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Does hydrilla grow an inch per day? Measuring short-term changes in shoot length to describe invasive potential

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INTRODUCTION

The ability of invasive plants such as hydrilla (*Hydrilla verticillata* [L.f.] Royle) and Eurasian watermilfoil (*Myriophyllum spicatum* L.) to grow and rapidly expand has been well described in both popular and scientific literature (Steenis 1967, Adams and McKracken 1974, Johnson and Manning 1974, Haller 1976, Sutton et al. 1992). Infestations are often reported in terms of percent cover or percent frequency at the lake scale, while dry weight biomass per square meter is generally reported for scientific studies at laboratory and field scales. Studies have also focused on growth from vegetative propagules and subsequent propagule production as endpoints (Van and Steward 1990, Sutton et al. 1992, Spencer et al. 2000). Nonetheless, when viewed in terms of overall productivity, submersed aquatic plants produce much less biomass when compared to their terrestrial counterparts (Westlake 1963, Grace and Wetzel 1978). Moreover, prior studies have demonstrated that Eurasian watermilfoil is not particularly productive when biomass production is compared to other submersed native species (Grace and Wetzel 1978, Smith and Barko 1990). While the vast majority of scientific trials have focused on changes in biomass or propagule production as an endpoint for evaluating growth or response of hydrilla or Eurasian watermilfoil to control methods, measuring the change in total stem length may be a useful technique for explaining rapid rates of lateral plant spread in a water body. Emphasis has often been placed on hydrilla and Eurasian watermilfoil concentrating biomass in a surface canopy (Haller and Sutton 1975, Grace and Wetzel 1978, Madsen 1997), yet production of numerous lateral stems and stolons and the subsequent rates of extensions may better explain rapid radial expansion. Hydrilla stolons, for example, have been documented to expand a colony radially at a rate of 4 cm d^{-1} (Madsen and Smith 1999). While the statement that "hydrilla can grow an inch a day" (Langeland 1996) initially sounds impressive, it is unlikely this rate of extension would explain the ability of hydrilla to form large contiguous surface canopies on hundreds or thousands of acres in lakes and reservoirs.

To evaluate the rate of growth of hydrilla and Eurasian watermilfoil, a series of mesocosm trials were conducted to mea-

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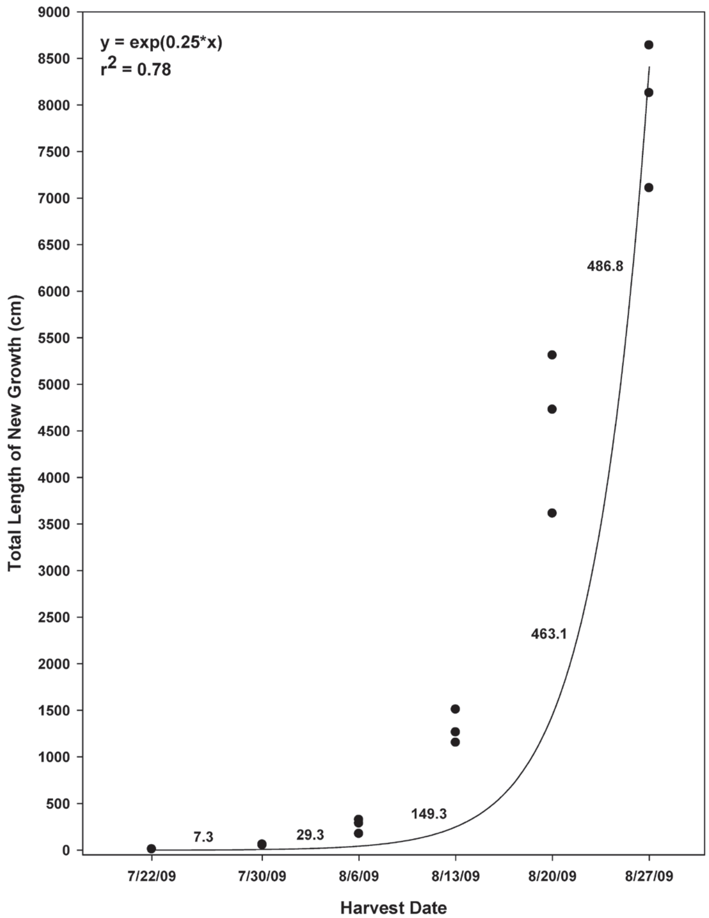

Figure 1. Mean hydrilla growth (cm) ± SE. Values reported directly on the graph represent the daily expansion rate in cm day^{-1} for weeks 1 through 5 of the study.

