Vegetative Spread of Dioecious Hydrilla Colonies in Experimental Ponds

JOHN D. MADSEN[1] AND DIAN H. SMITH[2]

ABSTRACT

Stolon formation and fragmentation are two vegetative mechanisms by which hydrilla colonies expand. These two mechanisms of spread were studied in ponds located in Lewisville, TX over a two-year period. Stolons were determined to be the predominant mechanism for localized expansion in undisturbed areas. While some fragments were produced, they accounted for only 0.1% of the establishment of rooted plants in new quadrats. Peak production of fragments occurred in October and November, with fragment densities of 0.15 N m^{-2} d^{-1}. Expansion by stolons occurred between June and November of each year, with higher rates of spread (up to 4.0 cm d^{-1} radial growth) observed in the second season.

[1]U.S. Army Engineer Waterways Experiment Station, CEWES-ES-P, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199.

[2]U.S. Army Engineer Waterways Experiment Station, Lewisville Aquatic Ecosystem Research Facility, R.R. #3 Box 446, Lewisville, Texas 75056-9720.

Key words: vegetative reproduction, fragment, stolon, dispersal, *Hydrilla verticillata.*

INTRODUCTION

Hydrilla (*Hydrilla verticillata* (L.f.) Royle) was first introduced into North America during the 1960s (Pieterse 1981), and since that time confirmed populations of dioecious hydrilla have been identified in thirteen states (AL, AZ, CA, CT, FL, GA, LA, MS, NC, OK, SC, TN, TX) (Les et al. 1997, Steward et al. 1984).

This highly invasive weed has two distinct biotypes in the USA, with a number of dispersal mechanisms. Viable seeds are produced by the monoecious biotype. Currently, the dioecious biotype within the United States develops only pistillate flowers, and thus does not produce seeds (Langeland and Smith 1984).

Like many submersed aquatic plants, both hydrilla biotypes expand by the production of vegetative propagules (Sculthrope 1967, Langeland and Sutton 1980). Root crowns develop stolons that extend into the area surrounding the parent plant and establish new plants. Tubers, also called

subterranean turions, are formed within the sediment and remain viable for many years after above ground vegetation has been destroyed (Van and Steward 1990). Fragments, which are produced by the mechanical breakage of plant stem apices, float away from the colony and settle to the sediment where they develop roots and produce new plants. Additionally, axillary turions, which are produced on and abscise from the stem, provide a mechanism for intermediate distance dispersal within a water body, and long distance dispersal between waterbodies (Sutton 1996, Spencer and Ksander 1991, Sutton and Portier 1985, Haller et al. 1976). Axillary turion production is often considered to be quite low on rooted dioecious plants, and may not provide the most important mode for intermediate-distance dispersal within a water body. Formation of turions on detached stems may provide an excellent means of intermediate and long distance dispersal.

The study objectives were to determine the prominence of two modes of vegetative population expansion (stolon and fragments) from a new, small colony of hydrilla; to determine the average daily rate of spread over two growing seasons; and to analyze seasonal dispersal patterns of the two modes of propagation.

MATERIALS AND METHODS

This study was conducted at the U.S. Army Corps of Engineers Lewisville Aquatic Ecosystem Research Facility in Lewisville, Texas, USA (Latitude 33°04'45" N, Longitude 96°57'33" W) in two 0.26 ha manmade ponds. An impervious barrier divided each pond, providing four separate study areas. Water depth within the ponds ranged from 70 cm to 148 cm (Madsen and Smith 1997). Lake Lewisville, a U.S. Army Corps of Engineers reservoir, was the source of water used for the experimental ponds. Water level was maintained by screened standpipes in each experimental pond (Smart et al. 1995). The water chemistry of the ponds was typically circumneutral (average pH of 7.1), with an average alkalinity of 100 mg $CaCO_3$ L^{-1}, average total phosphorus of 50 µg L^{-1}, average nitrate of 290 µg L^{-1}, and an average ammonium of 50 µg L^{-1} (Smart et al. 1995). The pond sediment was 28% sand, 33% silt, and 38% clay, with an average of 5% organic matter, 9.2 mg g^{-1} of exchangeable nitrogen, and a bulk density of 1.2 g cm^{-3} (Smart et al. 1995).

