* now placed within Hydrocharitaceae by some sources (Weakly 2012).

Kingdom	Plantae
Subkingdom	Tracheobionta
Superdivision	Spermatophyta
Division	Magnoliophyta
Class	Liliopsida
Subclass	Alismatidae
Order	Hydrocharitales
Family	Hydrocharitaceae
Genus	*Hydrilla*
Genus	*Blyxa*
Genus	*Egeria*
Genus	*Elodea*
Genus	*Enhalus*
Genus	*Halophila*
Genus	*Hydrocharis*
Genus	*Lagarosiphon*
Genus	*Limnobium*
Genus	*Nechamadra*
Genus	*Ottelia*
Genus	*Stratiotes*

Hydrilla is difficult to manage and causes significant economic and ecological damage across the United States (Langeland 1996). It may appear similar to other submersed aquatic plants (refer to taxonomic key in Figure 1), but what makes hydrilla unique is long-term quiescence of turions, rapid vegetative growth rates, low light compensation point, and C4-like photosynthesis. Turions are especially problematic for management as they allow hydrilla to resprout rapidly and revegetate after treatment or environmental stresses (Netherland 1997, Owens and Madsen 1998). Hydrilla may cause severe problems in infested water bodies (Langeland 1996). One significant problem is the disruption of water flow in drainage and irrigation canals. It also negatively impacts recreational uses of a water body, including boating, fishing, swimming, water skiing, and other uses of water resources (Langeland 1996). Hydrilla can displace native plant life and shift balanced ecosystems to monocultures with altered fish populations (Haller and

Aquatic herbs with leaves attached at multiple stem nodes. Leaves less than 4cm long and opposite or occurring in whorls of 2-8.

1 Leaves opposite or occurring in 4 or fewer per whorl.

    2 Leaves slightly narrowed or straight-sided to base, sessile; perianth present….***Elodea***

    2 Leaves broadened and sheathing at base, narrowing towards apex via "shoulders"; perianth absent….***Najas***

1 Leaves in whorls of 3 to 8, with 4-5 leaves per whorl common.

    3 Leaves 2 to 3 cm long or longer serrulate margins and rarely the midrib beneath; young leaves not noticeably scabrous (not rough to touch); leaf whorls generally spaced regularly on all stems; petals white and 9 to 12 mm long .....***Egeria***

    3 Leaves mostly 0.75 to 1.5 cm long, serrate margins and toothed along the midrib beneath; young leaves scabrous; leaf whorls generally crowded at stem terminal, not crowded on mature stems; petals translucent and 2 to 5 mm long...***Hydrilla***

Elodea

1 Most leaves 1.75 mm wide or greater…. **2**

1 Most leaves less than 1.75 mm wide ….**4**

    2 Leaves often overlapping with regular rows near stem apex and lying along stem, may appear oblong or ovate. ***E. canadensis***

    2 Leaves not usually overlapping near stem apex and may appear irregular and spreading, mostly elliptic to linear or lanceolate….**3**

3 Leaves often present in whorls of 4, lanceolate to elliptic, not usually parallel-sided, apex usually obtuse to widely acute…. ***E. potamogeton***

3 Leaves often present in pairs, no whorls of four; mostly linear and parallel sided with acute apex. ***E. bifoliata***

    4 Most leaves folded along midrib, slightly recurved, margins undulate, usually not greater than 10 mm long…. ***E. nuttallii***

    4 Most leaves flat, margins straight and spreading, some greater than 10 mm long…. ***E. callitrichoides***

Hydrilla

Leaf width 2.25 to 3.5mm; staminate flowers not present…**dioecious**

Leaf width 1.0 to 3.0 mm; staminate flowers sessile, at anthesis deciduous from plant...**monoecious**

Figure 1. Taxonomic key for Hydrocharitaceae genera *Elodea*, *Najas*, *Egeria*, and *Hydrilla* in the United States. *Hydrilla* keyed to biotype and *Elodea* keyed to species (Blackburn et al. 1969, Godfrey and Wooten 1979, Bowmer et al. 1995, Crow and Hellquist 2000, Weakley 2012).

Sutton 1975, Langeland 1996). The presence of hydrilla may impact wildlife higher up the food chain. It has been documented to host *Aetokthonos hydrillicola*, an epiphytic cyanobacterium in the order Stigonematales (Wilde et al. 2014). This cyanobacterium is believed to produce a neurotoxin that causes avian vacuolar myelinopathy (AVM), a neurological disease that impacts waterfowl and their predators in the southeastern United States, including bald eagles (Wilde et al. 2005, Williams et al. 2007).

In the United States, both a female dioecious biotype (staminate and pistillate flowers on separate plants) and a monoecious biotype (staminate and pistillate flowers on the same plant) of hydrilla have become naturalized (Cook and Lüönd 1982). Optimal growth and survival for the U.S.

dioecious type is found in warmer climates, whereas the U.S. monoecious form is better suited for more temperate climates with lower temperatures and shorter growing seasons (Ames et al. 1986, Steward and Van 1987, Van 1989, Netherland 1997, Madeira et al. 2000). Dioecious hydrilla typically thrives all year in the warm waters of the southern United States, whereas monoecious hydrilla dies back completely in the winter and acts as a herbaceous perennial (Harlan et al. 1985).

Monoecious and dioecious biotypes of hydrilla found in the United States have been shown to be genetically distinct (Verkleij et al. 1983, Ryan et al. 1991). A method of distinction between the two biotypes was conducted by Ryan and Holmberg (1994) and Ryan et al. (1995). They used random amplified polymorphic DNA (RAPD) and detected a marker that was only present in dioecious hydrilla, not the monoecious biotype. Madeira et al. (1997, 2000) continued this research examining samples of both U.S. hydrilla biotypes from around the world to examine origins of introductions. In 2004, Madeira et al. (2004) published an improved tool for distinguishing between monoecious and dioecious hydrilla that could be done without the reference samples required for the original method.

