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Fragment viability and rootlet formation in Eurasian watermilfoil after desiccation

CELIA ANN EVANS, D. L. KELTING, K. M. FORREST, AND L. E. STEBLEN*

ABSTRACT

Eurasian watermilfoil often invades aquatic ecosystems in North America via fragment transport from infested lakes to uninfested water bodies by watercraft and boat trailers. While fragments transported on watercraft and trailers are likely introduced to new water bodies in various stages of desiccation, surprisingly little is known about the desiccation tolerance and subsequent viability of Eurasian watermilfoil. We conducted *in situ* and laboratory experiments during the 2010 growing season to examine (1) the rate at which Eurasian watermilfoil desiccates, (2) the likelihood of new growth and rootlet formation in control fragments and fragments that had been desiccated for 3, 6, 18, 24, and 48 h, and (3) time until new growth and rootlet formation in the different treatment groups. We found that desiccation over time fits a Michaelis-Menten type function on which 87% and 96% desiccation occurred after just 3 and 6 h, respectively, and 100% desiccation of milfoil fragments occurred at approximately 13 h under laboratory conditions. Based on a logistic regression model, desiccation significantly reduced the likelihood of fragment viability from 98% in control fragments to 2% in fragments that were completely (100%) desiccated in the laboratory experiment. Desiccation also increased the time until new growth and rootlet formation. In control treatments, 20% of Eurasian watermilfoil nodes produced new growth (via lateral bud growth) after 5 weeks, and 90% of those produced rootlets. Although desiccation significantly reduced Eurasian watermilfoil fragment viability, a small proportion (2%) of fragments that were 100% dried were still viable and able to form rootlets.

Key words: desiccation tolerance, drying, logistic regression, watermilfoil physiology.

INTRODUCTION

Eurasian watermilfoil (*Myrophyllum spicatum* L.) is a submersed rooted, aquatic perennial (Smith and Barko 1990) that often exhibits nuisance growth in mesotrophic or slightly eutrophic lakes and can alter the structure and composition of littoral zone ecosystems (Madsen et al. 1991, Madsen 1998). In the Adirondack Park of Northern New York State, the Adirondack Park Invasive Plant Program (APIPP) reported 79 lakes infested with aquatic invasive plants in 2010, 55 of which were reported to contain Eurasian watermilfoil, making it the most common aquatic invasive plant in the Adirondack region (APIPP 2011).

Dispersal of Eurasian watermilfoil within lakes occurs primarily by stolon growth and secondarily by fragmentation; seeds are thought to be a relatively unimportant means of dispersal (Madsen and Smith 1997). Autofragmentation occurs in mid to late summer when biomass is greatest in the top 20 cm of growth. Some nodes develop rootlets and begin to abscise from the plant below and can be carried by currents to surrounding areas to settle and establish. Allofragmentation occurs from disturbance such as boat motors, paddles, and wind that breaks fragments free from rooted stems and similarly allows establishment of new colonies (Madsen and Smith 1997).

Long distance dispersal of Eurasian watermilfoil from one water body to another seems to be caused mainly by the transfer of fragments on water craft and water craft trailers. A study conducted in the Great Lakes Region showed that while high-pressure boat washing and visual inspection reduced the amount of macrophytes introduced to water bodies by boats by 88%, only about one-third of registered boaters always take these precautions (Rothlisberger et al. 2010). In a New Zealand study, nearly 20% of the aquatic wetland flora were introduced species, and the interlake movement of boats was almost exclusively the cause of the transfer of aquatic weeds. Johnstone et al. (1985) reported that none of the 5 invasive species they were studying were found in lakes with no boating or fishing activity. Working in collaboration with APIPP, the Adirondack Watershed Institute of Paul Smith's College manages a spread prevention initiative called the Watershed Stewardship Program. Stewards work at boat launches in the Adirondack Park to inspect watercraft, collect data on boater demographics, and educate boaters about the ways in which they can reduce the likelihood of transporting invasive species from lake to lake. While doing this work, stewards regularly pull fragments of aquatic plants off of boats and trailers. Stewards stationed at 7 boat launches in 2008 and 8 boat launches in 2009 (for varying numbers of days per week) identified and removed 21 and 12 Eurasian watermilfoil fragments (in those years, respectively) from boats and trailers preparing to launch into lakes without Eurasian watermilfoil populations (Watershed Stewardship Program 2008, 2009). These fragments were in various stages of desiccation.