Each of the four 18 m by 18 m sampling regions was delineated into 324 1 m^2 quadrats by a grid system using nylon rope suspended from contiguous 3 m by 6 m PVC pipe frames. The grid system was attached to floats and held stationary by metal posts driven into the sediment (Figure 1). A total of 1,296 quadrats were used in this study.

An Omnidata EasyLogger™ (Logan, Utah) underwater thermistor, affixed to a float and held below the surface of the water at a depth of 15 cm, measured water temperatures at five minute intervals. The five minute intervals were averaged to record an hourly average. Daily average water temperatures were calculated from logged hourly averages.

Localized spread of hydrilla was investigated by planting four root crowns in the sediment of each grid's center four quadrats (eight meters from each edge) in April 1995. The root crowns planted were from plants grown in small pots in the greenhouse from stem fragments planted in these pots in
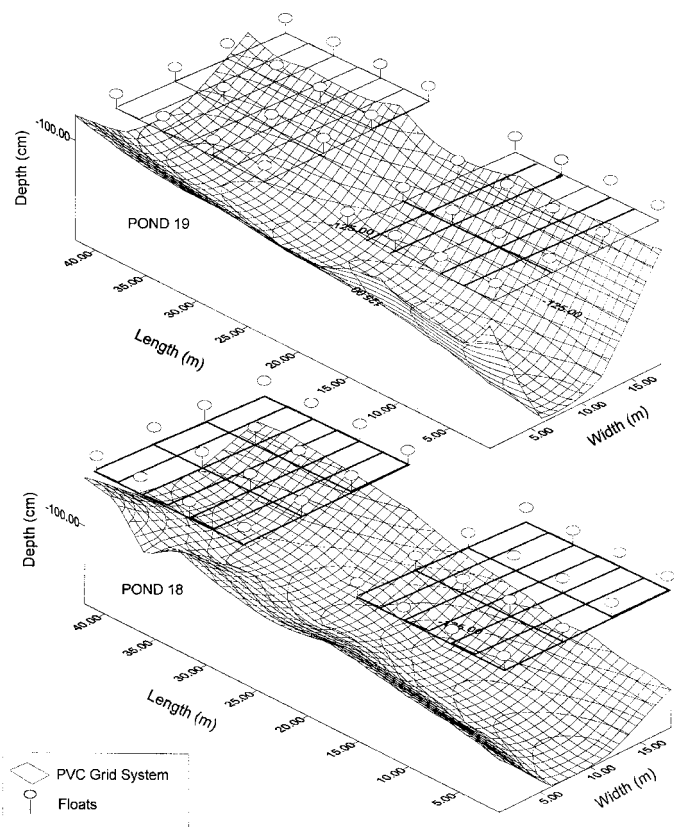

Figure 1. Schematic of grid system arrangement within experimental study ponds. Depth isopleths are in 25 cm intervals.

November 1994. From April 1995 through November 1996, presence or absence of rooted plants and fragments within the quadrats of each grid was recorded at three week intervals. No observations could be made from mid-November 1995 to mid-May 1996 due to high turbidity in the system.

During each observation period, the presence of rooted plants or fragments within all quadrats (planted and outlying) was used to calculate the percent frequency resulting from the two types of vegetative propagules and overall growth of the colonies. Quadrats which had fragments at one time, and rooted plants the next were generally assumed to have been colonized by fragments. Often, the stem fragment could still be observed in these quadrats. Although we examined plants for turions, none were observed throughout this experiment. Transition to presence or absence of the type of vegetative propagule observed within a quadrat from one sampling period to the next sampling period furnished data for calculation of average daily expansion or mortality rates.

