J. Aquat. Plant Manage. 36: 33-39

The Aquatic Macrophyte Seed Bank in Lake Onalaska, Wisconsin

D. G. MCFARLAND[1] AND S. J. ROGERS[2]

ABSTRACT

Submersed aquatic vegetation, dominated by *Vallisneria americana* Michx., declined dramatically in Lake Onalaska (Navigation Pool 7, on the Upper Mississippi River) following drought conditions in the late 1980s. Coinciding with the decline were marked increases in the abundance of *Myriophyllum spicatum* L., particularly in areas vacated by *V. americana*. Recent evidence indicates that much of the lake has remained unvegetated, but that since 1994, beds of *V. americana* have made a partial recovery. While the production of vegetative propagules may largely account for increases in populations of both species, the extent to which seed production may contribute to their expansion in the lake is unknown. To assess the germination potential and distribution of the aquatic macrophyte seed bank in Lake Onalaska, sediment cores (5 cm deep) were collected from 74 sampling sites in July 1996. Seedling emergence from sediments was observed in an environmental growth chamber operated at 25 C and a 14-hr photoperiod over a period of eight weeks. Fifteen species of aquatic macrophytes germinated in sediments from 55 sites. *V. americana* seedlings emerged from sediments from 36 sites throughout the lake, but were most prevalent in sediments collected within or downstream (within 250 m) of established *V. americana* beds. Seedlings of *M. spicatum* emerged from only two collected sediments that had supported this species in protected areas. These findings suggest that seed production may play a greater role in the dispersal of *V. americana* than *M. spicatum*, and further emphasize basic differences in their survival strategies, particularly in flowing water systems.

Key words: Aquatic plants, *Vallisneria americana*, *Myriophyllum spicatum*, sexual reproduction, germination.

INTRODUCTION

Sexual and asexual reproduction are the two fundamental means by which both terrestrial and aquatic macrophytes propagate (Sculthorpe 1967, Salisbury and Ross 1985). Because sexual reproduction provides genetic variation, it is considered the more advantageous mode in highly dynamic or heterogenous environments, such as those experienced mainly by terrestrial macrophytes. Conversely, asexual reproduction maintains genetic uniformity through cloning, and appears most effective in species adapted to relatively stable surroundings (Hartog 1970, Williams 1975, Grant 1981, Grace 1993, Philbrick and Les 1996). Despite differences that exist among aquatic systems, overall they tend to demonstrate greater chemical and thermal stability than terrestrial systems, and can function as temporary buffers against catastrophic events, e.g., dramatic shifts in temperature, flooding, fire, and wind storms (Sculthorpe 1967, Wetzel 1975, White et al. 1992, Philbrick and Les 1996). From an evolutionary standpoint, it is not surprising that asexual reproduction has become the dominant means of aquatic macrophyte population expansion. Yet, the abilities to flower and set seed have generally been retained even in the most clonal species of aquatic macrophytes (Sculthorpe 1967, Spencer and Bowes 1993).

The emphasis on asexual reproduction in aquatic macrophytes is reflected in their production of a variety of specialized vegetative propagules. Except for certain aquatic annual species in which reproduction is exclusively sexual, aquatic macrophytes are predominantly perennial (Sculthorpe 1967, Philbrick and Les 1996), producing such propagules as tubers, turions, corms, and stolons as a means of overwintering (Sculthorpe 1967, Hutchinson 1975, Grace 1993, van Vierssen 1993). In temperate species, these propagules are typically formed during short photoperiods of autumn; they remain dormant in the sediment throughout the winter, and germinate with warming temperatures of spring (Sculthorpe 1967, Hutchinson 1975, Grace 1993, van Vierssen 1993). During the growing season, lateral expansion of a population occurs vegetatively through rhizomes and stolons that root and form young plantlets at the nodes (Sculthorpe 1967, Grace 1993).

One of the most important mechanisms of long-distance dispersal is through stem fragmentation. However, the propensity for fragmentation varies substantially among macrophyte species with different growth forms. For example, the exotic species *M. spicatum* exhibits an elongated growth habit which concentrates much of the stem mass in the water column and especially on the water surface. Its long delicate stems are easily broken during senescence and can be widely distributed by water currents and wave action (Madsen et al. 1988). Unlike *M. spicatum*, germinable portions of the stem in the native species *V. americana* (i.e., stolons, rhizomes, tubers) are buried or anchored in sediment, and are less likely than stems of *M. spicatum* to be swept away by water movements. Notably, however, *V. americana* is well-adapted for water-mediated pollination (Korschgen and Green 1988) and has been observed to produce large numbers of fruits in established beds in the field (Korschgen and Green 1988; S. J. Rogers[2], pers. observ.). Thus, in sexually viable populations of this species, fruit and seed production may be the most effective mechanism of dispersal and colonization.

---

[1] US Army Engineer Waterways Experiment Station, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199.

[2] US Geological Survey, Environmental Management Technical Center, 575 Lester Avenue, Onalaska, WI 54650-8552. Received for publication October 3, 1997 and in revised form January 31, 1998.