INTRODUCTION AND SPREAD

Monoecious hydrilla may have been first documented within the United States in Delaware, and then in Washington, DC and the Potomac River in 1980 (Haller 1982, Steward et al. 1984). Steward et al. (1984) suggested that it was possibly introduced during caging and transplanting experiments where hydrilla, mistakenly identified as *Elodea canadensis*, was transplanted from Kenilworth Gardens in Washington, DC. Lilypons Water Gardens, located in Adamstown, Maryland, may have been the source of the Kenilworth Gardens infestation, as they were a popular commercial supplier of aquatic ornamental plants in the area, and Haller (1982) reported seeing a hydrilla-like plant with tubers there during a 1980 visit. Monoecious hydrilla was first documented in North Carolina in 1980 after reports of dense, weedy vegetation in Umstead Lake in the mid to late 1970s (Figure 2). The Delaware and North Carolina invasions seem to be relatively synchronous and it is possible that early monoecious hydrilla spread in the United States was facilitated by contaminated aquatic plant (especially water lily) shipments from Lilypons (Madeira et al. 2000) or other sources. Local spread and dispersal of monoecious hydrilla is often attributed to boaters moving plant fragments unintentionally, and new infestations often occur near boat ramps. Intentional spread also occurs when individuals believe that hydrilla will benefit fish and waterfowl habitat (Langeland 1996). Nonhuman dispersal is possible as well, with waterfowl able to transport turions, fragments, and seeds (Joyce et al. 1980, Langeland and Smith 1984, Miller 1988, Langeland 1996, Coley 1997).

The monoecious biotype spread and became the dominant hydrilla biotype found in the mid-Atlantic states (Langeland 1996). In 2000, Madeira et al. reported that monoecious hydrilla was found in drainages of the Atlantic Basin from central Georgia up to Pennsylvania and
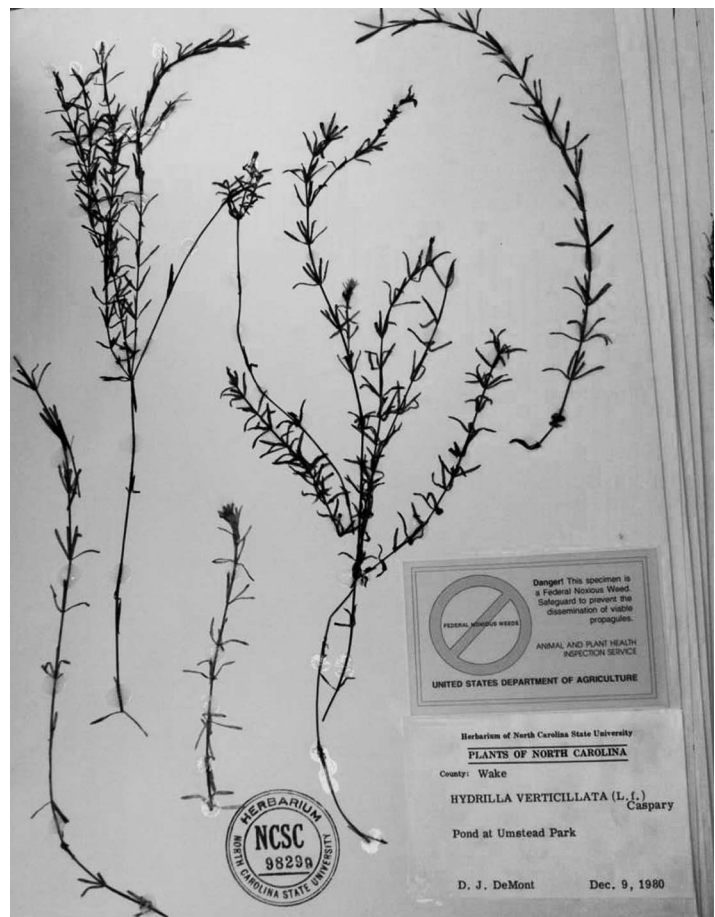

Figure 2. Herbarium specimen of monoecious hydrilla from Umstead Lake, Wake County, North Carolina, dated 9 December 1980.

