# The distribution of *Vallisneria americana* seeds and seedling light requirements in the Upper Mississippi River

**Anne Kimber, Carl E. Korschgen, and Arnold G. van der Valk**

**Abstract**: *Vallisneria americana* declined in backwaters of the Upper Mississippi River, U.S.A., after a drought in 1988. To determine whether viable seeds of *V. americana* occurred in the seed bank of navigation pool 7, Lake Onalaska, the upper 5 cm of sediment was collected from 103 sites in May 1990. These sediment samples were kept in pots at a depth of 0.4, 0.8, and 1.2 m in an outdoor pond for 12 weeks. *Vallisneria americana* seeds germinated from sites throughout the lake, and some seedlings produced overwintering buds by the end of the study. Seeds, spores, or fragments of 12 other species of aquatic plants also germinated. Seed germination trials with fresh and stored seeds in both greenhouse and ponds in which light availability was reduced with shade cloths indicated that seed germination was insensitive to light level. To determine the light requirements for seedling survival and bud production, sediment from Lake Onalaska was incubated in ponds under neutral density shade screens reducing light to 2, 5, 9, and 25% of full sun. Seeds germinated under all shade treatments but survival was significantly higher in the 9 and 25% light treatments, and bud production was restricted to these light levels.

*Key words*: aquatic macrophytes, seeds, germination, light response.

**Résumé** : La *Valisneria americana* a dépéri dans les eaux en amont de la partie supérieure de la rivière Mississippi, aux États-Unis, à la suite d'une sécheresse en 1988. Afin de déterminer si des graines viables de la *V. americana* se retrouvent dans les banques de graines du bassin de navigation 7, au lac Analaska, les auteurs ont récolté les 5 cm supérieurs des sédiments sur 103 sites, en mai 1990. Ces échantillons de sédiment ont été conservés dans des pots, à des profondeurs de 0,4, 0,8 et 1,2 m, dans un bassin extérieur, pendant 12 semaines. Les graines de la *V. americana* provenant de sites distribués tout autour du lac ont germé et quelques plantules ont produit des bourgeons d'hivernement, vers la fin de l'étude. Les graines, les spores et les fragments de 12 autres espèces de plantes aquatiques ont également germé. Des essais de germination de graines, sur des graines fraîches ou conservées, conduites en serre ou en bassin, avec une luminosité réduite par une ombrière en tissus, indiquent que la germination des graines est insensible à la lumière. Afin de déterminer les besoins en lumière pour la survie des plantules et la production des bourgeons, des sédiments du lac Onalaska ont été incubés dans des bassins sous des ombrières à densité neutre réduisant la lumière à 2, 5, 9 et 25% de la pleine lumière solaire. Les graines ont germé sous tous les traitements d'ombrage mais la survie a été significativement plus élevée avec des traitements de lumière situés entre 9 et 25% de la pleine lumière, et les bourgeons ne se sont formés qu'avec ces intensités lumineuses.

*Mots clés* : macrophytes aquatiques, graines, germination, réaction à la lumière.
[Traduit par la rédaction]

## Introduction

Studies of submersed aquatic plant populations generally conclude that these populations appear to be maintained by clonal reproduction and growth from overwintering buds, with little recruitment from seed banks (Sculthorpe 1967; Rogers and Breen 1980; Haag 1983; Kautsky 1990). Although flowering and seed set commonly occur in *Vallisneria americana* populations, seedlings appear to be rare in nature in temperate zones (V. Carter, personal communication; Titus and Hoover 1991). Nevertheless, seed banks may be important for the reestablishment of submersed vegetation that was eradicated by overgrazing, disease, or adverse environmental conditions. This could be analogous to the role of the seed bank in prairie wetlands for reestablishing extirpated emergent species during a drawdown (van der Valk and Davis 1978). The success of revegetation from the seed bank would depend on the abundance and viability of seeds of different species and on their physiological growth requirements.