Surprisingly little published information exists about how drying or desiccation influences the viability of aquatic inva-

*First author, Adirondack Watershed Institute and School of Science and Liberal Arts, Paul Smith's College, PO Box 265, Paul Smiths, NY 12970. Corresponding author's E-mail: cevans@paulsmiths.edu. Second author, Adirondack Watershed Institute and School of Forestry and Natural Resources, Paul Smith's College. PO Box 265, Paul Smiths, NY 12970. Third and fourth authors, Adirondack Watershed Institute, Paul Smith's College. PO Box 265, Paul Smiths, NY 12970. Received for publication November 23, 2010 and in revised form May 16, 2011.

sive plant fragments. Approximately <0.1% of angiosperms have been shown to be desiccation tolerant (Alpert 2000), though it is more common in bryophytes (Proctor 2000). A New Zealand study showed that survivorship of fragments decreased greatly with percent water loss and that there were differences in desiccation tolerance among the aquatic macrophyte species in that study (Johnstone et al. 1985). In the only information we could find on the effects of desiccation in Eurasian watermilfoil, Barnes et al. (2009) reported that desiccation after 1 h and 3 h was 70% and 90%, respectively, and that fragments that coiled as they dried were substantially less dry after the same time period. In most plants, particularly the higher plants (i.e., angiosperms), sufficient drying results in death. The term "desiccation tolerance" is used to describe the condition in which the adults of the species (not just the inactive stages such as seeds or spores) can tolerate drying.

The level of desiccation tolerance in Eurasian watermilfoil has yet to be established, but the rapid spread of this common invasive plant in North America via boats and boat trailers suggests that tolerance of plant tissue or dormant lateral buds to desiccation is likely a characteristic of at least some proportion of individuals in the species. Understanding the levels of tolerance of aquatic plants to desiccation is critical to eventually modeling the probability of new invasions. Indeed, a better understanding of drying affects on growth and development of Eurasian watermilfoil will provide valuable information for managers and educators as well.

To understand the viability of Eurasian watermilfoil, after different degrees of drying our aim was to determine (1) the rate at which desiccation occurs in Eurasian watermilfoil, (2) the proportion of fragments or nodes likely to form rootlets in undesiccated (control) fragments and in fragments desiccated for 3, 6, 18, 24, and 48 h, and (3) the length of time it takes rootlets to form in the different treatment groups.

MATERIALS AND METHODS

During summer 2010, we conducted 2 *in situ* experiments and one laboratory experiment to determine the viability of Eurasian watermilfoil after different drying times resulting in varying levels of desiccation. The 2 *in situ* experiments were conducted in Eurasian watermilfoil infested lakes: Second Pond (44.282755, -74.184237) and Little Lake Colby (44.329988, -74.151621), both located in the Saranac River watershed in the northern Adirondack Park of New York State.

Field experiments. Fragments of Eurasian watermilfoil were harvested from infested lakes in the northern Adirondack Park in the vicinity of Paul Smiths, New York, where beds were easily accessible by canoe or where hand harvesting operations were being conducted. We selected 60 strands of Eurasian watermilfoil, each 10 nodes long, for each experimental trial. The top 5 to 10 cm of growth was removed from each fragment because nodes at the apex of stems were extremely close together and were difficult to count. Individual fragments were measured, patted dry, and weighed. The samples were then laid out to air dry in a low humidity, room temperature laboratory for 3, 6, 18, 24, or 48 h, with 10 replicate strands in each treatment. After the sample groups had dried and were reweighed, each individual replicate was marked by loosely tying short lengths of embroidery thread between the second and third node on each end to track the progress of individual strands. The control treatments consisted of 10 fragments that were patted dry, weighed, measured, and put immediately back into lake water.

Six, cages, 50 by 40 by 40 cm, were constructed from 1 cm hardware cloth zip ties and placed at Second Pond (24 Jun 2010 to 15 Jul 2010) and in Little Lake Colby (23 Jul 2010 to 27 Aug 2010) in a sandy area of the littoral zone for 4 and 5 weeks, respectively. The cages were submerged to just below the surface in about 75 cm of water in the littoral zone and attached to narrow wooden stakes with zip ties.