Colony expansion via stolons was analyzed via rooted plants and their mortality. A stoloniferous expansion rate was characterized by the transition from absence of rooted growth within a quadrat during one sampling period to presence of rooted growth during the next sampling period. Mortality was characterized by transition from rooted growth present during one sampling period to the absence of observable rooted growth during the next sampling period. The units used to express these changes are given as N m^{-2} d^{-1}, or the number of new ramets per quadrat (or square meter) per day.

Distribution and colony expansion by fragments were analyzed via fragment settling, fragment persistence, establishment of fragments into rooted growth, and fragment mortality (Madsen and Smith 1997). Fragment settling was defined as a stem fragment having drifted to the bottom, but not yet rooted. Fragment persistence was defined as an unrooted fragment having settled the previous time period, and still occurring as an unrooted fragment. Fragment establishment was defined as a stem fragment forming adventitious roots that extended into the sediment. Fragment mortality was defined as a stem fragment occurring in the previous time period, but the quadrat being unoccupied in the current time period.

Data from all quadrats were combined across ponds and depths for analysis.

RESULTS AND DISCUSSION

The major period of expansion for the colonies of *Hydrilla verticillata* was in a six-month period from May 1996 through November 1996 when the percent of quadrats with rooted vegetation increased from 19.5% to 70% of the sampling quadrats (Figure 2B). Stoloniferous growth accounted for 99.9% of the colony expansion while only 0.1% of the expansion was attributable to fragmentation. Expansion followed a period of quiescence during the winter months when water temperatures ranged from zero to the mid-teens (Figure 2A).

During the major expansion period, the hydrilla colony expanded radially at 4.0 ± 0.39 cm d^{-1}. Stolons provided the colony with a daily rate of spread ranging from 0.56 ± 0.16 N m^{-2} d^{-1} to 1.48 ± 0.32 N m^{-2} d^{-1} during this major expansion period (Figure 2C). Stolon mortality was less than 0.12 ± 0.04 N m^{-2} d^{-1} throughout the investigation (Figure 2D).

In contrast to the major expansion of hydrilla colonies which occurred between May and November when water temperatures were above 20 C, Eurasian watermilfoil (*Myriophyllum spicatum* L.) grown under similar conditions demonstrated an earlier major expansion period between November and June when water temperatures were above 10 C (Madsen and Smith 1997). However, a similar radial population expansion rate of 3.9 cm d^{-1} was observed for Eurasian watermilfoil during its key expansion period (Madsen and Smith 1997). A slightly higher rate of stolon mortality was observed for Eurasian watermilfoil (≤ 0.20 N m^{-2} d^{-1}, Madsen and Smith 1997) as compared to the rate observed for hydrilla. Observed mortality was minimal for both species, suggesting that spread by stolons is a very efficient form of vegetative propagation.

Phenology of hydrilla grown in this southern region of the USA exhibits an active growth period during the summer months, with a period of senescence during the winter (Madsen and Owens 1998). The active growing period in Texas is somewhat later than observed for dioecious hydrilla in Florida (Bowes et al. 1979). In contrast, the active growth period for Eurasian watermilfoil in Texas is during spring when temperatures range from 10 to 25 C, with growth slowing during the summer months as temperatures exceed 25 C (Madsen 1997).