Connecticut. It was not found in Gulf Basin drainages, but was sporadically located in the Pacific basin, in California and Washington (Madeira et al. 2000). Monoecious hydrilla is also found in the Interior Basin in Maryland and North Carolina. More recent spread of hydrilla includes range expansion to states including Indiana, Ohio, Maine, New York, and Wisconsin as well as invasion of flowing systems including the Eno and Cape Fear Rivers (NC), Erie Canal (NY), and Ohio River (OH) (Owens et al. 2012, Netherland and Greer 2014, Shearer 2014, M. Netherland, pers. comm., R. Richardson pers. obs.). Langeland (1996) suggested that monoecious hydrilla could spread as far north as southern Canada, based on its range in Europe. Les et al. (1997) compiled the northernmost hydrilla distributions worldwide and Balciunas and Chen (1993) provided a comparison of January air temperatures in North America to those in Asia, where hydrilla has been documented. Based on reported worldwide hydrilla distribution and climate patterns, there are vast areas in North America at risk of invasion by hydrilla (Figure 3). New research examining the spectral signature of monoecious hydrilla under varying conditions may help in the use of remote sensing to assess the distribution and spread of the plant in the future (Blanco et al. 2012). In addition to distribution, research
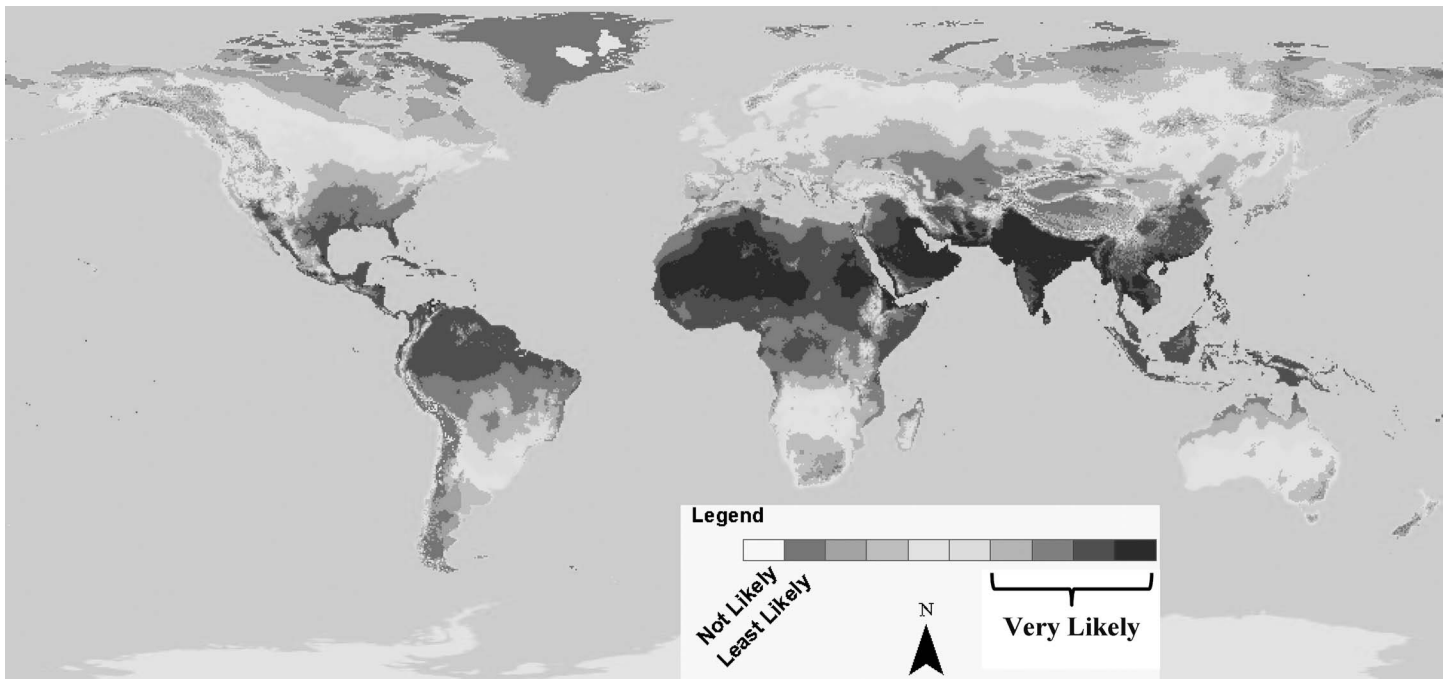
Figure 3. Establishment potential for *Hydrilla verticillata* based on known points of worldwide establishment for the genus and climate suitability (primarily air temperature) during the perceived growing season (June through August). Climate data derived as a 50-yr average mean monthly minimum temperature taken from the WorldClim data set and expanded upon by research at North Carolina State University (Hartis 2013).

should also evaluate the ecological fitness of the various hydrilla biotypes across various climates.

Benoit (2011) reported cryptic speciation in *Hydrilla*. Through phylogenetic and morphological analyses, she reported three lineages: "1) an Indian/Nepal/US dioecious species; 2) a Japan/Korean/European species; and 3) an Indonesian/Malayasian species" also found in Australia. Benoit (2011) indicated that both U.S. strains are triploid and that U.S. monoecious hydrilla is likely the result of hybridization between Indian and Indonesian populations. U.S. monoecious hydrilla populations had been previously linked to a population found in Seoul, Korea (Madeira et al. 1997). In the Kako River system of Japan, nine distinct hydrilla biotypes were reported, including monoecious and both diploid and triploid dioecious (Nakamura and Kadono 2000). Nakamura et al. (1998) previously reported that only one strain of triploid monoecious was present in Japan, but "17 and 23 electrophoretic phenotypes were" identified in dioecious diploid and triploid strains, respectively. Certainly, this level of genetic diversity has been underappreciated in the United States and poses many interesting questions for what genetic diversity would mean regarding invasion, growth, and reproduction across sites and climates. Hybrid vigor associated with polyploidy (i.e., triploid biotypes) may contribute to the invasion success of U.S. strains, but limit others such as European hydrilla (Benoit 2011).

Cook and Luond (1982) reported that monoecious hydrilla plants were typically found in climatically tropical regions, whereas dioecious hydrilla was typically found in temperate regions. However, this contrasts with other reports as well as the biology of the plant. Genetic analysis has confirmed monoecious hydrilla in Seoul, Korea, and in the Kako River of Japan (Madeira et al. 1997, Nakamura and Kadono 2000). Hydrilla reported from northwest Russia and northeast Kazakhstan were monoecious (Keldibekov 1972, Probatova and Buch 1981, as cited in Holm et al. 1997). Benoit's (2011) report that monoecious hydrilla may be the result of hybridization between two dioecious biotypes further muddies the water with regard to geographic origination of monoecious hydrilla. Future genetic research may be able to isolate this specific region, but there are currently no data to support the claim that monoecious hydrilla has specific tropical origins.

ANATOMY/LIFE CYCLE

Hydrilla grows as a rooted and submersed plant. Detached hydrilla stems can also survive on their own or in mats and may grow roots to attach to sediment. Hydrilla produces many stolons and rhizomes, as well as turions in the leaf axils, which detach upon maturity. Axillary turions are small, compact buds that are green in color (Figure 4). Subterranean turions are produced on the terminal end of rhizomes. Subterranean turions are larger and vary more in color, from white to yellow, or gray to red depending on the sediment (Figure 4). The subterranean turions are often referred to as tubers; true tubers and turions are morphologically distinct structures, but both serve as an overwintering propagule. Hydrilla leaves are whorled and serrated. The morphology of hydrilla has been described in detail by Cook and Lüönd (1982) and Yeo et al. (1984) and an excellent review of hydrilla turion ecology is also available (Netherland 1997).