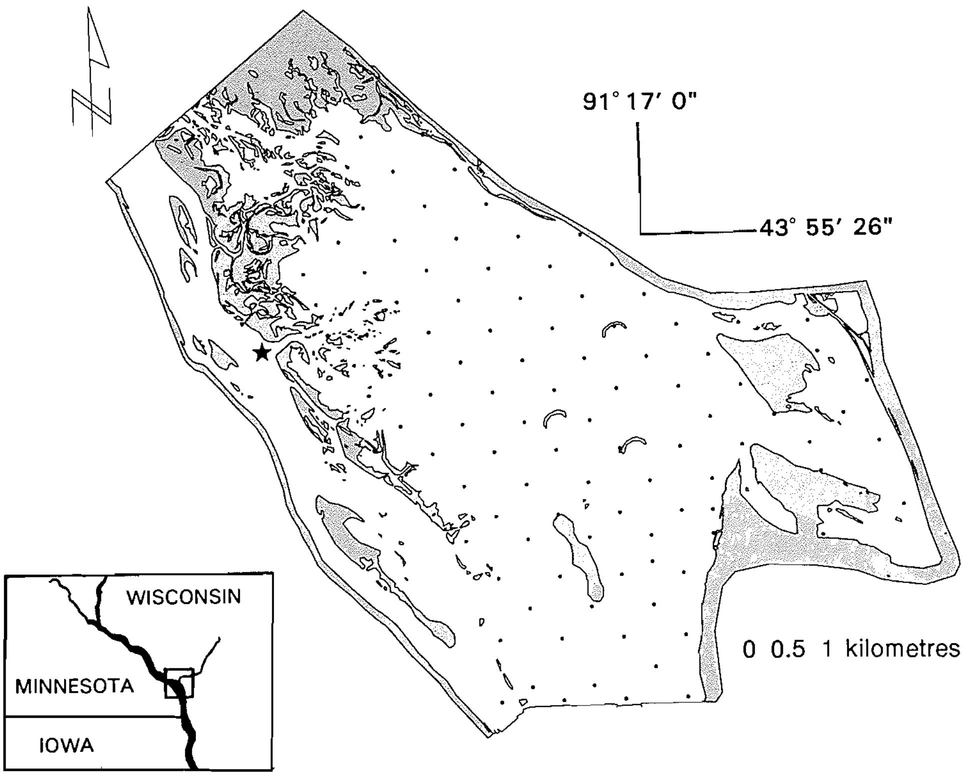
Unlike the positive- or neutral-buoyant seeds and fruits of

Received March 8, 1995.

**A. Kimber[1] and A.G. van der Valk.** Botany Department, Iowa State University, Ames, IA 50011, U.S.A.
**C.E. Korschgen.** National Biological Service, Upper Mississippi Science Center, P.O. Box 818, La Crosse, WI 54601, U.S.A.

[1] Author to whom all correspondence should be addressed.

**Fig. 1.** Lake Onalaska, navigation pool 7 of the Upper Mississippi River, showing seed-bank sampling grid. ★, location of Sommer's chute.




emergent aquatic vegetation, *Vallisneria* seeds and fruits are negatively buoyant, sinking to the sediment surface (McAtee 1917; Kaul 1978; Wilder 1974; Davis 1985). This implies that seed densities should be greatest in areas where adult plant densities are highest. Fruits may also be dispersed by water currents when plants are uprooted, by water fowl (Korschgen and Green 1988) because diving water fowl will consume fruits (McAtee 1917; Sculthorpe 1967), and possibly by fish as shown for *Najas* (Agami and Waisel 1988) since the crude protein content of fruits is high (Donnermeyer 1982). Seeds may secondarily be dispersed as bed-load transport in rivers, but the extent to which this occurs is unknown.

Although some physiological information is available about seed germination requirements and seedling growth of aquatic plants under laboratory conditions, i.e., Muenscher (1936), van Wijk (1989), recruitment, growth, and spread are not well understood and published studies give differing results. For example, Muenscher (1936) reported that seeds of *V. americana*, *Najas flexilis*, *Potamogeton* spp., *Heteranthera dubia* (now *Zosterella dubia*), and *Sagittaria* died if dried. However, Choudhuri (1966) reported that seeds of *Vallisneria spiralis*, which appeared to behave as an annual in monsoonal wetlands, germinated after drying.

Populations of *Vallisneria* declined in navigation pools 5–19 of the Upper Mississippi River after the summer of 1988, during which record low flows and high water temperatures were recorded (U.S. Army Corps of Engineers, unpublished data, Sullivan 1991). This native plant species, especially its overwintering buds, was highly valued in the backwater wildlife refuges along the Upper Mississippi River that were staging grounds for as much as 75% of the global canvasback duck population (Korschgen et al. 1987*a*). Its loss raised a number of questions related to the potential rate of recolonization of backwater habitats by native versus introduced species (especially the Eurasian watermilfoil *Myriophyllum spicatum*), e.g., what is the effective dispersal unit for submersed aquatic plants in rivers, what is the potential role of seed banks in recolonization, and what are the physiological requirements for seedlings to survive and produce overwintering buds?