The major episode of hydrilla fragment settling occurred between October and November 1995 when fragments settled into previously unvegetated quadrats at a rate of 0.02 N m^{-2} d^{-1} to 0.15 N m^{-2} d^{-1} (Figure 3A). However, fragment persis-
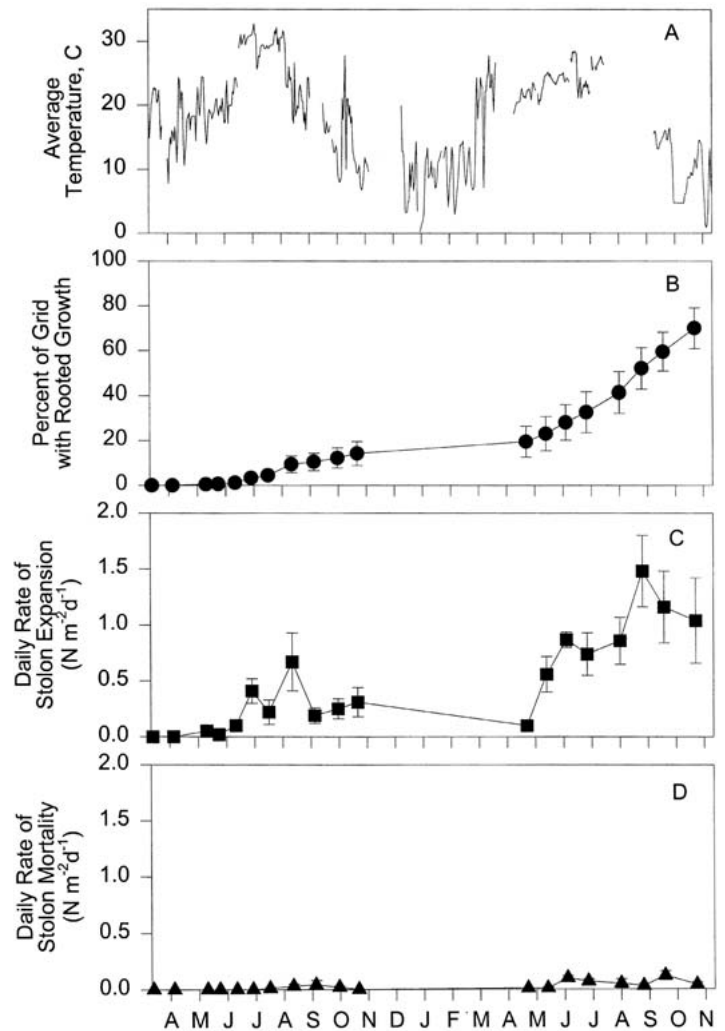

Figure 2. Stolon dynamics within the four experimental study pond areas. (A) Daily average water temperature during study period; (B) Percentage of sample areas vegetated by rooted growth; (C) Daily expansion rate of colonies by stolons; (D) Daily rate of stolon mortality.

tence was low with only one episode of persistence at the time of fragment settling. During November 1995, the persistence rate was 0.05 ± 0.04 N m^{-2} d^{-1} (Figure 3B). The mortality rate following the pulse of fragmentation was 0.02 N m^{-2} d^{-1} from October 1995 through May 1996 (Figure 3D). Establishment of fragments into rooted plants was observed between May and June 1996 when the rate of population expansion by fragments was 0.01 ± 0.01 N m^{-2} d^{-1} (Figure 3C).

Both hydrilla and Eurasian watermilfoil exhibit a peak in fragment settling during October and November. However, Eurasian watermilfoil fragments had a settling rate (or production rate) which was approximately 22 times greater, a persistence rate approximately 9 times greater, and an establishment rate which was approximately 67 times greater than hydrilla (Madsen and Smith 1997).