Monoecious hydrilla subterranean turions/tubers   **Monoecious hydrilla axillary turions**
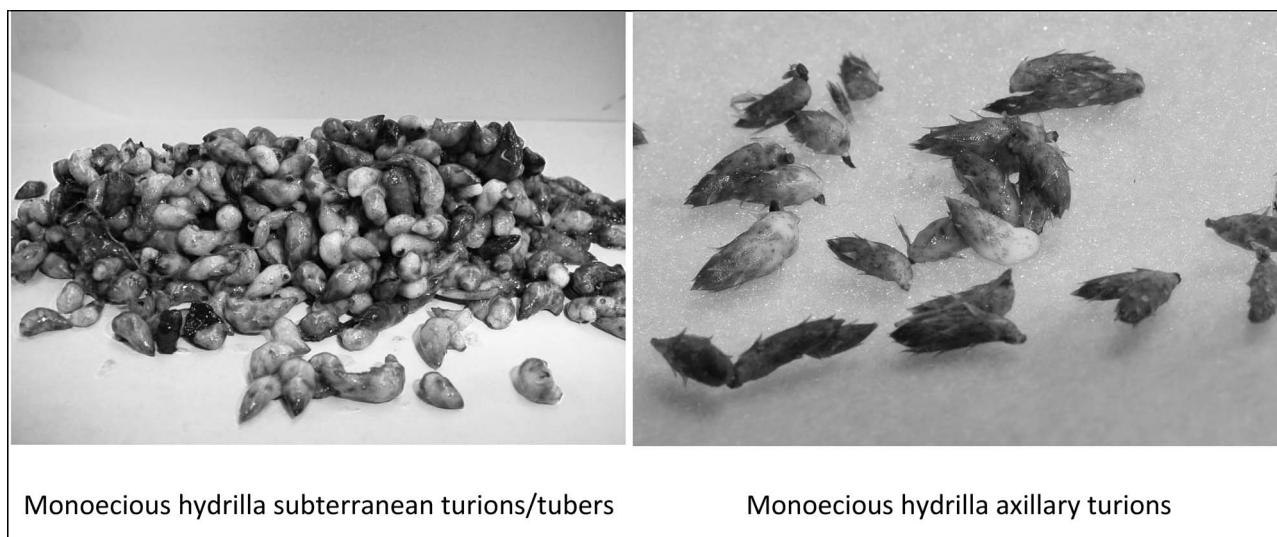
Figure 4. Monoecious hydrilla subterranean and axillary turions collected from Lake Gaston, NC in 2011 (J. J. Nawrocki, photo credit).

Pesacreta (1990) examined carbohydrate allocation in monoecious hydrilla and found that the majority of starch accumulation occurred in plant shoots when they were exposed to short photoperiods. Starch levels in tubers were found to decrease mostly in the first 2 wk after sprouting (Pesacreta 1990). Pesacreta (1990) also found that monoecious hydrilla displayed enhanced fragmentation after 8 wk of high temperatures (32 C).

Harlan et al. (1985) described the phenology of monoecious hydrilla in small North Carolina lakes. Tubers began sprouting in late March, when the hydrosoil was 11 to 13 C, and continued through August. The sprouting of axillary turions usually occurs prior to the sprouting of tubers in monoecious hydrilla (Spencer and Ksander 2001). Spencer and Ksander (2001) found that half of axillary turions sprout by mid-June in California and half of tubers by mid-July. After subterranean and axillary turions sprout, rapid shoot growth occurs laterally. On the Chickahominy River, Virginia, the most abundant hydrilla biomass was found in October (Shields et al. 2012). Tuber production in North Carolina has been reported to occur during long-day photoperiods in the summer. Tubers were formed from June through October in several small NC lakes (Harlan et al. 1985), whereas Meadows (2013) reported tuber formation in Lake Gaston, North Carolina occurred primarily from September through November with some formation in August and December. Axillary turions formed from October through December (Harlan et al. 1985). Following a final burst of subterranean turion production induced by short days, monoecious hydrilla biomass declines and then breaks away from the substrate, and mats loaded with axillary turions can shift locations (Steward and Van 1987). Harlan et al. (1985) found the majority of sprouting axillary turions in depths less than 0.5 m as a result of these mats floating to the shore. Monoecious hydrilla behaves as a herbaceous perennial in North Carolina and farther north, as plant stands and fragments do not overwinter (Harlan et al. 1985, Sutton et al. 1992, Owens and Smart 2007). Maximum growth is seen in the summer; in winter there is no shoot growth, plants die back, and regrowth is dependent on turions sprouting in the spring (Harlan et al. 1985, Sutton et al. 1992, Owens et al. 2012). This contrasts with dioecious hydrilla, which prefers to overwinter in vegetative form and produces fewer tubers. A comparison of monoecious hydrilla phenology in North Carolina to the phenology of dioecious hydrilla in Florida is shown in Figure 5. Monoecious hydrilla does, however, show some perennial characteristics in studies done in southern Florida, with growth all year long, but somewhat limited in winter months (Sutton et al. 1992, Steward 1993). Maki and Galatowitsch (2008) studied monoecious hydrilla axillary turion overwintering capacity, and found that 67 and 42% survived cold treatments (4 C) of 63 and 105 d, respectively.

Initial identification of hydrilla can often be difficult because of its highly polymorphic tendencies, and it is often misidentified as the morphologically similar *Egeria* spp. and *Elodea* spp. (Rybicki et al. 2013). Distinguishing between biotypes furthers the confusion, as growing conditions can have a significant effect on the appearance of the plant, and there is no way, visually, to distinguish between biotypes without flowers definitively (Figure 1). There are, however, some characteristics that can lead to a reasonable conclusion as to which biotype is being examined. For example, the monoecious plant is much less robust than the dioecious with leaf width of 1 to 3 mm and 2.25 to 3.5 mm, respectively (Benoit 2011). Monoecious hydrilla produces more tubers than does dioecious hydrilla; however, the tubers are smaller and weigh less (Van 1989, Sutton et al. 1992, Owens et al. 2012). A comparison of hydrilla tuber weights and densities is shown in Tables 1 and 2. Sprouting monoecious tubers send shoots out laterally, rather than vertically toward the surface as common in dioecious sprouting (Van 1989). And, staminate flowers are present with monoecious, but not dioecious hydrilla.