The cages were checked and data collected at weeks 2 through 4 at Second Pond and weeks 1 through 5 weeks at Little Lake Colby to determine viability of strands using proportion of new growth and rootlet formation as indices. Note that due to desiccation damage to plant tissue and various amounts of wave action, fragments from desiccation treatments were lost over time from cages in the field experiments; therefore qualitative data are presented here rather than statistical analyses (see *Observation of plant tissue integrity and growth*).

Laboratory experiment. We conducted a laboratory experiment using the same drying treatments and methods. After weighing, measuring, and drying we placed 10 Eurasian watermilfoil fragments (each with 10 nodes and apical tips removed as in the field experiment) from each treatment into clear plastic basins containing water from Lower St. Regis Lake in a temperature controlled laboratory (around 21 C) under grow lights set approximately 1.3 m above the basins. The lights were set to a cycle of 16 h on and 8 h off. Water levels in the basins were marked, and at least one-fifth of the water was changed every 3 to 5 d with freshly collected lake water to increase aeration and provide new nutrients. Starting at day 7, strands were examined and data collected on new growth and rootlet development for 5 weeks.

Desiccation controls. In 2009 (a preliminary study) and 2010, 10 (each) additional 10-node fragments were used as a desiccation control to determine the total percent water by weight in milfoil strands to determine the percent of total desiccation for each strand in each of the drying treatments. In each year these fragments were weighed and placed in an oven set at 45 C for 48 h or until no further mass loss. Percent water weight was determined as ([fresh mass – oven dry mass]/fresh mass) *100. There was no significant difference between percent water weight of Eurasian watermilfoil strands between years (88.9% ± 0.35 SD in 2009 and 88.2% ± 1.4 SD in 2010), so these data were combined to obtain a better estimate of the mean percent water weight.

Data analysis. Mean percent water weight was used to estimate the percent of total desiccation for each fragment that occurred as a function of the drying time. Because we subtracted the percent mass loss of each fragment from the mean percent water weight of the strands in the desiccation control trials, percent total desiccation is presented with 95% confidence intervals that occasionally exceed 100%. We decided this would be the most appropriate way to display the data on percent desiccation, even though plants could not, in reality, be >100% desiccated.

Percent desiccation due to drying time was not different for the fragments used in either of the 2 field experiments or the laboratory experiment; therefore, desiccation data from the 3 trials were pooled to analyze fragment drying rates. For statistical analysis, the 0, 87, and 96% desiccation categories correspond to the Control, 3, and 6 h drying times, and the 18, 24, and 48 h drying treatments are included in the 100% desiccation category. We used logistic regression on laboratory data only to determine the probabilities of fragments producing new growth and fragments producing rootlets in the different drying treatment. The growth data were coded as a binary dataset (0 = no growth, 1 = growth), and the binary variable was treated as the dependent variable in a multiple logistic regression model with drying treatment, experimental time, and the interaction as the independent variables. This full model was then reduced to a partial model based on model performance metrics. Independent variables with coefficient P-values <0.1 and 95% confidence intervals not bracketing 1 on the corresponding Odds Ratios were considered significant explanatory variables and thus were retained in the logistic regression model. An Odds Ratio of 1 means both events, root growth and no root growth, have an equal chance of occurring, basically meaning one event is not favored over the other. All statistics were done using Mini-tab (version 15). We present qualitative data for evidence of rootlet production in laboratory and field experiments because sample size was too small for logistic regression, and also for growth in *in situ* pond studies because logistic regression was not valid due to loss over time of fragments from cages in the lakes.

RESULTS AND DISCUSSION

Desiccation of Eurasian watermilfoil due to drying. We fit a Michaelis-Menten type function to the relationship between percent total desiccation and drying time (Figure 1). The strands were 87% desiccated after just 3 h of drying under our laboratory conditions of room temperature and low humidity. After 6 h of drying, the percent desiccation of fragments ranged between 93 and 99%. After 18 h of drying and beyond, all measurable water was lost from the fragments. Using the equation for the fitted function, we estimate that 100% desiccation occurs at approximately 13 h.

