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Stem fragment regrowth of *Hydrilla verticillata* following desiccation

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ABSTRACT

Hydrilla verticillata (L.f.) Royle, Hydrocharitaceae, is one of the most aggressive invasive aquatic weeds. It can regenerate from vegetative fragments, which may adhere to water vessels and become a possible source of infestation to otherwise uninfested water bodies. The objective of this study was to find out if, after a period of desiccation, a fragment of dioecious hydrilla would survive and produce new growth when it is rehydrated. Hydrilla was collected from four different sites in Central Florida, United States. Fragments with one and four whorls were desiccated for 0 to 8 h and were monitored for 14 d after reintroduction to water. There was a significant effect of desiccation time on fragment survival and production of new growth. One-whorl fragments desiccated for 2 h or more had low survival postdesiccation when compared to four-whorl fragments. Desiccation time of 2 h or longer significantly decreased the sprouting of four-whorl fragments compared to controls. The results of this study could be used to improve cultural control of hydrilla by preventing fragment introduction and the colonization of previously uninfested water bodies.

Key words: aquatic plant, cultural control, hydrilla, Hydrocharitaceae, invasive plant, management, prevention

INTRODUCTION

Hydrilla [*Hydrilla verticillata* (L.f.) Royle] has been nicknamed "the perfect aquatic weed" because of its ability to displace native plant species, its rapid growth, and its tolerance for a wide range of aquatic systems and conditions (Langeland 1996). This aggressive weed was first discovered in the United States near Miami, FL and in Crystal River, FL in 1960 (Blackburn et al. 1969) and established throughout the state of Florida within 20 yr (Schardt and Nall 1988, Langeland 1996). Today, hydrilla occurs throughout the United States from Maine to Washington state southward (U.S. Department of Agriculture 2014). Hydrilla impacts water bodies used for recreational purposes as well as restricting water flow, altering irrigation canals, causing flooding and limiting access (Langeland 1996). Economically, hydrilla control can cost several million dollars for management of a single lake. Mechanical removal alone costs $500 to $1,200 per acre (Hoyer et al. 2005).

As an aquatic vascular plant, hydrilla grows submersed either rooted or occasionally free-floating and can reproduce via turions (dormant buds in leaf axils), tubers (subterranean turions formed on shoots in sediment), seeds, or by sprouting from plant fragments. Subterranean rhizomes enable hydrilla to spread horizontally and its aboveground stolons allow it to spread vertically where it then branches near the water surface to maximize light interception (Langeland 1996).

Hydrilla can regenerate from vegetative fragments or even from individual whorls, a radial grouping of three to eight leaves emanating from a common node on the stem of hydrilla. In Florida, only the female dioecious form is present, so no sexual reproduction or seed production occurs, yet hydrilla is highly invasive and has spread rapidly throughout the state because of its ability to spread vegetatively (Langeland 1996). Hydrilla can grow up to 2.5 cm per day, which enables it to compete with other aquatic plants effectively, especially native species (Haller and Sutton 1975, Langeland 1996, Glomski and Netherland 2012). Habitat conditions, such as nutrient availability (Cook and Luond 1982), pH (Steward 1991), salinity (Haller et al. 1974, Steward and Van 1987), or light levels (Van et al. 1976, Bowes et al. 1977), do not limit hydrilla growth to the same extent as they do for some other species (Langeland 1996).

Mechanical harvesters, herbicides (Langeland 1996), and biological control (Van Dyke et al. 1984, Cuda 2014, Cuda and Weeks 2014) have been used to help manage hydrilla. However, herbicide resistance (Michel et al. 2004, Berger and MacDonald 2011, Giannotti 2013), harvester logistical issues, and creation of fragments that can disperse in the water column and rapidly regrow (Langeland 1996) emphasize the importance of integrated pest management (IPM) utilizing multiple approaches. Cultural control aimed at preventing the spread of hydrilla to uninfested water bodies may reduce the need for management. For example, removal of hydrilla from watercraft before leaving the launching area is currently recommended to prevent new infestations (Lietze and Weeks 2014). However, it is known that even small hydrilla fragments, which may go unnoticed, can be a potential source of new infestations via boat trailers, live wells, and other equipment such as draglines or mechanical harvesters (Langeland 1996). Anthropogenic infestations could be reduced if care is taken to ensure that masses of hydrilla are removed and any remaining hydrilla fragments are no longer alive. Removal of vegeta-

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tive clumps is important because desiccation of aquatic plant fragments outside of water has been shown to maintain a greater length, more "sprouts" (i.e., shoots/roots), a greater dry weight, and a larger adventitious root dry weight overall when dried on a substrate that could retain water like a clay sediment compared to sandy sediment (Silveira et al. 2009).