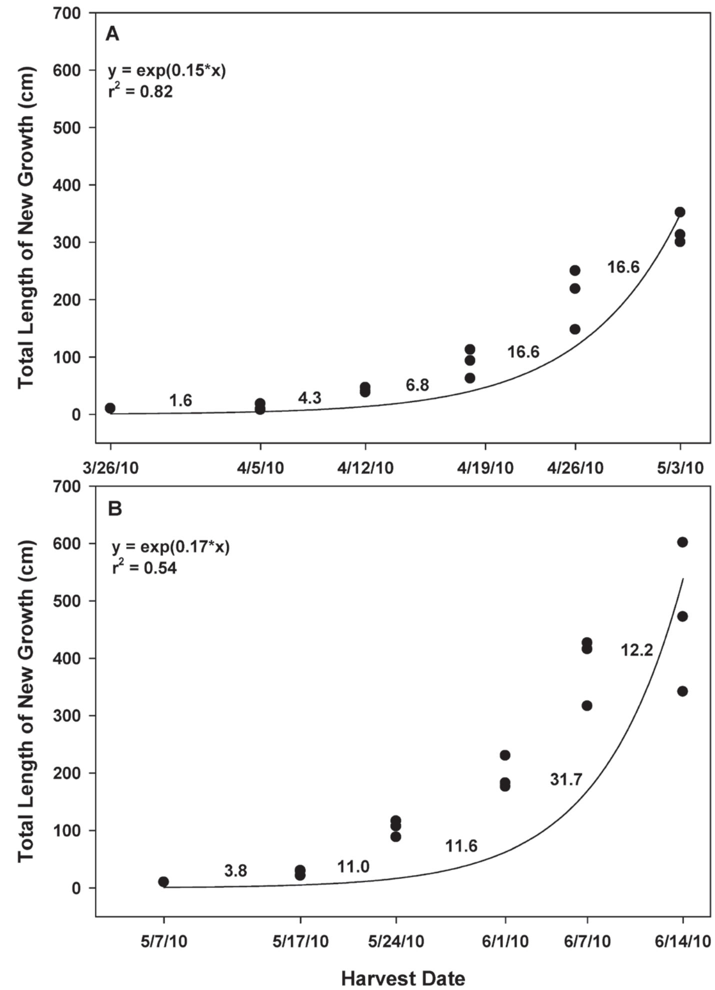

Figure 2. Mean Eurasian watermilfoil growth (cm) ± SE in A) study 1 and B) study 2. Values reported directly on the graph represent the daily expansion rate in cm day^{-1} for weeks 1 through 5 of the study.

sure the change in shoot length over a 35-day period during summer growth conditions. The objective of this study was to compare the shoot growth of two introduced and two native plant species and evaluate the data to determine if rates of overall shoot extension may help explain invasive properties.

MATERIALS AND METHODS

To determine the rate of shoot extension of hydrilla, Eurasian watermilfoil, American pondweed (*Potamogeton nodosus* Poir.), and water stargrass (*Heteranthera dubia* [Jacq.] MacMill.), mesocosm studies were conducted at the U.S. Army Engineer Research and Development Center, Lewisville Aquatic Ecosystem Research Facility (LAERF) in Lewisville, Texas. Hydrilla was evaluated 22 July through 27 August 2009. Eurasian watermilfoil was evaluated twice, 26 March through 3 May and 7 May through 14 June 2010, and temperature was recorded throughout both study periods. Both native species were evaluated 23 June through 2 August 2010. Eurasian watermilfoil exists as an evergreen and is typically active in the fall, winter, and spring in Texas. Therefore this portion of the study was conducted to compare early spring and late spring rates of growth. Hydrilla and both native species were evaluated during summer months when growth rates are expected to be at a maximum due to the increased photoperiod and mesocosm temperatures in the range of 28 to 30 C. Plants were obtained from LAERF ponds, and one 15 cm apical stem section was planted in pots (3.78 L) filled with LAERF pond sediment amended with 3 g L^{-1} Osmocote (16-8-12). Apical stem sections were planted so that 10 cm was initially above the sediment surface. Ten pots were placed into each of three 7000 L outdoor mesocosms, which were filled with lake water. Two pots from each replicate tank were harvested each week for 5 weeks, and all stems in the pot were measured for total length. To determine centimeters of growth per day for a given week, the previous week's average was subtracted from the current week's average and then divided by the number of days between the two harvests. The number of lateral branches, new stems, and stolons was also recorded. Lateral branches were defined as secondary branches, new stems as stems originating from the root crown or from nodes along the stolons, and stolons as horizontal stems atop the sediment surface originating from the root crown (Haller 1976, Yeo et al. 1984). Plant length data were subjected to regression analysis.