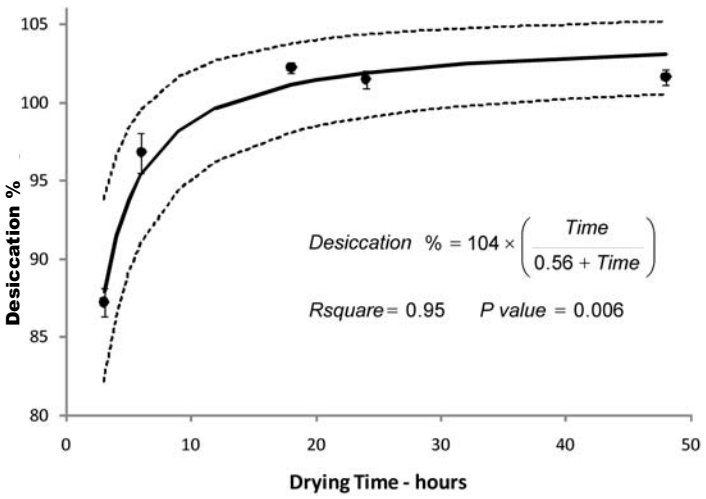

Figure 1. The average percent fragment desiccation vs. drying time with bars showing ± one standard error of the mean, n = 30. A Michaelis-Menten function was fit to the data, and the equation shows that drying time explained 95% of the variation in desiccation%, with 100% desiccation occurring in about 13 h drying time. Dashed lines are upper and lower 95% confidence intervals for the predicted desiccation percent.

Eurasian watermilfoil dried quickly under the conditions in this study. Rapid drying has been associated with desiccation tolerance, especially with bryophytes, but also in vascular plants (Gaff 1977). It has been proposed that rapid loss of water reduces damage that can occur during rehydration, and that the greatest amount of damage to plant tissues may be sustained at intermediate dryness levels (Alpert 2000). Our data for desiccation rates are close to those reported for Eurasian watermilfoil by Barnes et al. (2009) in which 3 h of drying resulted in 90% desiccation.

Fragment viability—effect of drying treatment and time on new growth in the laboratory. Full and reduced logistic regression models showed that drying treatment alone significantly reduced the likelihood of new growth on desiccated milfoil fragments ($z = -7.24$, $p \leq 0.001$, reduced model; Table 1). Using the reduced model (Table 1), we predicted the probability of new growth. Control fragments had a probability of 0.98 of producing new growth, while fragments dried for only 3 h resulting in 87% desiccation had a significantly reduced probability of viability of 0.06. Completely desiccated plants had a probability of viability of 0.02 (Table 2). A larger sample size would likely have reduced the variability in our study, thereby increasing the performance of our model. Regardless, there is a probability >0 of highly desiccated fragments producing growth.

No loss of tissue could occur over time in the laboratory experiment, which provided insight into the loss of fragments over time in the field experiments. Control treatment fragments were buoyant for the entire period of the experiment, while fragments from the 3 h drying treatment were initially buoyant and then began to sink in week 3. All other treatments were not buoyant after drying, as noted above. The only disturbance in laboratory basins was the changing of water every 3 to 5 d. Even this minimal disturbance began to break apart the most desiccated strands within 2 to 3 weeks. After 4 weeks of no evidence of new growth in the 18 through 48 h drying treatments (100% desiccated), we were ready to end the experiment when we observed new growth and rootlet development in both the 18 and 48 h drying treatments.

Observation of plant tissue integrity and growth after drying in pond experiments. The same disintegration of plant tissue we observed in the laboratory experiment led to the loss of fragments or partial fragments from cages in the field over time (aided in Second Pond by heavy wave action).

After 2 weeks in Second Pond, partial fragments remained in the control for 3, 6, and 18 h drying treatments. There was no new growth in any of the treatments, and there were no fragments remaining in the 24 or 48 h drying treatments. After 3 weeks, the remaining fragments in the control treatment had begun to grow and root. The 3 h treatment also showed new lateral bud growth but no rootlets. After 4 weeks, only several short fragments remained in the control cage.

TABLE 1. RESULTS OF LOGISTIC REGRESSION ANALYSIS ON THE PROBABILITY OF FRAGMENTS PRODUCING NEW GROWTH AS A FUNCTION OF PERCENT FRAGMENT DESICCATION AND INCUBATION DAYS FOR A LABORATORY INCUBATION STUDY.