To address these questions we developed three studies. In the first, sediment was sampled to determine the distribution and density of seeds of *Vallisneria* and of other submersed aquatic species. In the second, *Vallisneria* seed germination under several shade regimes was compared in greenhouse and pond settings to determine whether light levels affected germination. In the third, seedlings germinating from the seed bank were grown under replicated shade treatments to determine seasonal light requirements for production of overwintering buds.

## Methods

### Study area

Navigation pool 7, Lake Onalaska, was chosen for these studies because of its historical importance as a staging area for canvasback ducks and because long-term monitoring studies of *V. americana* populations (Korschgen and Green 1988; C.E. Korschgen, unpublished data) enabled comparisons between previous *Vallisneria* populations and the current distribution of the seed bank.

The lake (Fig. 1) is a large (2858 ha), shallow (mean depth 1.43 m) backwater area of the Upper Mississippi

River, inundated in 1937 during the construction of a 9-foot (2.7 m) navigation channel and associated locks and dams (Korschgen et al. 1987*b*). Water flows into the lake through two chutes from the Mississippi River channel running along the west side of the lake; from the southern chute, Sommer's chute, the lake may receive up to 80% of its water (Pavlou et al. 1982). From the north and the east, Black River water enters the lake. During 1990–1992 the following submersed species were observed in the lake: *Ceratophyllum demersum*, *Chara*, *Elodea canadensis*, *M. spicatum*, *N. flexilis*, *Potamogeton crispus*, *Potamogeton foliosus*, *Potamogeton natans*, *Potamogeton pectinatus*, *Potamogeton richardsonii*, *Potamogeton zosteriformis*, *V. americana*, and *Z. dubia*.

### Seed-bank study

From May 28 to June 1, 1990, sediment cores were collected at 103 uniformly spaced grid points in Lake Onalaska (Fig. 1). A LORAN positioning system was used to locate sites previously mapped using a grid system developed by Korschgen et al. (1987*b*). To increase the precision of seedling density estimates from sediments in which seed distribution was likely to be clumped (Bigwood and Inouye 1988), five cores were collected at each site using a 10-cm diameter clear PVC coring device. All but the top 5 cm of core was discarded and the cores were composited. The total volume collected per site was 2 L. Depth and all aquatic plant species present were recorded at each site. After roots, turions, and buds were removed, the cores were mixed and separated into three equal samples, and each sample was placed in a bucket (266 $cm^2$ surface area) that was then placed in an outdoor concrete pond (4.9 × 9.5 m, mean depth 1.1 m) at depths of 0.4, 0.8, or 1.2 m. Depths were chosen to determine whether germination was affected by light availability. The pond was located at the National Biological Service Upper Mississippi River Science Center, on an island between the Mississippi and Black Rivers, near La Crosse, Wisc. Pond water came from a shallow (23 m deep) Black River aquifer.

Germination, considered to be the appearance of leaves, was monitored every 2 weeks until seedlings were harvested at the end of August. This seedling assay method provided an estimate of the viable seeds present in the seed bank (the ecologically active portion of the seed bank; Haag 1983) but did not provide information about the total numbers of seeds of species present. Depths of sampling points, species distributions, and seed densities were mapped using a GIS system (ARC-INFO, version 6.1, 1992) on a digital base map provided by the National Biological Service Environmental Management Technical Center, La Crosse, Wis. Sampled depths were divided into increments of 0.25 m above the shallowest depth of 0.5 m or less. The distribution of seedlings was analyzed using a two-factor nested analysis of variance (SAS Institute Inc. 1987) to determine if species' seedling distributions were random or were significantly affected by depth and by location at any given depth.

### Light requirements for seed germination

*Vallisneria* fruits were collected in October 1990 and stored wet for 1 month at 4°C in a cold room. Seeds were washed from the fruits, sorted, and counted into lots of 20 using a dissecting microscope. Seeds were sown on sterilized sand in 0.5-L opaque plastic cups that were then filled with distilled water and either uncapped (full light), capped with black plastic shade cloth screens rated to reduce terrestrial light by 63, 80, or 92%, or covered with black plastic (dark). Cups were arranged on a greenhouse bench in two Latin Squares of six rows and columns each to control for position effects (12 replicates of each shade treatment). Natural light was augmented by metal halide lamps with a 14 h light : 10 h dark photoperiod. Seedlings were counted 3 weeks after planting. Instantaneous light levels in the cups under each treatment were measured in place using a LiCor underwater quantum sensor (LiCor Corp., Lincoln, Neb.).