Table 1. Number of lateral branches, new stems and stolons (± SE) produced by hyrilla, Eurasian watermilfoil (study 1 and 2), American pondweed, and water stargrass each week.

	Week 1	Week 2	Week 3	Week 4	Week 5
Hydrilla					
Lateral Branches	2 ± 2	13 ± 6	43 ± 11	129 ± 29	157 ± 38
New Stems	2 ± 0	6 ± 1	34 ± 13	71 ± 16	190 ± 63
Stolons	0 ± 0	1 ± 1	3 ± 2	9 ± 6	35 ± 20
Eurasian watermilfoil 1					
Lateral Branches	1 ± 1	3 ± 1	4 ± 0	10 ± 2	12 ± 0
New Stems	0 ± 0	0 ± 0	0 ± 0	1 ± 0	1 ± 0
Stolons	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Eurasian watermilfoil 2					
Lateral Branches	2 ± 0	3 ± 1	5 ± 1	8 ± 2	11 ± 4
New Stems	0 ± 0	0 ± 0	1 ± 0	2 ± 0	3 ± 0
Stolons	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
American pondweed					
Lateral Branches	1 ± 1	1 ± 1	1 ± 0	2 ± 1	1 ± 0
New Stems	0 ± 0	0 ± 0	2 ± 0	4 ± 0	8 ± 2
Stolons	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Water stargrass					
Lateral Branches	1 ± 0	1 ± 0	1 ± 0	1 ± 1	1 ± 1
New Stems	0 ± 0	0 ± 0	1 ± 1	1 ± 0	3 ± 0
Stolons	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

RESULTS AND DISCUSSION

Hydrilla increased by 7.3 cm d^{-1} in the first week of the study (Figure 1). New growth was primarily from elongation of the initial stem as well as the formation of lateral stems. In week 2, new stems originating from the base of the initial plant accounted for most of the new growth, and hydrilla grew 29.3 cm d^{-1}. By week 3, stolons and new stems along the stolon had formed, and the growth rate of hydrilla increased to 149.3 cm d^{-1}. The growth rates for hydrilla in weeks 4 and 5 were 463.1 and 486.8 cm d^{-1}, respectively (Figure 1). Hydrilla had also produced 190 new stems by week 5 (Table 1). From the original 10 cm shoot, hydrilla had increased to over 8000 cm of shoot tissue in a 35-day period. The early lag period was followed by rapid expansion in weeks 4 and 5. In terms of answering the question of whether hydrilla grows an inch a day, the current results would paint a more complex picture that suggests the initial 10 cm shoot was extending both vertically and horizontally by up to 191 inches per day. While growth of individual shoots may be closer to the 1 to 4 inches per day commonly cited, hydrilla was producing numerous stolons and lateral stems that resulted in a rapid three dimensional or radial expansion from the original single 10 cm shoot.

Compared to hydrilla, Eurasian watermilfoil shoot extension was considerably reduced in both trials. Overall, Eurasian watermilfoil growth was greater in study 2 than in study 1 (Figure 2A and B). This difference may have been related to temperatures, which ranged from 13 to 23 C in study 1 and 18 to 36 C in study 2. Eurasian watermilfoil can photosynthesize at temperatures as low as 10 C, with the optimal range occurring between 30 and 35 C (Stanley and Naylor 1972). The maximum growth rate for Eurasian watermilfoil was 16.6 and 31.7 cm d^{-1} in week 4 of study 1 and 2 respectively. The number of lateral branches produced by Eurasian watermilfoil was similar in both studies and along with elongation of the main stem accounted for most of the new growth (Table 1). While interspecific competition was not evaluated in these trials, such a large disparity between total stem lengths of hydrilla versus Eurasian watermilfoil suggests that hydrilla would have a strong competitive advantage under these growth conditions.

The growth rate of American pondweed ranged from 1.8 to 32.9 cm d^{-1} with the maximum during week 4 (Figure 3A). Water stargrass growth ranged from 2.4 to 12.6 cm d^{-1} with the maximum also occurring during week 4 (Figure 3B). The increase in shoot length was generally linear through the 5-week study, and the total stem values of approximately 200 and 400 cm was 20 to 40 times less than observed for hydrilla, but similar to that of Eurasian watermilfoil.