Predictor	Coefficient	S.E. Coefficient	Z Statistic	P value	Odds Ratio	Confidence Intervals for the Odds Ratio	
						Lower 95% CI	Upper 95% CI
				Model 1			
Constant	1.696	1.818	0.93	0.351			
Desiccation	-0.085	0.024	-3.50	<0.001	0.92	0.88	0.96
Days	0.139	0.125	1.11	0.268	1.15	0.90	1.47
Desiccation × Days	-0.0004	0.0014	-0.27	0.790	1.00	1.00	1.00
				Model 2			
Constant	4.031	0.970	4.15	<0.001			
Desiccation	-0.079	0.011	-7.24	<0.001	0.92	0.91	0.94

TABLE 2. PROBABILITY AND 95% CONFIDENCE INTERVALS FOR PROBABILITY OF FRAGMENTS PRODUCING NEW GROWTH AS A FUNCTION OF PERCENT FRAGMENT DESICCATION FOR A LABORATORY STUDY PREDICTED USING THE LOGISTIC REGRESSION MODEL 2 IN TABLE 1. THE 0, 87, AND 96% DESICCATION CATEGORIES CORRESPOND TO THE CONTROL, 3, AND 6 H DRYING TIMES. THE 18, 24, AND 48 HR DRYING TREATMENTS ARE INCLUDED IN THE 100% DESICCATION CATEGORY.

		95% Confidence Interval	
Desiccation %	Probability	Lower	Upper
0	0.98	0.89	1.00
87	0.06	0.00	0.72
96	0.03	0.00	0.61
100	0.02	0.00	0.55

In the Little Lake Colby experiment the control treatment showed new growth after just one week. The other treatments had no new growth and appeared to be in the process of disintegrating. In the second week, the Little Lake Colby control group had new growth on all 10 fragments, some with rootlet growth. The 3 h drying treatment had one fragment with new growth after 2 weeks, but the remaining samples showed no new development. By the third week, rootlets appeared on 8 of 10 control fragments, and new growth was found on every fragment; a second strand in the 3 h drying treatment also had new growth. By the fourth week, fragments remained only in the control and 3 h drying treatment.

Node viability and timing of growth and rootlet formation in the laboratory. Because all fragments remained in the laboratory basins for the entire experiment, unlike the *in situ* experiments, we could calculate the proportion of viability on a per node basis, which allows us consider viability in plant fragments of different lengths (number of nodes). New growth began during the first week in the control and 3 h (87% desiccation) drying treatments. The proportion of nodes with new growth increased through time in the control treatment. In the 3 h drying treatment, the new growth observed after the first week was not observed again until week 5 (day 33), with a proportion of viable nodes of only 0.01. No growth was observed in the 6 (96% desiccation), 18, 24, and 48 h (100% desiccation) drying treatments until week 5, when the proportion of viable nodes in the 6, 18, and 48 h drying treatments were each 0.01.

Rootlet production began in the control treatment after 3 weeks, when the proportion of nodes with new growth forming rootlets was 0.3. By the end of the experiment the proportion of nodes forming new growth in the control was 0.2, and the proportion of those nodes that formed rootlets was 0.9. These qualitative data suggest that at least 20% of Eurasian watermilfoil nodes may contain viable dormant lateral buds and that desiccation also may increase the length of time required for a viable node to produce new growth and, subsequently, rootlets.

All fragments in our experiments had the apical tip and between 5 and 10 cm of the upper stem removed because it was difficult to count the crowded nodes of the tips. The removal of the apical tips likely released some dormant lateral buds; however, the process of desiccation *per se* may initiate physiological changes leading to growth in some aquatic plant buds (Malek 1981). To predict the likelihood that desiccated fragments will be viable when introduced to new lakes we need to learn more about the ratio of lateral buds per node (Johnstone et al. 1985) and mechanisms of lateral bud growth initiation. If release from apical dominance is partially or mostly responsible for initiation of bud growth, then the likelihood of viability will be different for fragments that include the terminal growth and those that have had that terminal growth removed. In future research we recommend avoiding the removal of apical buds or comparing bud growth initiation between fragments with and without apical tips removed to better understand the control of bud development after desiccation.

Of the other 4 treatments that produced one instance of new growth, 2 (3 and 18 h drying treatments) did not produce a rootlet during the experiment, but the other 2 (6 and 48 h drying treatments) each showed rootlet growth. Note that new growth and rootlet development were delayed until after week 4 in these treatments. If we present these data in desiccation categories as we did for the regression analysis, the 96% desiccation (6 h drying) had a 0.01 probability of a node producing new growth, and the 100% desiccation (18, 24, and 48 h) showed new growth and rootlet development, a probability of 0.007 (2 of 300 nodes were viable). These data represent a valuable first estimate and could be useful in initial predictions of time until invasion of new lakes where boater traffic and incidents of fragment transport and number of nodes of Eurasian watermilfoil are available.