To examine the responses of overwintering seeds, fruits that had not been used for the greenhouse study were stored wet at 4°C until April 1991. Forty seeds each were sown in buckets on washed sand in outdoor concrete ponds 1 m deep, in randomized blocks of cells 1 $m^2$ with no shade cloth, or under 63, 80, or 92% shade screens. Germination (appearance of leaves) was counted after 6 weeks.

### Effects of light on seedling growth and bud production

Seedling emergence and seedling bud production were monitored as part of a 1992 study on the seasonal light requirements for plants to reproduce from overwintering buds (Kimber 1994). Sediment was collected in mid-April 1992 from Lake Onalaska from an area of a former *Vallisneria* bed. It was mixed and placed in buckets in two concrete ponds (4.9 × 9.5 m) at the National Biological Service Upper Mississippi River Science Center in La Crosse, Wis. Each pond ranged in depth from 0.9 to 1.1 m. Two submersible pumps in each pond circulated and aerated water such that the turnover rate was once every 2.5 days. Five buckets of lake sediment and 5 buckets of sand-amended lake sediment (4 parts sand to 1 part lake sediment), each bucket having 1 L of sediment, were placed in each of 48 shade cells (24 cells in each of two ponds), that were arranged in rows (randomized blocks) of four shade treatments each. Each cell (surface area 1 × 1 m) was isolated from the next by black plastic side walls that extended down to approximately 20 cm from the bottom of the ponds. The bottom was left free to increase water flow between cells and decrease temperature differences between light treatments. The tops of the cells were covered with removable frames having no shade cloth (open cell) or 63, 80, or 92% shade screens.

Terrestrial and underwater light was monitored continuously using LiCor quantum sensors. Estimates of the percentage of terrestrial light reaching the sediment surface in each light treatment were made for the period May 13 (emergence of leaves from overwintering buds) to October 13 (senescence and final harvest of plants grown from buds). In the open cells 25% of terrestrial light was transmitted to the sediment surface. Under the 63% shade screen, 9% of terrestrial light was transmitted, under the 80% shade screen 5% of terrestrial light was transmitted, and under the 92% shade screen 2% of terrestrial light was transmitted (Kimber 1994).

The experiment was planted on April 26. On June 24, all buckets were observed and seedling emergence recorded. Six harvests of seedlings were made over the growing season. During the summer buckets were removed, alternating between even-numbered and odd-numbered replicate cells so that at each harvest plants from 12 cells were collected. For the last two harvests (September 23 and October 12) plants

**Table 1.** Aquatic seedling species composition from Lake Onalaska.

| Species | No. of sites | Density[a] Mean | Density[a] SD | $P^b$ Depth | $P^b$ Latitude |
|---|---|---|---|---|---|
| *Ceratophyllum demersum* | 14 | 32.12 | 43.00 | 0.0001 | 0.0238 |
| *Chara* spp. | 26 | 46.12 | 69.62 | 0.0002 | 0.0509 |
| *Elodea canadensis* | 5 | 120.00 | 93.00 | 0.0002 | 0.0007 |
| *Myriophyllum spicatum* | 16 | 18.75 | 13.75 | 0.0038 | 0.0339 |
| *Najas flexilis* | 46 | 32.62 | 30.00 | 0.7675 | 0.5280 |
| *Pontederia cordata* | 7 | 12.50 | 0 | 0.0053 | 0.0002 |
| *Potamogeton crispus*[c] | 15 | 200.88 | 241.62 | 0.6965 | 0.4777 |
| *Potamogeton foliosus* | 24 | 12.50 | 0 | 0.0659 | 0.6721 |
| *Potamogeton pectinatus* | 3 | 12.50 | 0 | 0.0180 | 0.0422 |
| *Sagittaria* spp. | 13 | 39.38 | 37.12 | 0.0001 | 0.0001 |
| *Vallisneria americana* | 62 | 36.75 | 27.25 | 0.5396 | 0.4560 |
| *Zosterella dubia* | 25 | 17.50 | 8.12 | 0.4011 | 0.2304 |

**Note:** Sites could not be determined for *Lemna minor*.
[a]Density (plants/m$^2$) for sites where species were present.
[b]$P$-values were determined using a nested analysis of variance. Depth was the main effect; latitude was nested within depth.
[c]From fragments.