The desiccation of aquatic plant fragments has been studied at 24-h intervals for a period of up to 4 d (Doyle and Smart 2001, Silveira et al. 2009). However, the ability of small hydrilla fragments to regenerate once desiccated and reintroduced into a water body, as would likely occur with hydrilla fragments adhering to the propeller of a boat, has not been tested. In order to prevent hydrilla from spreading, cultural practices such as ensuring fragments on boats and boat trailers are removed or desiccated properly is an important part of an integrated management program. The aim of this study was to establish a desiccation threshold for cultural control of dioecious hydrilla by determining if fragments of various sizes would survive and produce new growth after desiccation.

MATERIALS AND METHODS

Hydrilla collection sites

Dioecious hydrilla was collected from four sites in Central Florida, including Lake Rowell, Bradford Co., FL (29°55′46″ N, 82°09′34″ W), Lake Tohopekaliga, Osceola Co., FL (28°12′8″ N, 81°23′23″ W), Natural Area Teaching Lab at the University of Florida, Alachua Co., FL (29°37′59″ N, 82°22′07″ W), and from the University of Florida Institute of Food and Agricultural Sciences Center for Aquatic and Invasive Plants, Alachua Co., FL (UF/IFAS CAIP; 29°43′35″ N, 82°25′4″ W).

Hydrilla cleaning and desiccation

Hydrilla was thoroughly rinsed in well water, hand cleaned by removing any insects or other unwanted debris, and cut into one-whorl or four-whorl fragments with scissors. Fragments were consistent in size ($\sim$ 1.5 to 3–cm one-whorl and $\sim$ 4 to 6–cm four-whorl fragments) and were not from the apical meristem. Whorls typically had three to five leaves. After being cut, whorls were rinsed again thoroughly and allowed to sit in well water for 1 d ($\sim$ 18 to 24 h). Fragments ($n = 30$ for one-whorl fragments; $n = 10$ for four-whorl fragments) were allowed to dry for 1, 2, 4, or 8 h at 26°C and ambient light conditions, then placed in separate aquaria and monitored for at least 14 d. A control with one- or four-whorl fragments also was set up, which consisted of fragments that were immediately placed in an aquarium with no time to dry out. Each replicate consisted of hydrilla from one of the four collection sites.

Postdesiccation

Aquaria (9.5 L; 16 W $\times$ 31 L $\times$ 21 H cm) were placed in a greenhouse maintained at 14 : 10 L : D photoperiod, 21 to 38 C, and were filled with 7.5 L of well water, aerated via a pump and fitted with a loose glass lid. For each aquarium, several variables were recorded daily for 14 d postdesiccation, which included fragment survival, shoot/root sprouting, as well as coloration, algal growth, and location of hydrilla fragments (i.e., clumped, spread out, sunk or floating). Once fragments began to fade in coloration and decay, they were no longer considered to be alive. Fragment survival was defined as green photosynthetically active whorls that maintained potential to produce shoots and was calculated by subtracting decaying whorls from total number of whorls. Fragments were examined for the presence of shoots and roots. Fragments that produced shoots or roots were considered to be alive even if they appeared faded and or decayed. The proportion of fragments that sprouted and the proportion of fragments that survived were evaluated with data from days 7, 11, and 14.

Data analysis

In order to achieve normality, a logit transformation of both proportion of fragments sprouted and survived was performed before data analysis. A linear mixed model that considered the fixed factors of postdesiccation time (7, 11, and 14 d), fragment length (one and four whorls) and desiccation time (0, 1, 2, and 4 h) together with all their interactions, and a random factor of collection site was fitted for each variable in the model. Because of data comprising repeated measures, residuals were modeled with the use of an autoregressive of order 1 error structure. In addition, a weight was included that consisted of the inverse of the number of fragments for each experimental unit. Significance of model terms was evaluated with the use of an approximated F-test with the Kenwards–Rogers correction for degrees of freedom. Multiple comparisons were obtained by least-square differences (LSDs) with the use of a significance level of 5%, and predicted means were calculated with the use of the inverse of the logit function. All models were fitted with the use of SAS v. 9.2 (SAS 2008).

RESULTS AND DISCUSSION

Desiccation time

Desiccation time of the hydrilla stem fragments had a significant effect on fragment survival and regeneration through shoot/root sprouting. In preliminary studies, no fragments survived or sprouted when desiccated for $\geq$ 24 h (Baniszewski et al., unpub. data), which is in agreement with Basiouny et al. (1978) in which drying hydrilla fragments longer than 16 h resulted in plant deterioration. Longer desiccation times significantly decreased the proportion of fragment survival ($P < 0.0001$) and fragment sprouting ($P < 0.0001$). A desiccation period of 2 h resulted in a significant reduction in fragment survival and sprouting compared to the control (Figure 1A). A desiccation time $>$ 2 h further reduced fragment survival and sprouting to $<$ 3%. These data are in agreement with Basiouny et al. (1978), who found a decrease in growth (length, fresh, and dry weight) of hydrilla fragments after 2 h drying. However, even in the