Monoecious hydrilla tubers have a very high germination rate in laboratory trials, often greater than 90% (Harlan et al. 1985, Van and Steward 1990, Owens et al. 2012, personal experience). However, although monoecious hydrilla tubers
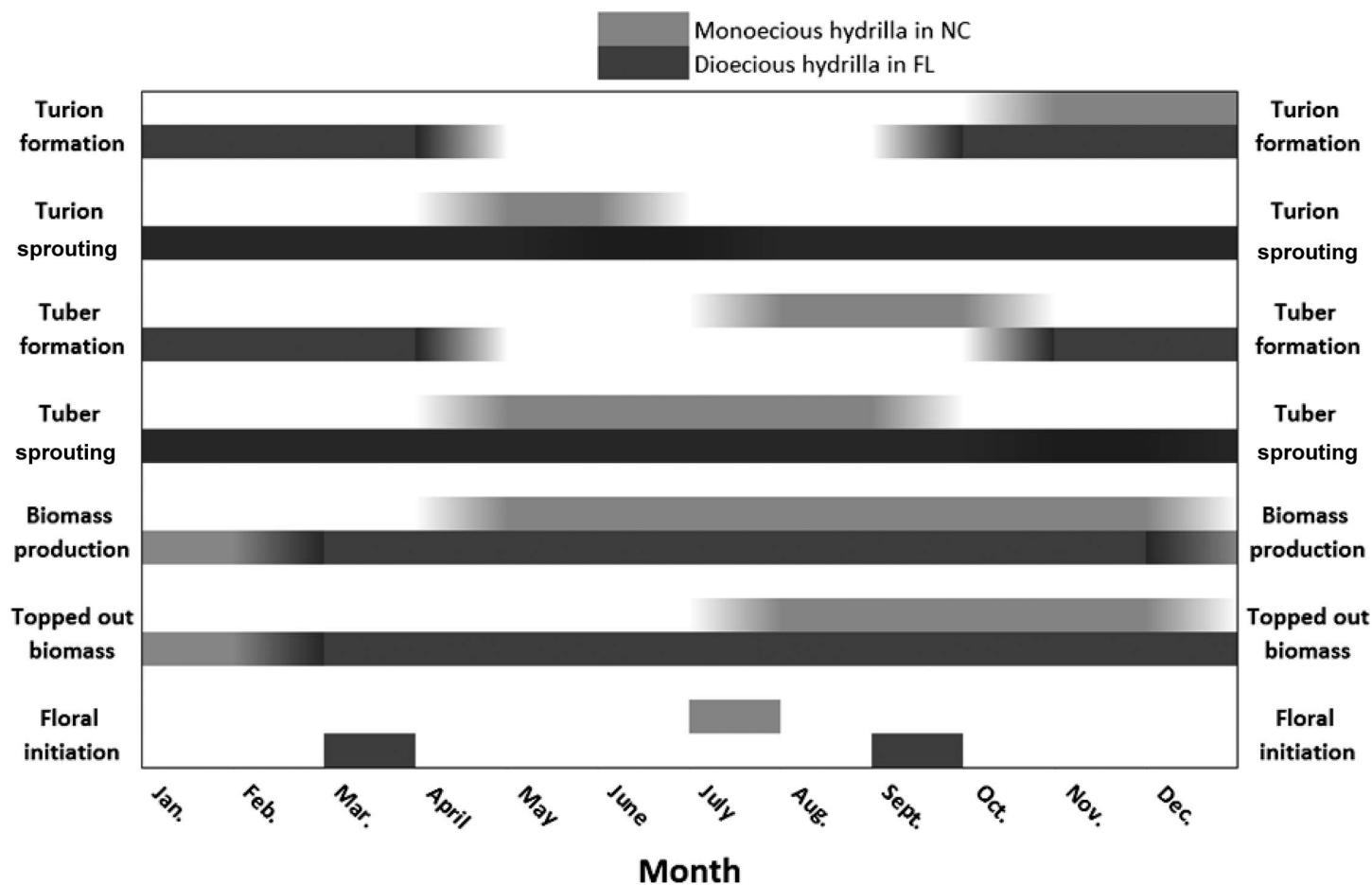
Figure 5. A comparison of monoecious hydrilla phenology in North Carolina to dioecious hydrilla phenology in Florida. Modified from Harlan et al. (1985).

readily germinate when removed from sediment, when left undisturbed in situ in southern Florida the germination rate was much lower (Van and Steward 1990). Carter et al. (1987) found that monoecious hydrilla tubers require a chilling period prior to sprouting which may prevent sprouting the same year of formation. Monoecious hydrilla tubers have been shown to remain in undisturbed soil for more than 4 yr after production in South Florida (Van and Steward 1990), and 6-yr-old tubers have still been viable in North Carolina (unpublished data). There appears to be an environmentally imposed dormancy that prevents depletion of tuber populations. Axillary turions will germinate within 1 yr or not at all (Van and Steward 1990). Nawrocki et al. (2011) also found that monoecious hydrilla tubers have

multiple axillary buds preformed within dormant tubers that can produce secondary shoots, even after terminal shoot removal. Recent studies on two hydrilla infestations in New York state suggest that frequency of monoecious hydrilla tuber sprouting exceeded 90% by late June in the year that management operations were implemented (Bob Johnson and Michael Netherland, pers. comm.). Thus, northern climates and extended chilling periods may increase sprouting of monoecious tubers and research should evaluate the impact of chilling period on dormancy.

TABLE 1. REPORTED TUBER WEIGHT FOR DIOECIOUS AND MONOECIOUS HYDRILLA.

Biotype	Tuber Weight (mg)	Situation	Citation
Dioecious	63–91	Mesocosm	Sutton et al. (1992)
	160–386	Mesocosm	Spencer et al. (1987)
	42–44	Mesocosm	Van (1989)
	188–290	Field, lake	Miller et al. (1976)
Monoecious	42–53	Mesocosm	Sutton et al. (1992)
	117–202	Mesocosm	Spencer et al. (1987)
	33–34	Mesocosm	Van (1989)
	30–320	Field, lake	Nawrocki (2011)

TABLE 2. REPORTED TUBER DENSITIES FOR DIOECIOUS AND MONOECIOUS HYDRILLA.