The use of large mesocosm tanks and the short-term nature of these studies prevented hydrilla from approaching carrying capacity. Moreover, interspecific competition was not a factor reducing the rates of growth. While the shoot expansion rates reported would slow greatly as hydrilla formed a canopy, this study demonstrates that following a short initial lag, hydrilla increased rapidly, and the production of numerous laterals stems and stolons helps to explain radial expansion as a key invasive trait. While this 35-day study was conducted during a period when maximum rates of growth would be expected, similar environmental conditions can generally exist from May through September in many southern states. In a Brazilian trial, hydrilla doubling times of 2.5 to 19 days were reported (Bianchini et al. 2010), and our current results with shoot extension would support this rate of expansion. While measuring stem extension is quite labor intensive compared to collecting plants for dry weight biomass, this type of data provides a unique look at how hydrilla expansion can be rapid as the plant fills the available water column with biomass.

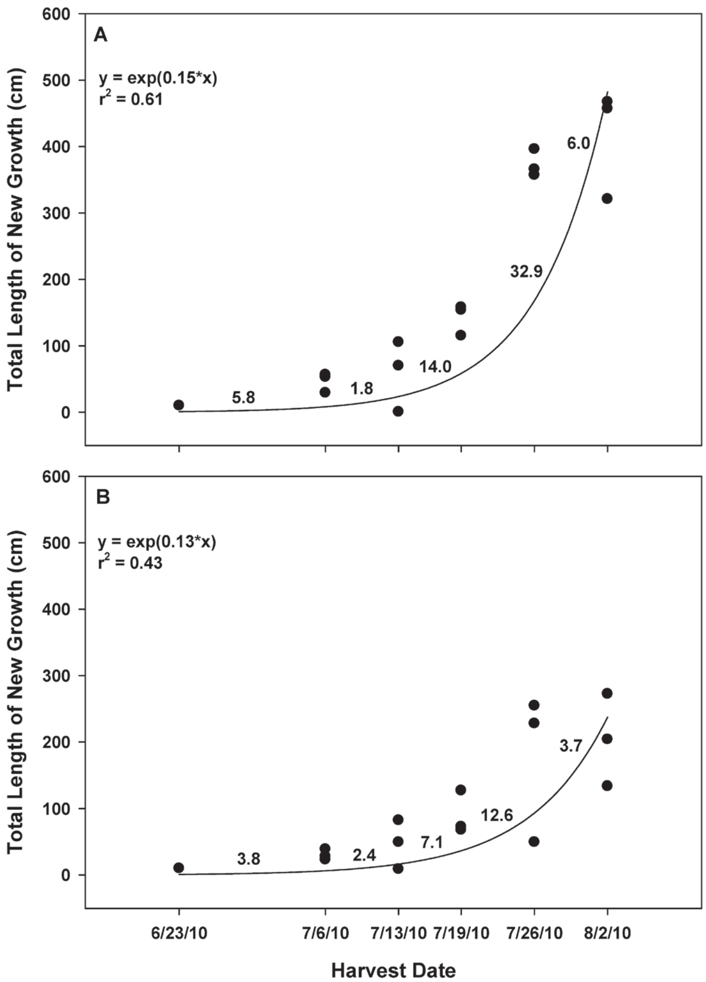

Figure 3. Mean (A) American pondweed and (B) water stargrass growth (cm) ± SE. Values reported directly on the graph represent the daily expansion rate in cm day^{-1} for weeks 1 through 5 of the study.

The reduced shoot extension rate for the native plants when compared to hydrilla was generally expected; however, the comparative performance of the Eurasian watermilfoil was much lower than expected. The lack of lateral shoot and new stem production by Eurasian watermilfoil during the two studies was in contrast to hydrilla and may, in part, explain lower shoot extension values observed during these short-term studies. Eurasian watermilfoil will overwinter as an evergreen, and new growth is often observed from large and well-established root crowns (Smith and Barko 1990). In this study, we were evaluating growth from single apical shoot fragments that do not contain starch reserves to support fast, copious shoot growth. Future studies evaluating rates of Eurasian watermilfoil expansion from established root crowns that have overwintered are planned.

Data generated from this trial may be useful in conveying the potential invasiveness of hydrilla to public and private stakeholder groups that have an interest, but not an expertise, in aquatic plant management. When describing hydrilla growth, a term such as "300 g dry weight m^{-3}" can be confusing and lack context , whereas reporting changes in length over a short period of time is intuitive and may better describe how hydrilla can readily dominate a given marina, cove, or waterbody.

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