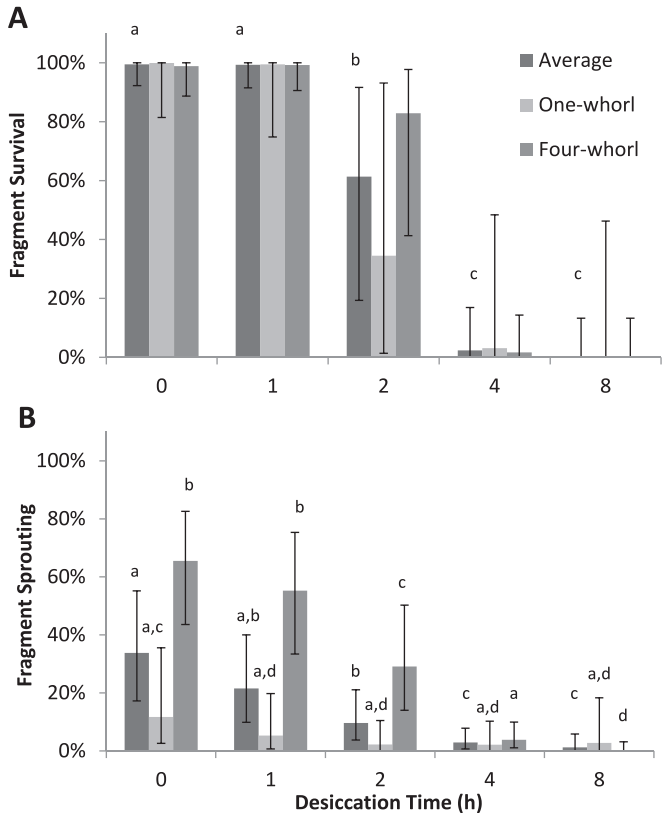

Figure 1. Effect of desiccation time on hydrilla fragments survival (A) and sprouting (B). Desiccation time is the time in hours that the hydrilla fragment was exposed out of the water. Control fragments spent no time out of water (0 h). Length of fragment may be one or four whorls. Bars represent predicted means ± 95% confidence intervals. Bars with different letters are statistically different ($\alpha = 0.05$). Average fragment spouting and fragment spouting with different size fragments were analyzed separately.

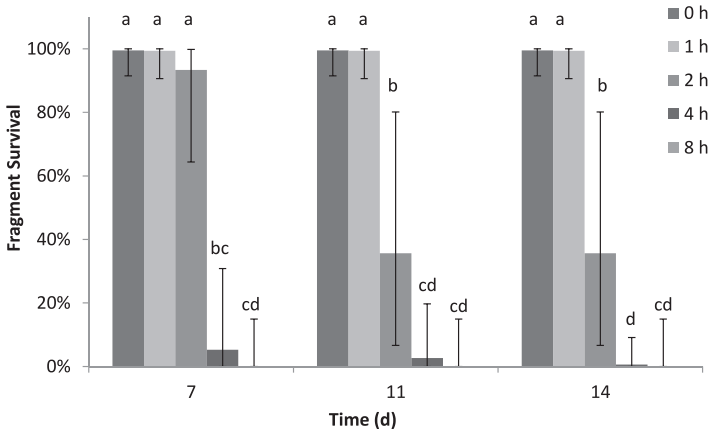

Figure 2. Effect of desiccation time on hydrilla fragment survival over time. Fragments were examined for survival every day; data presented for 7, 11, and 14 d only. Bars represent predicted means ± 95% confidence intervals. Bars with different letters are significantly different ($\alpha = 0.05$).

control group (0 h), where fragments spent no time out of water, not all fragments sprouted, with an average proportion of 34% (Figure 1B). There was a significant effect of the interaction between desiccation time and time postdesiccation on survival ($P = 0.0009$). Until day 7 postdesiccation, hydrilla fragments desiccated for up to 2 h were still surviving as well as the controls and fragments desiccated > 2 h had significantly lower survival compared to the controls (Figure 2). After 7, 11, and 14 d postdesiccation, there was a significant decrease in survival after a desiccation period of 2 h compared to the control.

Fragment length

Shoot/root sprouting was significantly affected by fragment length ($P = 0.0016$) and by the interaction between fragment length and desiccation time ($P = 0.0134$). There was no significant effect of fragment length on proportion of fragment survival ($P = 0.8441$; Figure 1A), and the interaction between fragment length and desiccation time also was not statistically significant ($P = 0.7675$). One-whorl fragments had low survival postdesiccation regardless of the desiccation time (Figure 1B). Four-whorl fragments showed significantly higher sprouting compared with one-whorl fragments when allowed to desiccate for ≤ 2 h. Desiccation time of 2 h or longer significantly decreased the proportion of sprouts of four-whorl fragments compared to the control. However, 2 h of desiccation still produced significantly more sprouts than any of the one-whorl fragment treatments or four-whorl fragments desiccated for 4 h or greater.