Biotype	Tuber Density per m^2	Situation	Citation
Dioecious	2,153	Mesocosm, 12 mo	Steward and Van (1987)
	2,293	Mesocosm, 7 mo	Steward (1980)
	257	Field, ponds	Haller and Sutton (1975)
	293–605	Field, lake	Miller et al. (1976)
	62–900	Field, ponds	Steward (1980)
Monoecious	2,099–9,053	Mesocosm, 16–28 mo	Steward and Van (1987)
	910–2,985	Mesocosm, 2 mo	Poovey and Kay (1998)
	189–1,312	Field, three lakes	Harlan et al. (1985)
	101–1,705	Field, two lakes	Nawrocki (2011)

Spencer and Anderson (1986) found in a greenhouse study that 38% of monoecious hydrilla grown from tubers and exposed to a 10-h photoperiod produced tubers by 28 d, and 100% produced tubers by 56 d with 24 C water temperature. They also observed that tuber production was the priority for the plants, overproduction of new root or shoot tissue (Spencer and Anderson 1986). Van (1989) found that monoecious hydrilla produced tubers under both a 10- and 16-h photoperiod, but production was much higher for the 10-h photoperiod. Tubers were produced in Van's study (1989) after 4 wk of exposure to this photoperiod with average water temperature of 22 C. Spencer et al. (1994) had similar results; monoecious hydrilla produced more tubers with an 11-h photoperiod than with a 15-h photoperiod. Spencer et al. (1994) also examined the carbon and nitrogen allocation of monoecious hydrilla and found that 43 times more carbon was allocated to new tubers than nitrogen.

Monoecious hydrilla tubers sprout at a lower temperature than does the dioecious type (Steward and Van 1987). The authors reported up to 95% sprouting of monoecious hydrilla after 3 to 4 wk at 15 C, whereas dioecious sprouting did not exceed 13%. This, along with its annual growth habit, shows why monoecious hydrilla may be better adapted for northern areas, which are colder and have short growing seasons. McFarland and Barko (1987) reported that dioecious hydrilla shoots lengthened more at high temperatures (32 C) than monoecious ones, and the authors speculated that the monoecious type appeared better adapted to moderate temperatures. However, McFarland and Barko (1999) found that monoecious hydrilla may be more adapted to warmer temperatures than previously reported. In their study, subterranean turion production occurred at unexpectedly high temperatures (35 C), although in reduced amounts (McFarland and Barko 1999). This lends to the theory that monoecious hydrilla could possibly spread and thrive farther south than typically thought. Nawrocki et al. (2011) also found similarities in sprouting of both biotypes under temperature and light manipulation. Although previous literature does not clearly show that monoecious shoots grow better in cooler water than dioecious, rapid sprouting of monoecious tubers at 15 C could better facilitate production of a new generation of tubers at 22 C, whereas dioecious tubers would just be sprouting (McFarland and Barko 1987, Steward and Van 1987, McFarland and Barko 1999). This could allow monoecious hydrilla to reach the 4-wk exposure to 22 C water necessary for tuber formation (Van 1989) in areas where dioecious sprouting is too constrained to produce a new generation.

Hydrilla turions vary greatly in abundance, size, and weight. Axillary turions are on average half the size of tubers (Van and Steward 1990). Spencer et al. (1987) found that the mean fresh weight for monoecious tubers ranged from 117 to 202 mg and 36 to 77 mg for axillary turions. Nawrocki (2011) reported that monoecious subterranean turion weight varied from 30 to 320 mg in North Carolina lakes.

Harlan et al. (1985) showed that the majority of monoecious hydrilla tubers in North Carolina lakes were found at soil depths between 0 and 8 cm, but that soil depths of 8 to 12 cm could hold up to 50% of the total turions.

Tubers were infrequently found deeper than 12 cm (Harlan et al. 1985). Monoecious hydrilla tubers have been found in densities of over 3,000 tubers m^{-2} in North Carolina (Nawrocki 2011). Nawrocki et al. (2011) examined monoecious hydrilla tuber sprouting dynamics at varying pH levels (4 to 10), and found few differences in initial growth. Monoecious hydrilla can tolerate salinities up to 13 ppt (Steward and Van 1987); however, Twilley and Barko (1990) reported little salinity tolerance in monoecious hydrilla. Shields et al. (2012) reported that hydrilla was limited to the upper estuary of the Chickahominy River, where salinity stays less than 3 ppt. Carter et al. (1987) reported that monoecious hydrilla vegetative growth was reduced when exposed to salinities of 7 and 9 ppt, and that there is a negative correlation between salinity and tuber germination. Greater than 92% of tubers in fresh water sprouted, 4 to 20% of tubers exposed to 5 to 9 ppt salinity sprouted, and no tubers sprouted with salinities greater than 9 ppt (Carter et al. 1987). Nawrocki et al. (2011) exposed tubers to salinity for 2 wk. Salinity of 12 ppt had little to no effect on tuber sprouting, whereas tubers exposed to 24 ppt did not sprout under constant salinity exposure but sprouted when moved into a solution of deionized water (Nawrocki et al. 2011).

Although there have been no reports of seed production from the dioecious biotype of hydrilla (Steward 1993), viable seed production has been reported in monoecious hydrilla (Conant et al. 1984, Langeland and Smith 1984, Lal and Gopal 1993, Langeland 1996). A monoecious population in New Delhi, India produced seed profusely during late winter (Lal and Gopal 1993). The seeds showed light sensitivity and germinated within a week at 23 to 28 C, and readily germinated when exposed to light after being stored wet or dry in darkness for up to 1 yr (Lal and Gopal 1993). Sexual reproduction of monoecious hydrilla could result in variations that would allow adaptations to a wider range of environments than are already exploited by this plant, by aiding in dispersal and overwintering. Lal and Gopal (1993) suggest that hydrilla seed production may offer a long-term strategy for plant survival after long dry periods, such as in regions with a monsoon climate.