Although seed banks of terrestrial and wetland species have been extensively studied (e.g., Major and Pyott 1966, Wein and Bliss 1973, Huiskes et al. 1995, Leck and Simpson 1995, Henry and Armoros 1996, van der Valk and Rosburg 1997, Westcott et al. 1997), few studies have examined the seed banks of submersed aquatic macrophytes (Haag 1983, Madsen et al. 1993, Kimber et al. 1995). This may be due in part to the fact that seeds of submersed macrophytes are quite small and are rarely observed to grow into mature plants in nature. Consequently, their role in population dynamics is largely overshadowed by that of vegetative propagules and often presumed to be minor. Yet, for certain species, as in *V. americana*, seed production may not only be the primary means of propagule dissemination, but an important source of propagule longevity. Despite the small size and little carbohydrate reserve in submersed macrophyte seeds, they appear to withstand adverse conditions and can remain viable for several years (Sculthorpe 1967). With these considerations, the availability of a viable seed bank could be crucial to the recovery of an aquatic plant community following a severe or prolonged habitat disturbance (e.g., drought or drawdown).

The need to investigate the aquatic macrophyte seed bank in Lake Onalaska, Wisconsin became evident following a widespread three-year drought that peaked in 1988. Over 1214 ha of submersed aquatic vegetation dominated by *V. americana* dramatically declined, and by 1990, less than 121 ha were estimated to remain (Rogers 1994, Kimber et al. 1995, Rogers et al. 1995). The loss of this species prompted concern over increasing populations of *M. spicatum*, a potentially nuisance species that had begun to colonize areas vacated by *V. americana*. The restoration of *V. americana* was favored because of its highly valued contributions to lake ecology (Rogers et al. 1995). Established stands of *V. americana* help to improve water quality by stabilizing sediments and filtering out suspended particles. Also, the rootstocks and winter buds of this species are an important food resource for canvasback ducks and other waterfowl (Korschgen and Green 1988, Korschgen et al. 1988).

In this article, we present results of an investigation of the germination potential and distribution of the seed bank of aquatic macrophytes in Lake Onalaska. The study was conducted jointly by the US Geological Survey (USGS), Onalaska, Wisconsin, and the Environmental Laboratory of the US Army Engineer Waterways Experiment Station (WES), Vicksburg, Mississippi. The specific objectives of the investigation were to: 1) examine seedbank diversity by identifying seedlings that emerge from sediments from different sampling locations, 2) compare densities of germinable seeds at different sediment depths, and 3) determine frequencies of species that germinate in the laboratory for comparison with frequencies of species observed in the field. The results are intended to provide insight into the role of seed banks in the recurrence and spread of aquatic macrophyte populations, with particular reference to *V. americana* and *M. spicatum.*

STUDY AREA

Lake Onalaska is a large (2,835-ha), irregularly-shaped impoundment located in the backwaters of the Upper Mississippi River System (UMRS, Figure 1). The lake is situated in the lower half of Navigation Pool 7, the region in the UMRS extending from Lock and Dam 6 near Trempealeau, Wisconsin downstream to Lock and Dam 7 near Dresback, Minnesota. Pool 7 was inundated by the US Army Corps of Engineers in 1937 and is operated to help maintain adequate depths for navigation in the river channel during periods of low-water flow (Chen and Simons 1986, Hendrickson and Hasse 1994[3]). West of the Mississippi River, Lake Onalaska is bordered by hills, bluffs, and scattered farmlands, and east of the river, by a narrow strip of marshlands and the city of Onalaska, Wisconsin (Korschgen et al. 1987; S. J. Rogers[2], pers. observ.). At normal full-pool elevation (195 m based on National Geodetic Vertical Datum, 1912 adjustment; NGVD), water depths in the lake range up to about 2.5 m, with a mean depth of 1.4 m (Korschgen et al. 1988, Hendrickson and Hasse 1994[3], Kimber et al. 1995). The Black River, the primary tributary, enters the lake directly from the north and east, and indirectly through a network of distributaries joined to the Mississippi River. Inflows from the Mississippi are received through seven secondary channels that cut through a long chain of barrior islands. The largest of these channels, Sommer's Chute, delivers up to 80% of the total input from the Mississippi River (Pavlou et al. 1982, Hendrickson and Haase 1994[3]). The outlet structure for Pool 7 has both surface and below-surface discharge ports; flood flows (in excess of 82,000 cfs) are allowed to pass with minimal blockage through vertical slide gates that can be lifted completely out of the water and an earthened fixed-crest spillway that can be overtopped (Sparks 1995). Lake levels are typically stable except during major floods because of the close proximity of the lake to Lock and Dam 7 and the associated spillway structure (Korschgen et al. 1988). Peak discharge rates (above 80,000 cfs) from Pool 7 usually occur during snowmelts of spring and decrease to an overall seasonal minimum (typically < 20,000 cfs) by late summer or fall (St. Paul District 1971[4], Hendrickson and Hasse 1994[3]). As rates of inflow to Pool 7 change, the water surface elevation at the dam is adjusted to 639 ft (195 m) NGVD, while elevations are allowed to vary at all other points in the pool (St. Paul District 1971[4]).

Lake Onalaska historically has been a productive lake, supporting an abundance of wildlife, sport fish and aquatic vegetation (Fleener 1975[5], Holzer and Ironside 1977[6], Rach and Meyer 1982, Mohlenbrock 1983[7], Korschgen et al. 1987 and 1988, Rogers 1994). An important feature of the lake is

---

[3] Hendrickson, J. S. and F. R. Haase. 1994. Dynamic conditions in the Black River Delta/Lake Onalaska area, Pool 7, Upper Mississippi River, 1980-81 and 1991-92. US Army Corps of Engineers, St. Paul District, St. Paul, MN 55101-1638.

[4] St. Paul District. 1971. Mississippi River Nine Foot Channel Navigation Project, Appendix 7, Lock and Dam No. 7, La Cresent, Minnesota. US Army Corps of Engineers, St. Paul, MN.