There was no significant interaction between the effect of fragment length over time on survival ($P = 0.0571$). However, a four-whorl fragment desiccated for 2 h did not reach 50% mortality at 14 d postdesiccation (average 62.5%), but a one-whorl fragment desiccated for 2 h exhibited 50% mortality by day 10. By day 14 only 25% of fragments were still alive (Figure 4). The mortality of fragmented hydrilla is important to understand because free-floating fragments of hydrilla are more likely to produce new shoots than rooted hydrilla and can generate a new plant from a single-whorl (Haller et al. 1976). Nearly 50% of all single-whorl fragments

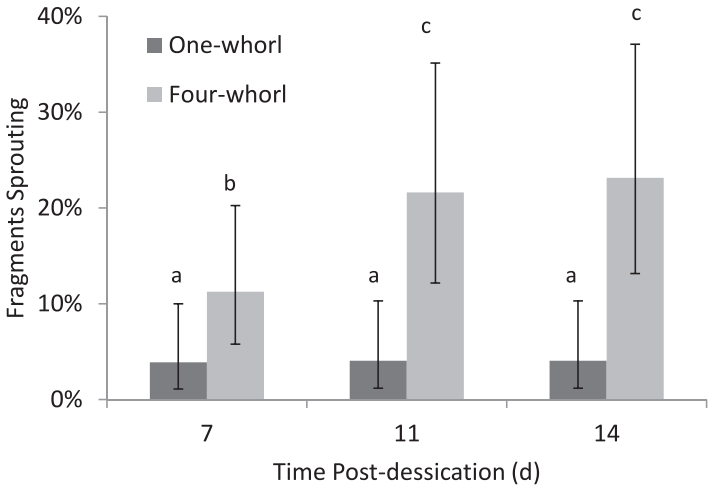

Figure 3. Effect of fragment length on hydrilla fragment sprouting over time. Length of fragment may be one or four whorls. Fragments were examined for sprouting every day; data presented for 7, 11, and 14 d only. Bars represent predicted means ± 95% confidence intervals. Bars with different letters are significantly different (a = 0.05).