Data from this study of the spread of hydrilla and a similar study of the spread of Eurasian watermilfoil (Madsen and Smith 1997) delineate distinctive vegetative strategies utilized by these nuisance weeds when grown in southern states.
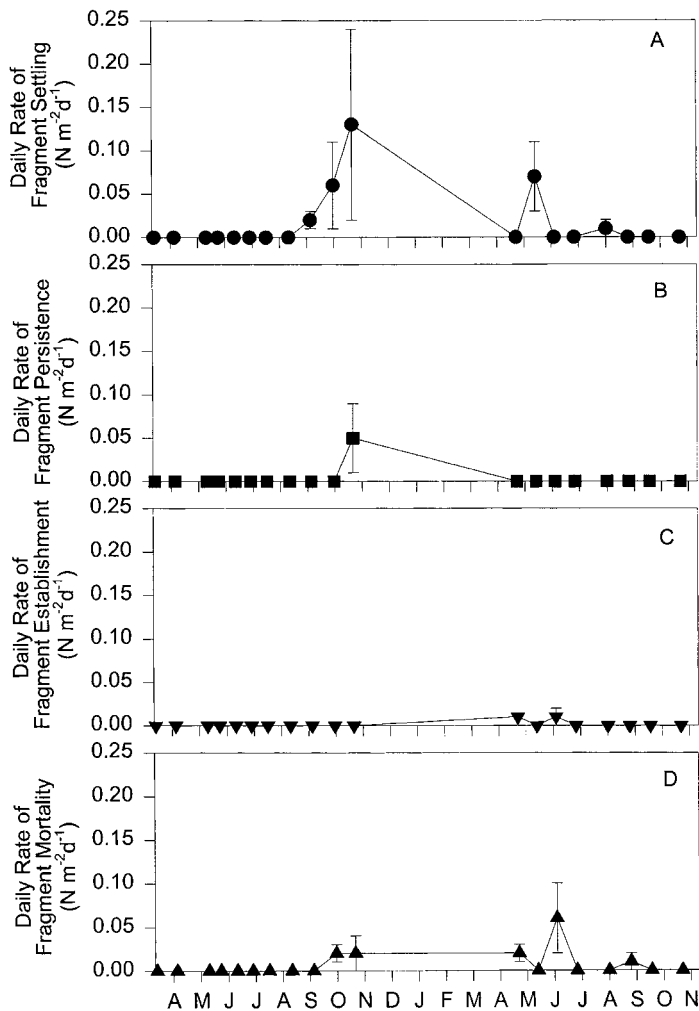
Figure 3. Fragment dynamics within the four experimental study pond areas. (A) Daily rate of fragment settling; (B) Daily rate of fragment persistence; (C) Daily rate of fragment establishment into rooted plant; (D) Daily rate of fragment mortality.

formation. Our observations indicate that turions are often formed on detached stems in Texas, as has been observed for dioecious hydrilla in Florida (Miller et al. 1993).

Hydrilla depends on stoloniferous growth for localized radial spread of a colony. In areas of relatively undisturbed environments, vegetative expansion by stolons abet the establishment of new ramets by transporting nutrients from parent plants; thereby reducing new ramet mortality (Grimes 1981). Production of subterranean tubers provides the species with a vegetative strategy for localized regrowth or revegetation after periods of high disturbance, such as drawdown or herbivory. Finally, vegetative strategies for intermediate distance dispersal (within and between connected waterbodies) are provided by the development of axillary turions and vegetative fragments which allow clones of the species to colonize areas further away from the rooted colony.

This study indicates that dioecious hydrilla is only spreading during the time of active growth, from June through November in Texas. The primary mechanism of spread in this study was through stolon growth. Few fragments were formed autochthonously. Therefore, other vectors of stem breakage, either through human activity or from wave action or water movement, are required to form large numbers of fragments. Therefore, the spread of dioecious hydrilla within a lake or river system may be reduced by reducing the level of human activity in areas infested with hydrilla. Hydrilla spread also exhibited a "lag phase" during the first year, in which little spread occurred. Hydrilla did not form a dense canopy on the surface during the first year, as well. Hydrilla populations in lakes and reservoirs may exhibit a lag phase in the initial year of introduction and establishment, during which the plants do not form a dense canopy or spread widely, and in the following year a large colony will then reach the surface, forming a dense canopy.

LITERATURE CITED

Bowes, G., A. S. Holaday, and W. T. Haller. 1979. Seasonal variation in the biomass, tuber density, and photosynthetic metabolism of *Hydrilla* in three Florida lakes. J. Aquat. Plant Manage. 17: 61-65.

Bowes, G., T. K. Van, L. A. Garrard, and W. T. Haller. 1977. Adaptation to low light levels by hydrilla. J. Aquat. Plant Manage. 15: 32-35.

Grimes, J. P. 1981. Plant strategies and vegetation processes. Wiley and Sons, New York, 222 pp.

Haller, W. T., J. L. Miller, and L. A. Garrand. 1976. Seasonal production and germination of hydrilla vegetative propagules. J. Aquat. Plant Manage. 14: 26-29.