[5] Fleener, G. G. 1975. The 1972-1973 sport fishery survey of the Upper Mississippi River. Upper Mississippi River Conservation Committee, Rock Island, IL.

[6] Holzer, J. A. and S. J. Ironside. 1977. Basic lake inventory of Lake Onalaska, La Crosse, Wisconsin. Wisconsin Department of Natural Resources, La Crosse, WI.

[7] Mohlenbrock, R. H. 1983. Annotated bibliography of the aquatic macrophytes of the Upper Mississippi River covering the area from Cairo, Illinois to St. Paul, Minnesota. US Fish and Wildlife Service, Rock Island, IL.

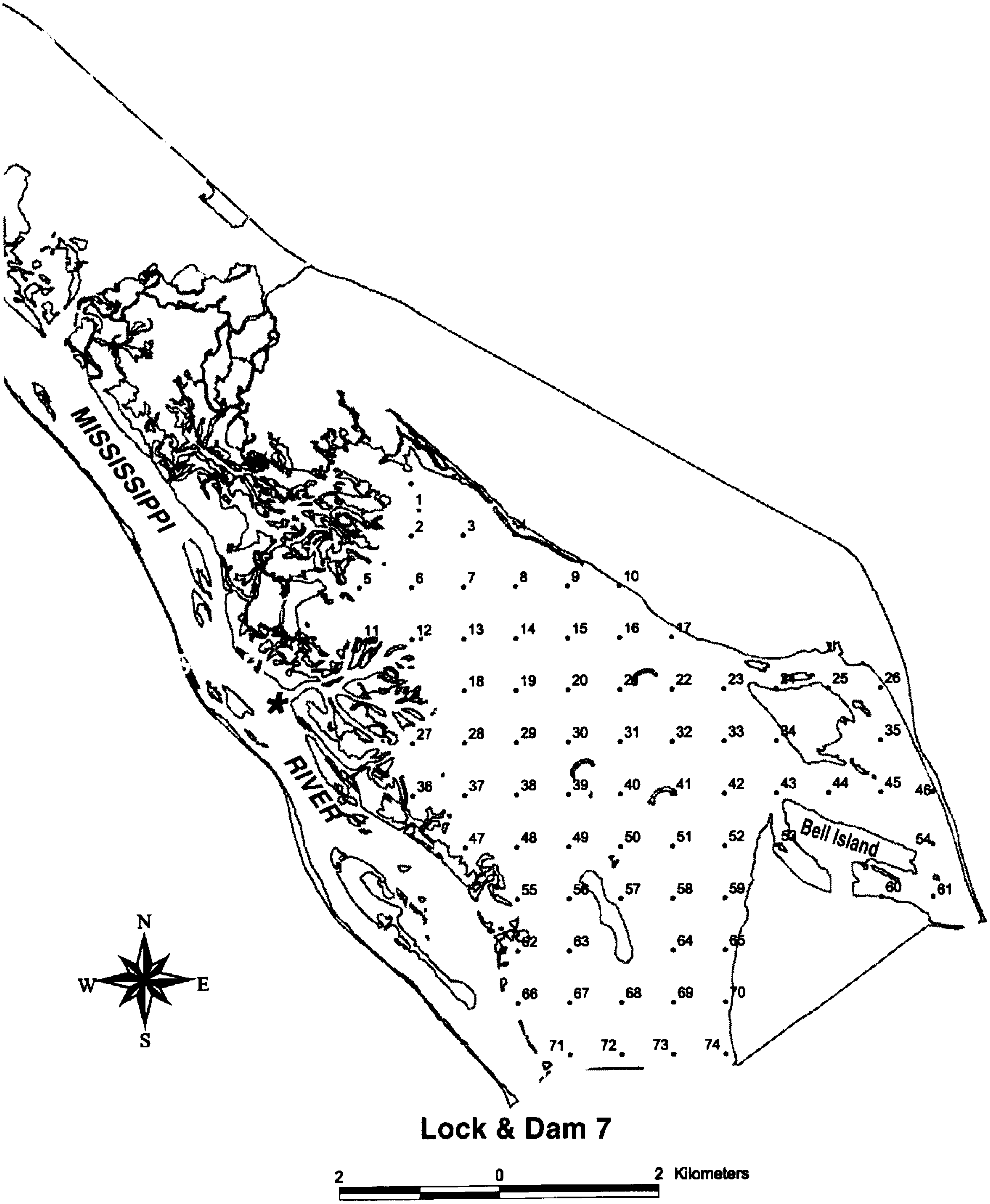

Figure 1. Lake Onalaska (Pool 7 of the Upper Mississippi River), Wisconsin with sampling site locations. Asterisk (*) indicates inlet of Sommer's Chute.

that it is managed as a wildlife refuge that serves as the staging ground for up to 75% of the world's canvasback duck population (Korschgen et al. 1988). The lake provides an extensive open water habitat with beds of aquatic macrophytes occurring mainly near the lake margins and island perimeters. Surveys of aquatic vegetation over a period from 1990 to 1996 indicate that at least 14 species of submersed aquatic macrophytes occurred in the lake (i.e., *V. americana*, *Heteranthera dubia* (Jacq.) MacM., *Potamogeton crispus* L., *Ceratophyllum demersum* L., *Najas flexilis* (Willd.) Rostk., *P. richardsonii* (Benn.) Rybd., *P. pectinatus* L., *P. foliosus* Raf., *Chara* sp., *Zannichellia palustris* L., *P. zosteriformis* Fernald, *Elodea canadensis* Rich. in Michx., *M. spicatum*, and *P. nodosus* Poiret) and that *V. americana* and *M. spicatum* were among the most common (Rogers 1994, USGS unpubl. data).