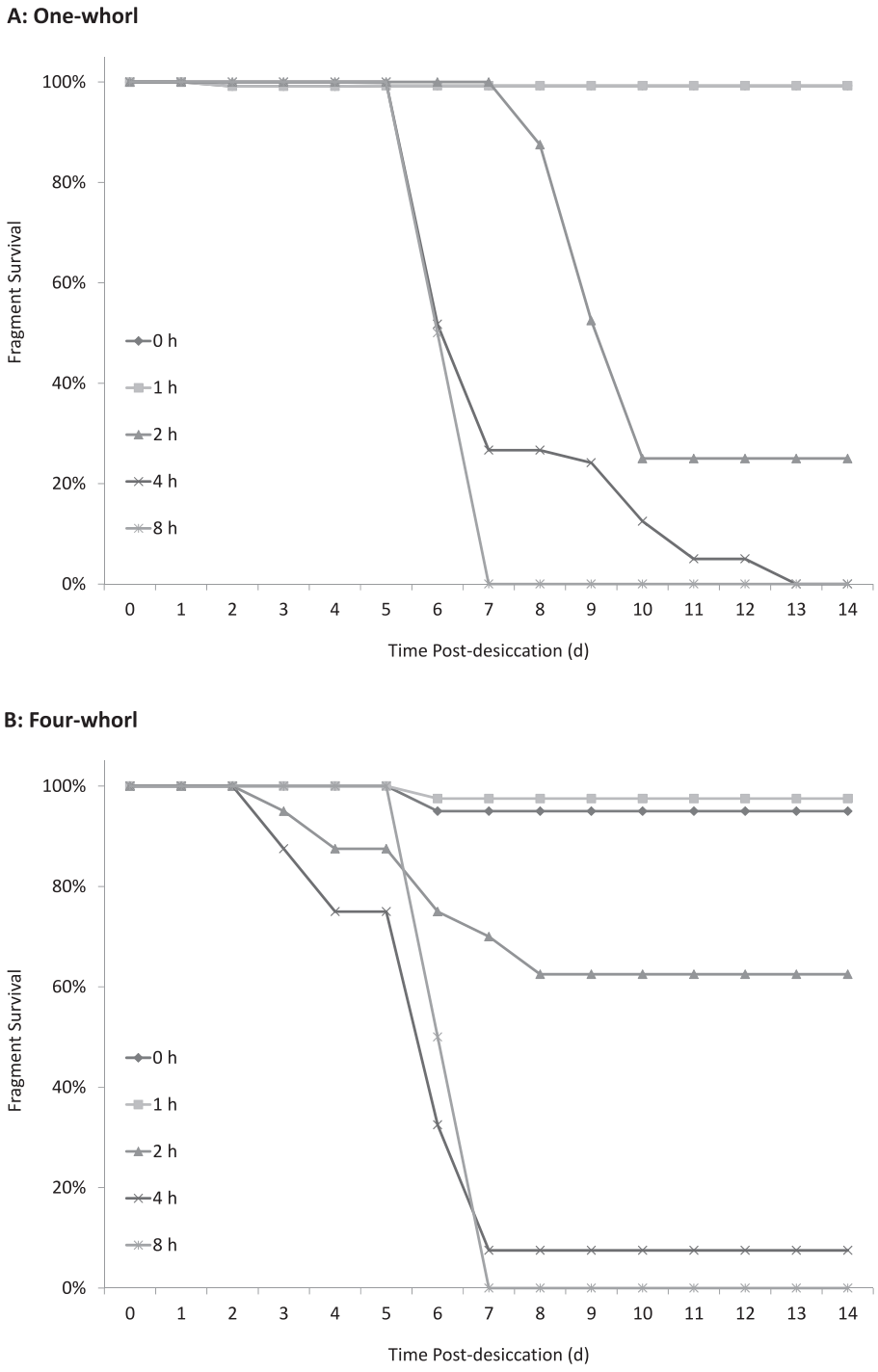

Figure 4. Survival of one- and four-whorl fragments for each period of desiccation. Desiccation time is the time in hours that the hydrilla fragment was exposed out of the water. Control fragments spent no time out of water (0 h).

with leaves can regenerate to form a new plant and larger fragments have a higher rate of regeneration (Langeland and Sutton 1980). A fragment of five whorls has been shown to regenerate 98% of the time in field conditions, indicating that introductions of even these small fragments can be a source of infestation into new water bodies (Langeland and Sutton 1980).

Sprouting potential

There was a clear difference in sprouting potential over time between one-whorl and four-whorl fragments, which could be a function of the higher total carbohydrate content available in the longer fragments. Four-whorl fragments had the potential to continue sprouting even after 7 d; whereas

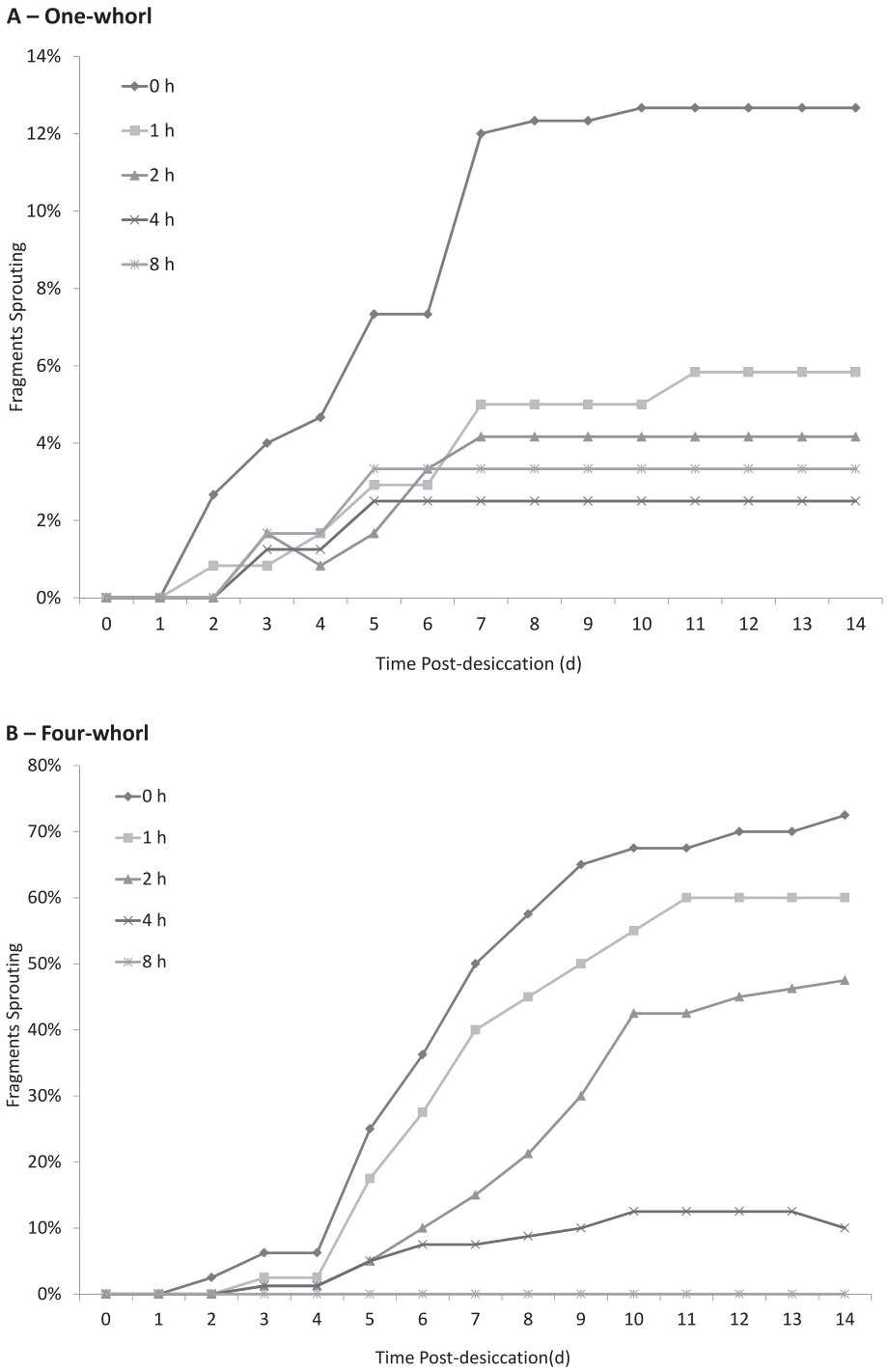

Figure 5. Cumulative daily sprouting for one- and four-whorl fragments for each period of desiccation. Desiccation time is the time in hours that the hydrilla fragment was exposed out of the water. Control fragments spent no time out of water (0 h).