Steward (1993) found that 71% of test crosses between dioecious and monoecious hydrilla resulted in the production of seed. Of the seeds from these successful crosses, 90% were viable and the majority of seedlings survived (Steward 1993). Lake Gaston, on the North Carolina–Virginia border, is the first location where both biotypes of hydrilla were found in one body of water (Ryan et al. 1995); however, dioecious hydrilla is no longer present. Recently, the two biotypes have been reported to co-occur on numerous Tennessee Valley Authority reservoirs (Netherland and Greer 2014). Steward (1993) hypothesized that if hydrilla starts sexually reproducing, there could be serious detrimental effects. Genetic variability would increase, and individuals could develop with adaptations for thriving in a greater number of environments. This could lead to greater difficulty in managing and controlling hydrilla.

Monoecious hydrilla can establish and then displace native plants. It has been reported to persist alone and competitively with *Elodea canadensis* (Michx.) in flowing systems like streams and waterways in New Zealand (Hofstra

et al. 2010). Spencer and Ksander (2000) showed the strong competitive ability of monoecious hydrilla mixed with American pondweed, and Meadows and Richardson (2012) found that monoecious hydrilla outcompeted four other submersed aquatic plants [Eurasian watermilfoil (*Myriophyllum spicatum* L., invasive), curly leaf pondweed (*Potamogeton crispus* L., invasive), *Elodea canadensis* Michx. (native), and *Vallisneria americana* Michx. (native) in a mesocosm trial]. Chadwell and Engelhardt (2008) reported that monoecious hydrilla establishment was inhibited by previous colonies of *V. americana* (Michx.) in greenhouse trials, but not in field trials, and Steward (1991b) showed that monoecious hydrilla biomass was on average 45% higher when grown with *V. americana* in mesocosms. Meadows and Richardson (2012) and Hofstra et al. (1999) found hydrilla growth in outdoor tanks to be greater when planted close to the same time as competitor species than if the competitor was given more time to establish before monoecious hydrilla introduction.

Steward (1991a) found that monoecious hydrilla in the Potomac River would most likely not grow at less than 5% of incident solar PAR, and therefore would be restricted to the limnetic zone. Estes et al. (2011) conducted a survey after the discovery of monoecious hydrilla in Cumberland County, Tennessee, the first infestation found in a rocky, rugged mountain stream system. They found hydrilla mainly in pool and run habitats (Estes et al. 2011). Hydrilla can take advantage of disturbances and rapidly colonize these areas. On the Chickahominy River a high-salinity, low-water-clarity disturbance event occurred in 2001 to 2002, which led to bare sediment (Shields et al. 2012). Monoecious hydrilla took advantage of the lack of competition and became the dominant species; however, smaller amounts of noninvasive submersed aquatic vegetation also became established in these areas (Shields et al. 2012). In North Carolina, monoecious hydrilla is now invading highly disturbed systems like flowing rivers, estuaries, and reservoirs with high water fluctuation.

CONTROL/MANAGEMENT

Hydrilla is a difficult weed to eradicate, and research on management of the monoecious biotype is more limited than dioecious. Monoecious hydrilla active management should begin several weeks after tubers first sprout, or as soon as possible after discovery of new infestations. However, new infestations of monoecious hydrilla are often not detected until much later in the season, when shoot growth reaches the surface of the water body, which increases the level of difficulty to achieve control. Treatments to control monoecious hydrilla are generally the same as for dioecious hydrilla, with chemical control and grass carp generally being the most effective. Mechanical control is usually not recommended for hydrilla management because of the fragmentation that occurs, the cost, and other negative impacts. Serafy et al. (1994) found that hydrilla biomass was greater 21 d after harvesting than at an undisturbed site, and mechanical harvesting had short-term negative effects on fish populations. Haller et al. (1980) estimated that mechanical harvesting of dioecious hydrilla

caused a loss of 32% of fish numbers and 18% of fish biomass in Orange Lake, FL.

Herbicide treatments are a popular and effective method for managing hydrilla infestations. Current herbicides registered for hydrilla control in the United States include bispyribac-sodium, copper, diquat, endothall, flumioxazin, fluridone, imazamox, and penoxsulam, although the majority of research conducted for product registration was done on dioecious hydrilla, and not the monoecious biotype. Treatments of diquat and endothall (both dipotassium and monoamine salts) produced similar results on both U.S. biotypes (Van and Steward 1986, Steward and Van 1987, Van et al. 1987). Diquat and endothall are often more successful when applied early to mid-June, when monoecious hydrilla biomass is more manageable (Langeland and Pesacreta 1986). A second application can be applied in mid-August if regrowth occurs (Langeland and Pesacreta 1986). Van et al. (1987) reported that a concentration of 0.25 mg/L diquat for 2 d was lethal to both monoecious and dioecious hydrilla. Hodson et al. (1984) showed that endothall was effective on monoecious hydrilla, but appropriate exposure times must be met. Langeland and Pesacreta (1986) also reported that granular endothall was more effective in areas with more water exchange, and Poovey and Getsinger (2010) found that endothall applied at 2 mg ai L^{-1} with 72-h exposure times reduced monoecious hydrilla biomass grown from shoot fragments. Monoecious hydrilla sprouted tubers needed an increased rate (4 mg ai L^{-1}) or longer exposure times (96 h) to achieve the same result (Poovey and Getsinger 2010). Bensulfuron methyl, when applied in rates of 0.05 to 0.2 mg L^{-1} to monoecious hydrilla, causes biomass reduction for only 2 mo before regrowth occurs (Van and Vandiver 1992). However, it has been shown to inhibit subterranean turion production in monoecious hydrilla (Van and Vandiver 1992). Fluridone will control monoecious hydrilla (Langeland and Pesacreta 1986) and has been documented to cause tuber numbers to decrease over time (Nawrocki 2011). However, after years of repetitive fluridone treatments within Florida, fluridone-resistant dioecious hydrilla has been documented (Michel et al. 2004). Mutations of the phytoene desaturase (pds) gene at codon 304 have been shown to confer fluridone resistance in dioecious hydrilla (Benoit and Les 2013). Benoit and Les (2013) have reported that of the 24 samples of monoecious hydrilla collected across 11 states no pds mutations were observed at codon 304 upon genetic analysis. However, because of the possible existence of yet-undiscovered mutations that may confer resistance in monoecious hydrilla, the exclusive annual use of fluridone (or any single herbicide mode of action) is not recommended. It is important to alternate herbicide modes of action or other management techniques in any long-term weed management plan.