MATERIALS AND METHODS

In July 1996, sediments were collected by the USGS from 74 sampling sites (Figure 1). The positions of the sites were generated using a systematic sampling grid and located in the field with a Precision Lightweight GPS (Global Positioning System) unit. At each location, five sediment cores were obtained using a 10-cm diameter coring device, and sediment within the upper 5 cm of each core was retrieved. As the sediments were collected, they were divided equally into two 2.5-cm-deep sections. Shallow sections were selected to allow comparisons between sediment depths from which seedlings were most likely to emerge (cf. Hartleb et al. 1993). The upper sections of sediment were composited as were the lower sections to reduce sampling error associated with seed clumping (Bigwood and Inouye 1988). Afterwards, the composites were sifted by hand to remove unwanted debris (e.g., rocks and twigs) and any asexual propagules (e.g., fragments, tubers, and turions). When sediment collection was completed, there were 148 (≈ 980-ml) composites: 74 each from the upper (0 to 2.5 cm) and lower (2.5 to 5.0 cm) sediment sections. These composites were placed separately in gallon-sized Zip-loc bags, and shipped in coolers to WES within five days.

At WES, the composites were established in plastic planting containers and observed under controlled environmental conditions for seedling emergence. The containers (20 cm × 20 cm × 8 cm deep) were each filled with 600 ml of a single well-mixed composite spread evenly to depth of 1.5 cm. Standard culture solution (described below) was then poured into each flat, producing a 6-cm-deep water column overlaying the sediment. A clear Plexiglas lid was placed on top of each container to help reduce evaporative losses. Prepared containers were aligned on benches in an environmental growth chamber operated to maintain a 14-hr photoperiod, at 350 $\mu E \cdot m^{-2} \cdot s^{-1}$ PAR (photosynthetically active radiation), and a constant temperature of 25 C. Assessments of seedling emergence were based on direct counts and recorded at weekly intervals over a period of eight weeks. A detailed description of the growth chamber and ancillary equipment is presented by Barko and Smart (1980 and 1981).

The low alkalinity culture solution that was used in the study was prepared according to Smart and Barko (1985). This solution, formulated with reagent-grade salts and deionized-distilled water, provides major cations (Na^+ = 16.0, K^+ = 6.0, Ca^{+2} = 25.0, and Mg^{+2} = 6.8 $mg \cdot L^{-1}$) and anions (Cl^- = 44.2, HCO_3^- = 51.8, and SO_4^{-2} = 26.9 $mg \cdot L^{-1}$) but lacks N and P, specifically omitted to reduce algal growth. Upon preparation, the solution had a pH of 7.9 and an electrical conductivity of 278 $\mu S \cdot cm^{-1}$ at 25 C. A single air line per container provided filtered-humidified air to enhance mixing and air/water CO_2 exchange. The solution was replaced at least twice weekly to minimize cloudiness from transplanting and invertebrate activity.

Approximately two weeks after emergence, individual seedlings were transplanted using procedures similar to those for aquatic plant cultures (Smart and Barko 1985). The tiny seedlings were gently uprooted from their original culture flats and planted singly in sediment contained in 300-ml plastic cups. The sediment that was used was collected from Brown's Lake, WES and was amended with nitrogen by adding 0.8 g $NH_4Cl \cdot L^{-1}$ wet sediment. Physical and chemical characteristics of this substrate are presented by McFarland and Barko (1987) and McFarland et al. (1992). When planted, a thin layer of washed builder's sand was placed over the sediment surface and the cups were submersed in culture solution in 200-L fiberglass tanks. The seedlings were grown under chamber conditions for at least four weeks after transplanting to allow ample time for plant development needed for species identification. The identifications here are based on descriptions of plant morphology provided by Fernald (1970), Fassett (1975), and Godfrey and Wooten (1979 and 1981).

Data from this study were analyzed using analysis of variance (ANOVA) and post-ANOVA procedures of the Statistical Analysis System (SAS Institute, Inc. 1991). The general linear model (GLM) procedure was applied in cases involving unequal sample sizes. Tests of normality were performed using the Shapiro-Wilk statistic; homogenity of variance was evaluated using the Levene's test. Separation of means was accomplished as appropriate using Duncan's multiple range test or Fisher's LSD (Least Significant Difference) Test. Hereafter, statements of statistical significance without precise indication of probability level refer to $P \leq 5\%$.

RESULTS AND DISCUSSION

A total of 15 aquatic plant species, representing a variety of growth forms, emerged from sediments from 55 of the 74 sampling sites (Table 1). Among these, ten species were submersed (i.e., *V. americana*, *N. flexilis*, *H. dubia*, *P. foliosus*, *P. crispus*, *M. spicatum*, *P. richardsonii*, *C. demersum*, *Chara* sp. and *Nitella* sp.), three were emergent (i.e., *Sagittaria latifolia* Willd., *Lindernia dubia* (L.) Pennell, and *Sparganium eurycarpum* Engelm.), and two were free-floating aquatic plants (i.e., *Lemna minor* L. and *Spirodela polyrhiza* (L.) Schleiden). The emergence of seedlings continued over the entire eight weeks of the study, but there was little increase in the number of seedlings beyond six weeks. Seedlings of *S. latifolia*, *P. crispus*, *H. dubia*, and *N. flexilis* began appearing within the first week of study initiation, while *V. americana* and *M. spicatum* seedlings took nearly two weeks or more to emerge. The most widespread species was *V. americana*, occurring in sediments from 36 sites. *C. demersum* was the rarest species, occurring in samples from only one site. The number of seedlings (or sporelings) of each species did not vary significantly

TABLE 1. AQUATIC PLANT SPECIES GERMINATED IN SEDIMENTS FROM LAKE ONALASKA, WISCONSIN.