**Fig. 2.** The distribution of depths for sampled sites in Lake Onalaska.

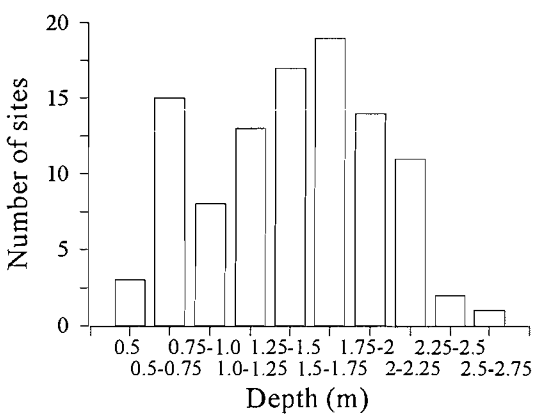



**Table 2.** Germination of *Vallisneria* seeds as a function of light availability.

| Treatment | Midday light ($\mu$mol · m$^{-2}$ · s$^{-1}$) $N$ | Mean | SD | % germination Mean[a] | SD |
|---|---|---|---|---|---|
| 25% light (open cell) | 12 | 228 | 104 | 37*a* | 24 |
| 9% light (63% shade) | 12 | 75 | 28 | 39*a* | 28 |
| 5% light (80% shade) | 12 | 48 | 22 | 48*a* | 23 |
| 2% light (92% shade) | 12 | 11 | 5 | 30*a* | 26 |
| Dark | 12 | 0 | 0 | 68*b* | 27 |

[a]Student's $t$-test, $P$ = 0.05. Means with the same letter are not significantly different from each other.

were harvested from all cells (24 replicates). At harvest the number of seedlings of each species present was recorded for each bucket. For each *Vallisneria* seedling, the presence of winter buds were recorded. Data were analyzed statistically by one-way analysis of variance for unequal sample sizes (GLM procedures, SAS Institute Inc. 1987). Student's $t$-test was used to determine significant differences among means (SAS Institute Inc. 1987).

## Results

### Seed-bank study

The depth at which buckets containing seeds were placed had no effect on germination or seedling survival; the analyses presented here are based on the number of seedlings or sporelings found of each species at a site, pooled for all three buckets. Seeds generally had germinated by 6 weeks after the experiment started. Seedlings were found in 90 of the 103 sites sampled (Table 1), consisting of species of rooted submersed, floating submersed, emergent, and floating plants. *Vallisneria americana* was the most common and widespread species (Fig. 2), present in 62 of the sites, followed by *N. flexilis*). Seedlings of *Potamogeton pectinatus* were the rarest encountered in this survey.

A mean depth of 1.35 m was calculated for the sampled locations. Most sites were between 0.5 and 2.0 m deep, and changes in depth were gradual (Fig. 2). The total number of species that occurred at a given depth declined slightly beyond 1.75 m (Fig. 3), but individual species' distribution was not consistently affected by depth (Table 1).

Species that occurred at 24 or more sites (*Najas*, *Potamogeton crispus*, *Potamogeton foliosus*, *Vallisneria*, and *Zosterella*) had random distributions (Fig. 3), reflected in high $P$-values for depth and for location within depth (Table 1), with the exception of *Chara*, which occurred in 26 sites but with a consistently greater percent occurrence at depths less than 1.25 m (Fig. 3). Seedlings that were less common (*Ceratophyllum*, *Elodea*, *Myriophyllum*, *Pontederia*, *Potamogeton pectinatus*, *Sagittaria*) typically had significantly low $P$-values (less than 0.05) for both depth and location.

*Vallisneria*, *Zosterella*, and *Potamogeton foliosus* seedlings had the widest distribution, being found in all depth classes at which seedlings were found (Fig. 3). In contrast, viable seedlings of *Ceratophyllum* and *Potamogeton pectinatus*

**Fig. 3.** The distribution of species with depth in Lake Onalaska. The percent occurrence is the number of sites in which a species was found divided by the total number of sites in the depth class, multiplied by 100.