Our quantitative analysis shows a significant reduction in viability as a function of desiccation, which is corroborated by our qualitative observations. However, even after long desiccation time and 100% loss of measurable water, some small fraction of fragments (nodes within fragments) was able to produce growth. Our data suggest that once new growth is initiated, rootlets usually follow. In this study, initiation of new growth in Eurasian watermilfoil does not seem to be the rehydration of leaf tissue, but rather the rehydration of dormant lateral buds that produce new stems and rootlets. Eurasian watermilfoil does not seem to have a high tolerance to desiccation; however, some lateral buds can withstand full drying and eventually produce new growth. This finding is similar to that of Johnstone et al. (1985) for several aquatic invasive species in New Zealand. They reported that after 50% mass loss of fragments (due to desiccation), all leaves on the fragments died, but fragments were still able to grow from lateral buds.

Mechanisms of tolerance to desiccation probably include both cellular and subcellular level responses to oxidative damage and possibly mechanisms that reduce physical damage to cell membranes when desiccated cells begin to lose turgor (Alpert 2000). If there is variability within Eurasian watermilfoil populations for tolerance to desiccation, then fragments transported via watercraft that ultimately are successful in colonizing new lakes will be those that can withstand desiccation. If desiccation has a genetic basis, then long distance transport of milfoil strands could create a strong selection for desiccation tolerance in subsequently colonized lakes. Note that nongenetic factors such as carbohydrate storage due to season and environmental conditions are also potential influences on viability after desiccation, and that understanding the relative importance of these various factors will be important for future research.

In conclusion, Eurasian watermilfoil fragments dry out quickly, at least under the conditions in our study (room temperature and relatively low humidity); after 3 h, fragments averaged only 13% of the original moisture. Loss of tissue integrity and a significant reduction in viability are associated with desiccation. Decreased viability was a function of percent desiccation, was statistically significant, and was shown qualitatively by both the reduction in production of new growth and rootlets and also by the longer time required to develop new growth and rootlets in dryer fragments. While the likelihood of growth and root production of a desiccated or partially desiccated fragment is much reduced, it is not eliminated. Our data suggest that even 100% dry fragments have a 0.02 probability of new growth, and that the new growth will likely form rootlets. Moreover, one of the incidences of rootlet formation in the 100% desiccation group was in the 48 h drying treatment. Based on our desiccation rate curve, full desiccation occurred in 13 h, so this lateral bud was still viable after having been fully desiccated for 35 h. This suggests that at least a small number of Eurasian watermilfoil dormant lateral buds are highly desiccation tolerant.

Our data can not estimate the likelihood of establishment of fragments once introduced to a new lake because environmental variables such as lake sediment texture, nutrient composition, and light environment (Grace and Wetzel 1978, Madsen 1998) will also play a role in the establishment of any viable Eurasian watermilfoil fragments. Nor can our data be used to determine a minimum drying time to reduce viability to zero (1) because our treatments did not result in zero viability, and (2) because drying conditions in the environment where fragments are clinging to watercraft may be very different than in this study. Fragments transported along with watercraft in wells, on bunks of trailers, and other locations are likely kept more moist during transport. Barnes et al. (2009) found that coiled Eurasian watermilfoil fragments desiccated much more slowly than uncoiled fragments. Additional research is needed to better understand the relationship between desiccation and viability under different environmental conditions, drying scenarios, and in different populations of Eurasian watermilfoil.

Our results emphasize the need for continued vigilance on the part of educators and boaters because fragments that look, feel, and are dry may still be viable. Once Eurasian watermilfoil has established in a lake it is rarely possible to eradicate it through management efforts. Among other methods, benthic matting (Mayer 1978) and hand-pulling operations (Kelting and Laxson 2010) have been shown to be effective at significantly reducing milfoil density; however, the cost of programs like these are exorbitant. Results of this study support the idea that efforts to prevent initial invasion are likely the best option for uninfected lakes. To reduce invasion of Eurasian watermilfoil into new lakes, the inspection and removal of all plant material (regardless of the observed apparent condition) and careful boat washing are critical practices.

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