Species	No. of Sites	Estimated Density
Vallisneria americana Michx.	36	36.2 (4.6)
Sagittaria latifolia Willd.	25	56.8 (13.4)
Lindernia dubia (L.) Pennell	22	54.4 (11.6)
Najas flexilis (Willd.) Rostk.	11	17.9 (3.6)
Sparganium eurycarpum Engelm.	10	30.2 (7.9)
Chara sp.	10	40.8 (14.1)
Heteranthera dubia (Jacq.) MacM.	9	20.4 (4.4)
Potamogeton foliosus Raf.	6	32.9 (12.6)
Nitella sp.	5	28.9 (9.7)
Potamogeton crispus L.	5	21.0 (3.2)
Lemna minor L.	4	44.0 (12.2)
Spirodela polyrhiza (L.) Schleiden	4	26.3 (7.6)
Myriophyllum spicatum L.	2	19.7 (6.6)
Potamogeton richardsonii (Benn.) Rybd.	2	19.7 (6.6)
Ceratophyllum demersum L.	1	13.1 (0.0)

*Density = no. of seedlings (or sporelings)/m^2. Values are means (± 1 std. err.), where n = no. of sites.

between sediment depths ($P > 0.05$); therefore, the results presented here are based on calculations where data for upper and lower sediment sections were combined.

Figure 2 presents a synopsis of seedling emergence from sediments from the 74 sampling sites. Within each subfigure, the sites are categorized according to position within a 250-m radius of the center of an established plant bed. This information was derived using point data provided by the USGS indicating the positions of aquatic plant beds in Lake Onalaska in 1996. According to those determinations, 31 sampling sites were located in open areas (i.e., outside the set 250-m radius), and of the remaining 43 sampling sites, 16 were situated in the center of a plant bed, 13 were generally south, and 14 generally north of a vegetated area (Figure 2A). The percentage of sites that showed germination was greatest in sites located either in the middle or downstream (south) of established vegetation (Figure 2B); those same sites also demonstrated significantly higher densities of seedlings ($P < 0.05$) and numbers of species ($P < 0.05$) than sites in the other two categories (Figures 2C and 2D). A similar trend was apparent when the distribution of *V. americana* seedlings was considered (not shown). Densities of *V. americana* seedlings taken from the center or south of a *V. americana* bed (31.4 and 40.7 seedlings/m^2, respectively) were significantly greater than those taken from open areas or upstream of a *V. americana* bed (14.4 and 6.6/m^2 for sites, respectively). Maps of water movements in Lake Onalaska show a prevailing southward flow pattern in the lake (USGS unpubl. data), coinciding with the observed southward drift and deposition of seeds relative to plant bed location.

Although 30 sampling sites were located in the vicinity of *M. spicatum* beds, sediments from only two sites showed emergence of *M. spicatum* (Table 1). Interestingly, the two sites (60 and 61) occurred in protected areas that had supported stands of this species near Bell Island (Figure 1). On-site observations by the USGS indicated a typical absence of flowering and seed set in *M. spicatum* since at least 1991 (S. J. Rogers[2], pers. observ.). Restricted sexual reproduction appears to have had little impact on *M. spicatum*'s occurrence as it was relatively common in Lake Onalaska according to 1996 surveys (USGS unpubl. data). The scarcity of its seedlings in the present study, along with previous USGS data, suggest that: 1) seed production and dispersal may be of minor importance to the spread of *M. spicatum* in Lake Onalaska, and that 2) the capacity of *M. spicatum* to develop a substantial seed bank in the lake appears minimal compared to that of *V. americana.*

Numerous studies have reported moderate to high rates of germination in seeds of *V. americana* (Muenscher 1936, Kimber et al. 1995) and *M. spicatum* (Patten 1955, Coble and Vance 1987, Madsen and Boylen 1988[8], Hartleb et al. 1993). However, few have demonstrated the growth of seedlings of these species under favorable conditions after emergence. Although early attempts to grow seedlings of *M. spicatum* in the laboratory failed to produce healthy plants (Anonymous 1981[9]), subsequent efforts of McDougall (1983[10]) suggested that *M. spicatum* seedlings could achieve a mature size (Hartleb et al. 1993). Additionally, Titus and Hoover (1991) reported that seedlings of *V. americana* transplanted in Otsego Lake accrued a substantial mean of 1.9 g dry mass and 6.3 rosettes ($n = 16$) in less than 16 weeks. In the present study, seedlings of most species grew better than expected and had to be transferred (singly) from cups into larger (3-L) sediment containers. Twelve weeks after the initial transplanting, seedlings of *M. spicatum* had reached 188.1 (± 22.3) cm in height (mean ± 1 std. err., $n = 3$) and 10.7 (± 1.2) g total dry mass. Over approximately the same growth period, seedlings of *V. americana* reached a height of 91.9 (± 6.8) cm and a total dry mass of 17.3 ± 1.3 g ($n = 6$). These were not the only species to demonstrate such capacities. Seedlings of *P. crispus*, *P. foliosus*, *P. richardsonii*, *S. latifolia*, *L. dubia*, and *H. dubia* all demonstrated substantial growth subsequent to transplanting.