Grass carp [*Ctenopharyngodon idella* (Val.)] are often recommended and used for hydrilla management, as stocking a body of water with these fish can cause a reduction or elimination of aquatic plants. These fish have been called "selective generalists" as they feed on aquatic plant species in order of decreasing palatability; hydrilla and pondweeds (*Potamogeton* spp.) are the most common species reported to be consumed by grass carp (Dibble and

Kovalenko 2009). A major concern with using grass carp as a vegetation control method is the possible negative impacts on aquatic communities, both direct and indirect, and more research is needed in this area. One major benefit of using grass carp is that it is a multiyear solution. Regulations for grass carp stocking differ on a state-by-state basis. In many states a permit from a state resource management agency is needed for stocking grass carp. The majority of published research on grass carp and hydrilla has been done with the dioecious biotype; however, Hodson et al. (1984) found a stocking rate of 50 or more grass carp per hectare effectively controlled monoecious hydrilla when stocked in winter or spring before significant hydrilla growth. In North Carolina, recommendations on stocking grass carp are 38 fish per hectare in small ponds, and 38 to 50 fish per vegetated hectare in larger water bodies (Richardson and Getsinger 2014). Stich et al. (2013) observed a significant inverse relationship between the biomass of grass carp (up to 16 yr of age) at a given time and hydrilla coverage in Lake Gaston. Incorporating a 4-yr lag time between grass carp stocking and hydrilla impact analysis produced the model with the strongest relationship between grass carp biomass and hydrilla coverage (Stich et al. 2013). Stich et al. also stress the need to include older fish in stocking models, as these fish appeared to contribute to changes in hydrilla coverage on Lake Gaston. Combining two methods of control is often recommended and can be beneficial. Stocking a water body with grass carp is often used in tandem with herbicide treatments. However, timing is critical, as treated hydrilla plants have been found to be less desirable for grass carp in greenhouse trials (Kracko and Noble 1993).

The hydrilla leaf-mining fly (*Hydrellia pakistanae* Deonier and *Hydrellia balciunasi* Bock), has been suggested as a biological control agent for monoecious hydrilla, as it has had success on dioecious hydrilla (Doyle et al. 2002, Owens et al. 2006, Doyle et al. 2007, Owens et al. 2008). However, Dray and Center (1996) suggest that *H. pakistanae* would be useful for control of monoecious hydrilla only where it can grow as a perennial, and Grodowitz et al. (2010) and Harms and Grodowitz (2011) show that monoecious hydrilla is not a suitable host, as the plant provides no overwintering habitat for the fly. The larvae of *Cricotopus lebetis*, a chironomid midge, have been observed to mine the apical meristems of dioecious hydrilla. In no-choice survival and development tests, Stratman et al. (2013) found that monoecious hydrilla supported higher survival (100%) of *Cricotopus lebetis* as compared to dioecious hydrilla (56.6%). Although the midge was observed to be a generalist in other experiments conducted by the authors, the high survival rate on monoecious hydrilla may warrant further investigation (Stratman et al. 2013). The search for new biological control agents should be conducted in temperate climates to find agents with compatible overwintering strategies to monoecious hydrilla.

Prolific tuber production is one of the main challenges to monoecious hydrilla management. Nawrocki (2011) predicted that with consistent yearly herbicide treatments in North Carolina, it would take 7 to 10 yr to reduce an initial monoecious hydrilla tuber bank 99.5%. When 1 yr of treatment was omitted, tuber densities rebounded up to 74% of the original amount (Nawrocki 2011). Spencer and Ksander (1999) found that exposure to acetic acid inhibited sprouting of tubers by 80 to 100%, and suggested this method may be useful in tandem with drawdown treatments. Hodson et al. (1984) found that drawdown treatments were ineffective on monoecious hydrilla in North Carolina because of the location of the tubers in the soil profile; many tubers were found in the clay substrate layer under an organic detrital layer, and drawdowns of a few months were not successful in completely drying this clay layer. Poovey and Kay (1998) further examined summer drawdowns as a control measure for monoecious hydrilla and found that a drawdown of only 1 wk on sandy soil completely killed hydrilla and allowed for no tuber production, whereas on silt loam a 2-wk or more drawdown period was needed to reduce tuber numbers greatly and suppress regrowth. Unfortunately the timing of summer drawdowns is not feasible for many water bodies. Another method proposed for control of monoecious hydrilla and other aquatic invasives is the altering of organic matter contents of sediments (Gunnison and Barko 1989). However, this method has had mixed results, and Spencer et al. (1992) found it unsuccessful for monoecious hydrilla biomass reduction.

Although hydrilla is one of the most often studied submersed aquatic plants, the majority of research has been conducted with the dioecious biotype and additional research is greatly needed on the monoecious biotype. Monoecious hydrilla now represents a new and distinct threat to glacial lakes and there is very little literature that would indicate how well hydrilla will grow and compete in these cooler waters. The effect of latitude (cool water temperatures and compressed warm period) along with winter duration on monoecious hydrilla should also be evaluated as this biotype continues to spread north. Development of strategies to increase tuber sprouting within a narrow time frame is an area of great importance, as this would allow management efforts to be more effective. *In situ* documentation of the relevance of monoecious hydrilla seed production is also needed. This includes quantity of seed produced, viability of seed, potential for seed dispersal, and ability of seed to establish new plants. Additionally, research to increase the effectiveness of management techniques, while limiting damage to non-target organisms is also needed. As monoecious hydrilla spreads into glacial lakes in the northern tier states, a different native plant species spectrum will be present from that in its southern range and management techniques will need specificity for glacial lake plant diversity. This would include best management practices for herbicide use, but also other management options and proper integration of multiple techniques. In order to achieve these goals, cooperation between industry, academia, regulatory agencies, and land managers is vital.

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