one-whorl fragments reached maximum sprouting potential at 7 d after being rehydrated postdesiccation regardless of desiccation time (Figure 5). Sprouting over time for four-whorl fragments continued to increase and reached a threshold around 10 to 11 d postdesiccation.

Although there was no significant effect of the interaction between desiccation time and time postdesiccation on proportion of sprouting ($P = 0.3467$), there was variation in the effect of desiccation time on sprouting relative to fragment length over time (Figure 3; $P = 0.0082$). Although there was little change in the number of developing sprouts for one-whorl fragments over time (Figure 3), four-whorl fragments showed a significant increase in sprouting from 7 to 11 d.

Longer desiccation of the hydrilla fragments correlated with reduced sprouting potential for both one- and four-

whorl fragments. A 4 h desiccation time resulted in almost complete mortality and prevented sprouting by individual hydrilla fragments. Kar and Choudhuri (1982) described hydrilla desiccation in three phases: shock, recovery, and deteriorative. Shock occurs immediately after drying, typically for 4 h, but up to 12 h, and is temporary deterioration in plant tissues, increased tissue permeability induced by impairment of the membrane system, and reduced carbohydrate concentration because of high respiration. Recovery follows shock, lasting up to 16 h, and is characterized by recovery of plant tissue deterioration, decreased tissue permeability and phospholipid concentration, and some repair to the damaged membrane system. The recovery phase has a carbohydrate accumulation and reduced respiration, which is reversed in the final stage. Finally, after 16 h, the vegetative tissue is degraded to a point that it cannot recover and is considered the deteriorative phase, characterized by another increase in tissue permeability and phospholipid concentration (Kar and Choudhuri 1982). In comparison, Eurasian watermilfoil, *Myriophyllum spicatum,* another fragmenting invasive aquatic plant, had reduced viability with longer desiccation time during boat transport (Jerde et al. 2012). Even 1 h of desiccation of single Eurasian watermilfoil fragments reduced survival and root sprouting potential, regardless of size.

Hydrilla sprouting potential was affected by fragment size, unlike Eurasian watermilfoil (Jerde et al. 2012). With no desiccation, four-whorl fragments have the potential to regenerate over 70 new sprouts within 14 d from every 100 fragments that are reintroduced into water, with each sprout having the potential to grow into a new hydrilla plant. In contrast, one-whorl fragments only have the potential of producing approximately 13 new sprouts for every 100 fragments reintroduced. Decreased viability in one-whorl fragments resulted in less sprouting. Even with four times as many fragments there would still be more new plants resulting from four-whorl fragments than one-whorl fragments. Fragment potential is important to understand because of potential dispersal if introduced into a new water body. Berković et al. (2014) illustrated the potential of vegetative fragments of a seagrass, *Zostera noltii,* to disperse several thousand kilometers, whereas seeds had a dispersal potential of only a few centimeters. This finding illustrates the importance of limiting the introduction of hydrilla fragments, especially large fragments (i.e., four-whorl or longer) into new water bodies or the potential that fragmenting hydrilla, whether by a boat motor or harvester, may have on the spread of hydrilla.

Ecological impact

Vegetative reproduction has been shown to play an important role in survival and regeneration of other aquatic plant species, especially those that fill an ecological role as floating vegetation in water bodies (Barrat-Segretain et al. 1998). The difference in the ability of four-whorl hydrilla fragments to continue sprouting for a longer time compared to one-whorl fragments is important when considering the invasion potential of fragmented hydrilla. Hydrilla is a fast-growing plant, and the high relative growth rate may be responsible for the difference in sprouting capacity between the two types of fragments. Nutrients alone may not limit colonization and regrowth of hydrilla; thus this vegetative regeneration potential is an important consideration for many watersheds (James et al. 2005).

Aquatic plant reproduction and life-history patterns are likely correlated with colonization and regeneration ability in lotic environments such as streams. There is a trade-off in colonization ability between plants with slow root growth ($>$ 10 wk) but higher regeneration ability, such as new propagule development from fragments (Barrat-Segretain et al. 1998). Hydrilla is likely to optimize colonization via fragment regeneration, but also has rapid growth, which maximizes survival of hydrilla in a new aquatic environment and enables this invasive weed to outcompete other aquatic vegetation. Because hydrilla is able to regenerate without roots for initial colonization, it can readily infest uncontaminated water bodies simply by being transported between water bodies and can quickly spread via fragment dispersal and sprouting potential.