Given the potential for submersed macrophyte seedlings to accrue significant amounts of biomass, it is important to understand mechanisms that affect their establishment and survival. A variety of environmental factors such as water movements, sedimentation, competition, and grazing undoubtedly limit seedling growth *in situ.* Moreover, the environmental tolerances of newly-emerged seedlings are probably narrower than those of established plants, and in nature, their survival may be severely restricted by suboptimal conditions that might exist (Smith et al. 1991). Nevertheless, the fact that a forbidding array of limitations may be imposed on seedlings *in situ* does not eliminate altogether the prospects for successful seedling establishment. One of the clearest examples is apparent in Lake Onalaska where over the past four years submersed annuals including *P. folio-*

---

[8] Madsen, J. D. and C. W. Boylen. 1988. Seed ecology of Eurasian watermilfoil (*Myriophyllum spicatum* L.). Rensselaer Fresh Water Institute Report 88-7. Rensselaer Polytechnic Institute, Troy, NY.

[9] Anonymous. 1981. A Summary of Biological Research on Eurasian water milfoil in British Columbia. Information Bulletin. British Columbia Ministeries of Environment, Aquatic Studies Branch.

[10] McDougall, I. A. 1983. A study of the germination potential in *Myriophyllum spicatum* L. seeds. Studies on Aquatic Macrophytes Part XXIV. Province of British Columbia Ministry of Environment, Water Management Branch, Victoria.

[11] Korschgen, C. E. US Geological Survey, Upper Mississippi River Science Center, P.O. Box 818, La Crosse, WI 54602-0818.

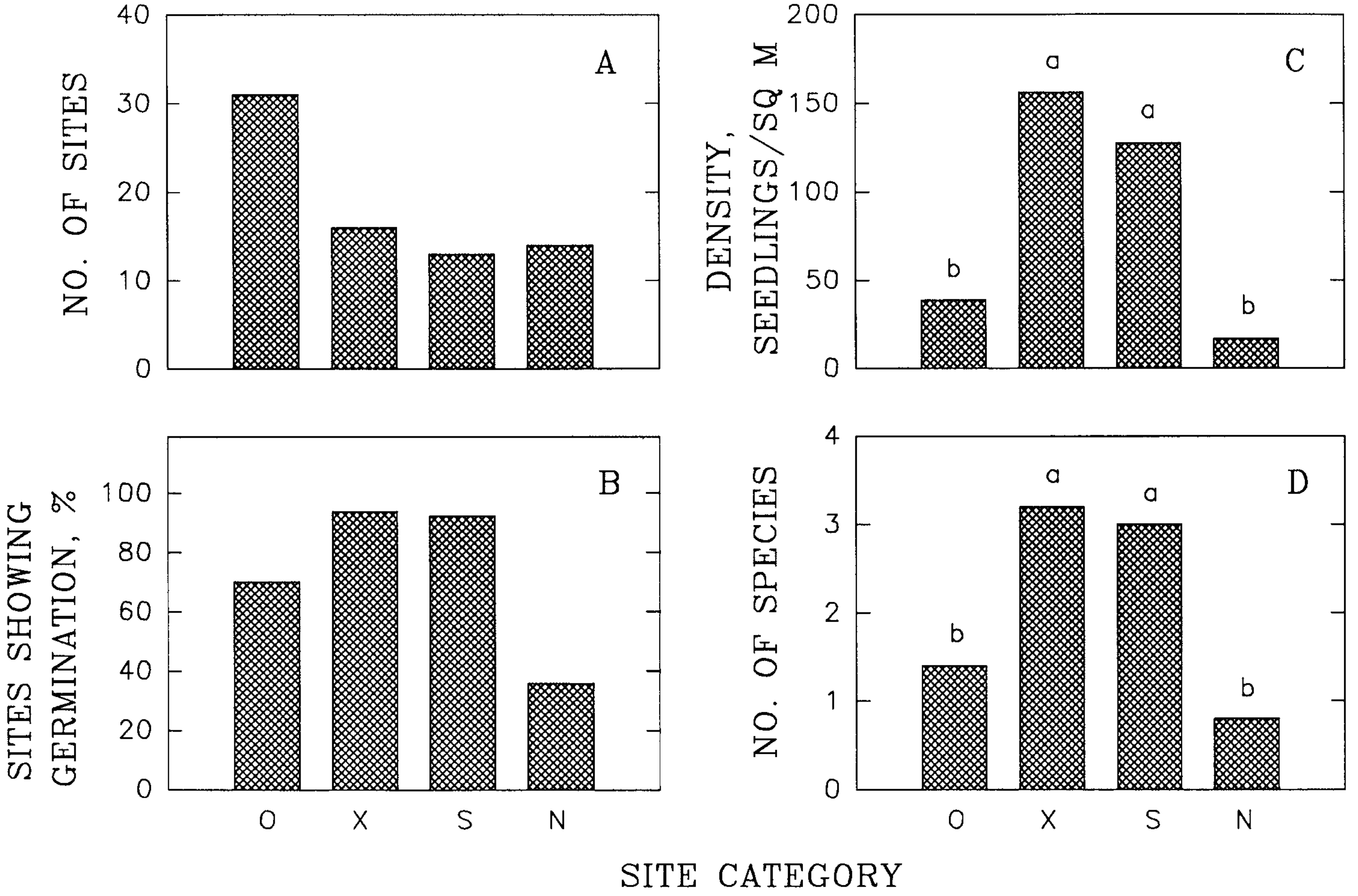

Figure 2. Number of sites (A), percentage of sites showing germination (B), seedling density (C), and number of species (D) in different site categories ('O' indicates sites in open areas; 'X,' sites in the center of a plant bed; 'S,' sites south or downstream of a plant bed; 'N,' sites north or upstream of a plant bed). Within subfigures C and D, means sharing the same letter (in lower case) do not differ at the 5% level of significance according to Fisher's Least Significant Difference Test.