Holaday, A. S. and G. Bowes. 1980. C4 acid metabolism and dark CO_2 fixation in a submersed aquatic macrophyte (*Hydrilla verticillata*). Plant Physiol. 65: 331-335.

Langeland, K. A. 1990. Hydrilla (*Hydrilla veritcillata* (L.F.) Royle) a continuing problem in Florida waters. University of Florida, circular 884, 21 pp.

Eurasian watermilfoil begins its growing season when water temperatures are low and vigorously grows to the surface, forming a mat which shades many species from required light. The spread of an Eurasian watermilfoil colony slows as water temperatures increase, in contrast to hydrilla which begins its active growth period when higher water temperatures prevail, growing rapidly to the surface and branching profusely. Hydrilla has low light and carbon dioxide compensation points, and is tolerant of high water temperatures and high oxygen concentrations. It is therefore capable of maintaining photosynthesis when many other submersed plants are photosynthetically inactive, which provides a competitive advantage for hydrilla (Bowes et al. 1977, Holaday and Bowes 1980, Langeland 1990). Once a surface mat is formed, hydrilla also shades other submersed species from light.

In this study, there were no disturbances to cause breakage of hydrilla stems (e.g., boat traffic, wave action, harvesting, or other physical injuries to plants). This not only reduced the production rate of hydrilla fragments in this study, but may have also reduced the rate of hydrilla turion

Langeland, K. A., and C. B. Smith. 1984. Hydrilla produces viable seed in North Carolina lakes—a mechanism for long distance dispersal. Aquatics 6(4): 20-21.

Langeland, K. A., and D. L. Sutton. 1980. Regrowth of hydrilla from axillary buds. J. Aquat. Plant Manage. 18: 27-29.

Les, D. H., J. Mehrhoff, M. A. Cleland, and J. D. Gabel. 1997. *Hydrilla verticillata* (Hydrocharitaceae) in Connecticut. J. Aquat. Plant Manage. 35: 10-14.

Madsen, J. D. 1997. Seasonal biomass and carbohydrate allocation in a southern population of Eurasian watermilfoil. J. Aquat. Plant Manage. 35:15-21.

Madsen, J. D., and C. S. Owens. 1998. Seasonal biomass and carbohydrate allocation in dioecious hydrilla. J. Aquat. Plant Manage. 36: 138-145.

Madsen, J. D., and D. H. Smith. 1997. Vegetative spread of Eurasian watermilfoil colonies. J. Aquat. Plant Manage. 35:63-68.

Miller, J. D., W. T. Haller, and M. S. Glenn. 1993. Turion production by dioecious hydrilla in north Florida. J. Aquat. Plant Manage. 31: 101-105.

Pieterse, A. H. 1981. *Hydrilla verticillata*–a review. Abstracts on Tropical Agriculture 7(6): 9-34.

Sculthrope, C. D. 1967. The biology of aquatic vascular plants. Arnold, London, 610 pp.

Smart, R. M., J. D. Madsen, J. R. Snow, G. O. Dick, and D. Honnell. 1995. Physical and environmental characteristics of experimental ponds at the Lewisville Aquatic Ecosystem Research Facility. Misc. Paper A-95-2, U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS, 22 pp.

Spencer D. F., and G. G. Ksander. 1991. Comparative growth and propagule production by *Hydrilla verticillata* grown from axillary turions or subterranean turions. Hydrobiologia 222: 153-158.

Steward, K. K., T. K. Van, V. Carter, and A. H. Pieterse. 1984. Hydrilla invades Washington, D.C. and the Potomac. Amer. J. Bot. 71: 162-163.

Sutton, D. L. 1996. Depletion of turions and tubers of *Hydrilla verticillata* in the North New River Canal, Florida. Aquat. Bot. 53: 121-130.

Sutton, D. L., and K. M. Portier. 1985. Density of tubers and turions of hydrilla in South Florida. J. Aquat. Plant Manage. 23: 64-67.

Van, T. K., and K. K. Steward. 1990. Longevity of monecious hydrilla propagules. J. Aquat. Plant Manage. 28: 74-76.