Hydrilla vegetative tissues have a relatively fast desiccation rate of 9.96 g/h (Barnes et al. 2013), which explains why hydrilla fragment viability is greatly reduced when removed from the water for periods longer than 4 h. The rapid desiccation rate of hydrilla could help reduce its spread if boats and other watercraft that may inadvertently carry hydrilla fragments after removing large clumps of aquatic vegetation refrain from coming in contact with a new water body within several hours. Strong disturbances have been shown to reduce hydrilla biomass, number of nodes, and shoot length compared to other submerged macrophyte plants (Zhang et al. 2014), which may decrease viability if hydrilla fragments are chopped by a boat propeller before reintroduction.

Study limitations

The focus of this study was to determine the effects of desiccation followed by rehydration of hydrilla fragments and the survival potential such fragments may have when boats or other watercraft unintentionally transport hydrilla to another water body. A limitation of this study is that it did not consider the impact of a substrate or a mass of hydrilla on the desiccation time of fragments. Previous studies that investigated resistance to desiccation in aquatic plants have provided a substrate, such as clay, silt loam, or sandy soil. Hydrilla desiccated on a substrate has the potential for faster elongation compared to other species of Hydrocharitaceae, especially if it is reintroduced into water within 2 d (Silveira et al. 2009). Although hydrilla stems and leaves may be quick to dry out, other structures, such as tubers, may prolong the desiccation time of hydrilla (Barnes et al. 2013). It has been shown to take 1 wk to suppress hydrilla growth in a drawdown with soil substrates (Poovey and Kay 1998). Consequently, fragment survival and potential to sprout and produce roots would likely increase if hydrilla fragments were in contact with damp soil substrate. Similarly, Eurasian watermilfoil fragments were better able to survive if coiled, such as around a propeller

(Jerde et al. 2012). However, current cultural practices emphasize the manual removal of large clumps of plant material before moving boats from boat ramps, so the spread of hydrilla is likely from smaller, more easily overlooked fragments that may have been missed when cleaning a water craft.

CONCLUSION

Hydrilla vegetative tissues are highly susceptible to desiccation without a medium from which to absorb water. In this study, all hydrilla fragments exhibited decreased survival and potential for sprouting after a desiccation time of > 1 h. Even without desiccation, single-whorl fragments were less likely to sprout compared to four-whorl fragments. Preventing larger hydrilla fragments from being released into lotic water bodies during management may be more important for reducing the likelihood of colonization of new sites. Although ensuring that watercraft dry out for longer than 4 h may significantly reduce sprouting by larger fragments, even this recommendation may not be sufficient to avoid contamination of new water bodies. To ensure desiccation, it is essential to remove potential water sources for the hydrilla, such as soil and other plant material. In summary, this study has provided information that is vital to improving cultural control of hydrilla in order to prevent colonization of previously uninfested water bodies. Watercraft still should be cleaned before leaving the dock area. Additionally, to prevent the movement of smaller fragments that may go unnoticed, all watercraft should be subjected to a drying period of at least 4 h prior to entering new water bodies so that individual hydrilla fragments become desiccated.

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LITERATURE CITED

Barnes MA, Jerde CL, Keller D, Chadderton WL, Howeth JG, Lodge DM. 2013. Viability of aquatic plant fragments following desiccation. Invasive Plant Sci. Manage. 6:320–325.

Barrat-Segretain MH, Bornette G, Hering-Vilas-Bôas A. 1998. Comparative abilities of vegetative regeneration among aquatic plants growing in disturbed habitats. Aquat. Bot. 60:201–211.

Basiouny FM, Haller WT, Garrard LA. 1978. Survival of hydrilla (*Hydrilla verticillata*) plants and propagules after removal from the aquatic habitat. Weed Sci. 26(5):502–504.

Berger S, MacDonald G. 2011. Suspected endothall tolerant hydrilla in Florida (poster abstract). Proc. Southern Weed Sci. Soc. 64:331.

Berković B, Cabaço S, Barrio JM, Santos R. 2014. Extending the life history of a clonal aquatic plant: Dispersal potential of sexual and asexual propagules of *Zostera noltii*. Aquat. Bot. 113:123–129.

Blackburn RD, Weldon LW, Yeo RR, Taylor TM. 1969. Identification and distribution of certain similar-appearing submersed aquatic weeds in Florida. Hyacinth Contr. J. 8:17–23.

Bowes G, Holaday AS, Van TK, Haller WT. 1977. Photosynthetic and photorespiratory carbon metabolism in aquatic plants, pp. 289–298. In: Proceedings of the 4th International Congress of Photosynthesis, Reading, United Kingdom.

Cook CDK, Luond R. 1982. A revision of the genus *Hydrilla* (Hydrocharitaceae). Aquat. Bot. 13:485–504.