sus, *N. flexilis*, and *H. dubia* have been increasing in abundance (USGS unpubl. data). Furthermore, young plants of *V. americana* with seed coats still attached have been observed growing in slow-flow areas of Lake Onalaska (Korschgen and Green 1988, Kimber et al. 1995; S. J. Rogers[2], pers. observ., C. E. Korschgen[11], pers. comm.). Kimber et al. (1995) also speculated that seedlings were the source of *V. americana* beds where they had been absent for five years or more. These observations and ours concerning the potential for seedling growth, suggest that the role of seed banks in vegetation recovery may be greater than previously surmised. Further studies of environmental influences on the growth of submersed macrophyte seedlings would be useful in assessing relative production potential of seedlings under site-specific conditions.

ACKNOWLEDGMENTS

The authors gratefully acknowledge Ms. Mary McGregor and Mr. Frank A. Boyd for their technical efforts in the setup, maintenance, and take-down of this study. Mr. Shawn Weick of the USGS is also acknowledged for his help in sample collection and processing, and for his assistance in the field. Our appreciation is extended to Mr. Dennis Brandon for his guidance in performing statistical analyses, and to Dr. Victor A. McFarland for a preliminary review of portions of this manuscript. Funding in support of this research was provided by the US Army Engineer Aquatic Plant Control Research Program and the Long Term Resource Monitoring Program for the Upper Mississippi River. Permission to publish this information was granted by the Chief of Engineers.

LITERATURE CITED

Barko, J. W. and R. M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biol. 10: 229-238.

Barko, J. W. and R. M. Smart. 1981. Sediment-based nutrition of submersed macrophytes. Aquat. Bot. 10: 339-352.

Bigwood, D. W. and D. W. Inouye. 1988. Spatial pattern analysis of seed banks: an improved method and optimized sampling. Ecology 69: 497-507.

Chen, Y. H. and D. B. Simons. 1986. Hydrology, hydraulics, and geomorphology of the Upper Mississippi River System. Hydrobiologia 136: 5-20.

Coble, T. A. and B. D. Vance. 1987. Seed germination in *Myriophyllum spicatum* L. J. Aquat. Plant Manage. 25: 8-10.

Fassett, N. C. 1975. A Manual of Aquatic Plants. University of Wisconsin Press, Madison, WI. 405 pp.

Fernald, M. L. 1970. Gray's Manual of Botany. D. van Nostrand Company, New York, NY. 1632 pp.

Godfrey, R. K. and J. W. Wooten. 1979. Aquatic and Wetland Plants of Southeastern United States: Monocotyledons. University of Georgia Press, Athens, GA. 712 pp.

Godfrey, R. K. and J. W. Wooten. 1981. Aquatic and Wetland Plants of Southeastern United States: Dicotyledons. University of Georgia Press, Athens, GA. 933 pp.

Grace, J. B. 1993. Adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. Aquat. Bot. 44: 159-180.

Grant, V. 1981. Plant Speciation. Columbia University Press, New York, NY. 563 pp.

Haag, R. W. 1983. Emergence of seedlings of aquatic macrophytes from lake sediments. Can. J. Bot. 61: 148-156.

Hartleb, C. F., J. D. Madsen, and C. W. Boylen. 1993. Environmental factors affecting seed germination in *Myriophyllum spicatum* L. Aquat. Bot. 45: 15-25.

Hartog, C. Den. 1970. The seagrasses of the world. Verh. K. Ned. Akad. Wetensch. Afd. Natuurk. 59: 5-257.

Henry, C. P. and C. Amoros. 1996. Are the banks a source of recolonization after disturbance: an experiment on aquatic vegetation in a former channel of the Rhone River. Hydrobiologia 330: 151-162.

Huiskes, A. H. L., B. P. Koutstaal, P. M. J. Herman, W. G. Beeftink, M. M. Markusse, and W. De Munck. 1995. Seed dispersal of halophytes in tidal salt marshes. J. Ecol. 83: 559-567.

Hutchinson, G. E. 1975. A Treatise on Limnology. Vol. 3: Limnological Botany. John Wiley and Sons, New York, NY. 660 pp.

Kimber, A., C. E. Korschgen, and A. G. van der Valk. 1995. The distribution of *Vallisneria americana* seeds and seedling light requirements in the Upper Mississippi River. Can. J. Bot. 73: 1966-1973.

Korschgen, C. E., L. S. George, and W. L. Green. 1988. Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River. In: Weller, M. W., ed. Waterfowl in Winter. University of Minnesota Press, Minneapolis, MN, pp. 237-249.

Korschgen, C. E. and W. L. Green. 1988. American wildcelery (*Vallisneria americana*): ecological considerations for restoration. US Fish and Wildlife Service, Technical Report 19, US Department of the Interior, Washington, DC. 24 pp.

Korschgen, C. E., G. A. Jackson, L. F. Muessig, and D. C. Southworth. 1987. Sedimentation in Lake Onalaska, Navigation Pool 7, Upper Mississippi River, since impoundment. Water Resour. Bull. 23: 221-226.

Leck, M. A. and R. L. Simpson. 1995. Ten-year seed bank and vegetation dynamics of a tidal freshwater marsh. Amer. J. Bot. 82: 1547-1557.

Madsen, J. D., L. W. Eichler, and C. W. Boylen. 1988. Vegetative spread of Eurasian watermilfoil in Lake George, New York. J. Aquat. Plant Manage. 26: 47-50.

Madsen, J. D., R. M. Smart, L. W. Eichler, C. W. Boylen, J. W. Sutherland, and J. A. Bloomfield. 1993. Submersed littoral vegetation distribution: field quantification and experimental analysis of sediment types from Onondaga Lake, New York. Technical Report A-93-14, US Army Engineer Waterways Experiment Station, Vicksburg, MS. 50 pp.

Major, J. and W. T. Pyott. 1966. Buried viable seeds in two California bunchgrass sites and their bearing on the definition of a flora. Vegetatio 13: 253-282.

McFarland, D. G. and J. W. Barko. 1987. Effects of temperature and sediment type on growth and morphology of monoecious and dioecious *Hydrilla*. J. Freshwat. Ecol. 4: 245-252.

McFarland, D. G., J. W. Barko, and N. J. McCreary. 1992. Effects of sediment fertility and initial plant density on growth of *Hydrilla verticillata* (L.f.) Royle and *Potamogeton nodosus* Poiret. J. Freshwat. Ecol. 7: 191-200.

Muenscher, W. C. 1936. Storage and Germination of Seeds of Aquatic Plants. Bulletin 652. Cornell University Agricultural Station, Ithaca, NY. 17 pp.

Patten, B. C. 1955. Germination of the seed of *Myriophyllum spicatum* L. in a New Jersey lake. Bull. Torrey Bot. Club 83: 5-18.

Pavlou, S. P., W. G. Hines, and W. Hom. 1982. The development of a diagnostic model of PCB transport, distribution and fate in Pool 7, Upper Mississippi River. Vol. 1. Hydrology and sediment transport. Columbia National Fishery Research Laboratory, Fish and Wildlife Service, US Department of the Interior, Columbia, MO. 73 pp.

Philbrick, C. T. and D. H. Les. 1996. Evolution of aquatic angiosperm reproductive systems. BioScience 46: 813-826.

Rach, J. J. and F. P. Meyer. 1982. Winter harvest of bluegills in 1976-1977 from Lake Onalaska, Wisconsin. N. Amer. J. Fish. Manage. 2: 28-32.

Rogers, S. J. 1994. Preliminary evaluation of submersed macrophyte changes in the Upper Mississippi River. Lake and Reserv. Manage. 10: 35-38.

Rogers, S. J., D. G. McFarland, and J. W. Barko. 1995. Evaluation of the growth of *Vallisneria americana* Michx. in relation to sediment nutrient availability. Lake and Reserv. Manage. 11: 57-66.

Salisbury, F. B. and C. W. Ross. 1985. Plant Physiology. Wadsworth Publishing Company, Belmont, CA. 540 pp.

SAS Institute, Inc. 1991. SAS/STAT Release 6.03 Edition. Cary, NC. 1028 pp.

Sculthorpe, C. D. 1967. The Biology of Aquatic Vascular Plants. Edward Arnold (Publishers) Ltd., London. 610 pp.

Smart, R. M. and J. W. Barko. 1985. Laboratory culture of submersed freshwater macrophytes on natural sediments. Aquat. Bot. 21: 251-263.

Smith, C. S., J. W. Barko, and D. G. McFarland. 1991. Ecological considerations in the management of Eurasian watermilfoil in Lake Minnetonka, Minnesota. Technical Report A-91-3, US Army Engineer Waterways Experiment Station, Vicksburg, MS. 49 pp.

Sparks, R. E. 1995. Need for ecosystem management of large rivers and their floodplains. BioScience 45: 168-182.

Spencer, W. and G. Bowes. 1993. Ecophysiology of the world's most troublesome aquatic weeds. In: Pieterse, A. J. and K. J. Murphy, eds. Aquatic Weeds: The Ecology and Management of Nuisance Aquatic Vegetation. Oxford University Press, New York, NY, pp. 39-73.

Titus, J. E. and D. T. Hoover. 1991. Toward predicting reproductive success in submersed freshwater angiosperms. Aquat. Bot. 41: 111-136.

van der Valk, A. G. and T. R. Rosburg. 1997. Seed bank composition along a phosphorus gradient in the northern Florida Everglades. Wetlands 17: 228-236.

van Vierssen, W. 1993. Relationships between survival strategies of aquatic weeds and control measures. In: Pieterse, A. J. and K. J. Murphy, eds. Aquatic Weeds: The Ecology and Management of Nuisance Aquatic Vegetation. Oxford University Press, New York, NY, pp. 238-253.

Wein, R. W. and L. C. Bliss. 1973. Changes in Arctic *Eriophorum* tussock communities following fire. Ecology 54: 845-852.

Westcott, K., T. H. Whillans, and M. G. Fox. 1997. Viability and abundance of seeds of submerged macrophytes in the sediment of disturbed and reference shoreline marshes in Lake Ontario. Can. J. Bot. 75: 451-456.

Wetzel, R. G. 1975. Limnology. Saunders College Publishing, Fort Worth, TX. 767 pp.

White, I. D., D. N. Mottershead, and S. J. Harrison. 1992. Environmental Systems. Chapman and Hall, New York, NY. 616 pp.

Williams, G. C. 1975. Sex and Evolution. Princeton University Press, Princeton, NJ. 200 pp.