Cuda JP. 2014. Insects for biocontrol of aquatic weeds, pp. 59–66. In: L. A. Gettys, W. T. Haller, and D. G. Petty (*eds.*). Biology and control of aquatic plants: A best management practices handbook. 3rd ed. Aquatic Ecosystem Restoration Foundation, Marietta, GA.

Cuda JP, Weeks ENI. 2014. Featured creatures: The hydrilla tip mining midge, pp. 96–100. In J. Gillett-Kaufma, V.-U. Lietze, and E. Weeks (*eds.*). Hydrilla: Integrated management. University of Florida, IFAS Extension, Gainesville, FL.

Doyle RD, Smart RM. 2001. Effects of drawdowns and desiccation on tubers of hydrilla, an exotic aquatic weed. Weed Sci. 49(1):135–140.

Giannotti AL. 2013. Hydrilla shows tolerance to fluridone and endothall in the Winter Park Chain of Lakes: Considerations for management strategies and treatment options in urban systems. 37th Ann. Training Conference, Florida Aquatic Plant Manage. Soc., 2013 Book of Abstracts, pp. 5–6.

Glomski LM, Netherland MD. 2012. Does hydrilla grow an inch per day? Measuring short-term changes in shoot length to describe invasive potential. J. Aquat. Plant Manage. 50:54–57.

Haller WT, Miller JL, Garrard LA. 1976. Seasonal production and germination of hydrilla vegetative propagules. J. Aquat. Plant Manage. 14:26–29.

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

Haller WT, Sutton DL, Barlowe WC. 1974. Effects of salinity on growth of several aquatic macrophytes. Ecology 55:891–894.

Hoyer MV, Netherland MD, Allen MS, Canfield DE, Jr. 2005. Hydrilla management in Florida: A summary and discussion of issues identified by professionals with future management recommendations. https://plants.ifas.ufl.edu/wp-content/uploads/files/caip/pdfs/HydrillaMgmt__Final__June05a.pdf; accessed 27 April 2016.

James CS, Eaton JW, Hardwick K. 2005. Responses of three invasive aquatic macrophytes to nutrient enrichment do not explain their observed field displacements. Aquat. Bot. 84:347–353.

Jerde CL, Barnes MA, DeBuysser EK, Noveroske A, Chadderton WL, Lodge DM. 2012. Eurasian watermilfoil fitness loss and invasion potential following desiccation during simulated overland transport. Aquat. Invasions 7(1):135–142.

Kar RK, Choudhuri MA. 1982. Effect of desiccation on internal changes with respect to survival of *Hydrilla verticillata*. Hydrobiol. Bull. 16(2–3):213–221.

Langeland KA. 1996. *Hydrilla verticillata* (L.f.) Royle (Hydrocharitaceae), "the perfect aquatic weed." Castanea 61(3):293–304.

Langeland KA, Sutton DL. 1980. Regrowth of hydrilla from axillary buds. J. Aquat. Plant Manage. 18:27–29.

Lietze V-U, Weeks ENI. 2014. Early detection, pp. 17–26. In J-L Gillett-Kaufman, V-U Lietze, and E N I Weeks (*eds.*). Hydrilla: Integrated management. University of Florida, IFAS Extension, Gainesville, FL. pp. 17–26.

Michel A, Arias RS, Cheffler BE, Duke SO, Netherland MD, Dayan FE. 2004. Somatic mutation-mediated evolution of herbicide resistance in the nonindigenous invasive plant hydrilla (*Hydrilla verticillata*). Mol. Ecol. 13:3229–3237.

Poovey AG, Kay SH. 1998. The potential of a summer drawdown to manage monoecious hydrilla. J. Aquat. Plant Manage. 36:127–130.

SAS. 2008. SAS/STAT® 9.2 User's guide. Statistical Analysis System Institute Inc., Cary, NC.

Schardt JD, Nall LE. 1988. 1988 Florida aquatic plant survey. Florida Department of Natural Resources Technical Report No. 89-CGA, Tallahassee, FL. p. 118.

Silveira MJ, Thomaz SM, Mormul RP, Comacho FP. 2009. Effects of desiccation and sediment type on early regeneration of plant fragments of three species of aquatic macrophytes. Int. Rev. Hydrobiol. 92(2):169–178.

Steward KK. 1991. Growth of various hydrilla races in waters of differing pH. Fla. Sci. 54:117–125.

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

U.S. Department of Agriculture. 2014. Plants database. *Hydrilla* Rich. Hydrilla. http://plants.usda.gov/core/profile?symbol=HYDRI

Van TK, Haller WT, Bowes G. 1976. Comparison of the photosynthetic characteristics of three submersed aquatic plants. Plant Physiol. 58:761–768.

Van Dyke JM, Leslie, AJ Jr., Nall LE. 1984. The effects of grass carp on the aquatic macrophytes of four Florida lakes. J. Aquat. Plant Manage. 22:87–95.

Zhang Q, Xu YS, Huang L, Xue W, Sun GQ, Zhang MX, Yu FH. 2014. Does mechanical disturbance affect the performance and species composition of submerged macrophyte communities? Sci. Rep. 4(4888):1–6.