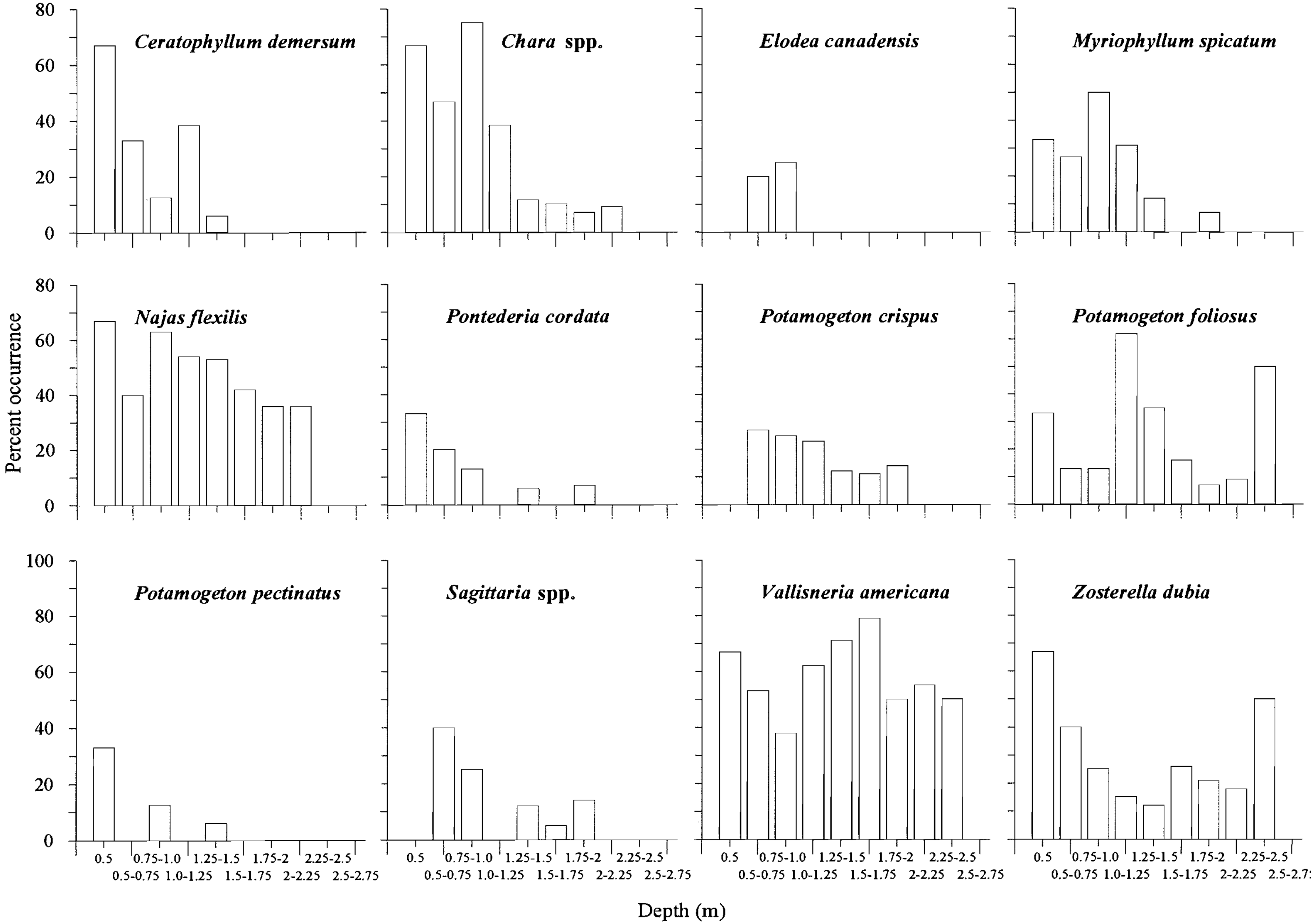


**Table 3.** Seed-bank germination and survival dynamics (total seed bank).

| *N* | Harvest date | Initial census[a] | Harvest[b] New | Survived | Total | No. of *Vallisneria* seedlings |
|---|---|---|---|---|---|---|
| | | **25% light (open cell)** | | | | |
| 12 | 30 June | 5 | 1 | 2 | 3 | 2 |
| 12 | 27 July | 6 | 4 | 3 | 7 | 2 |
| 12 | 15 Aug. | 4 | 2 | 2 | 4 | 3 |
| 12 | 29 Aug. | 1 | 6 | 0 | 6 | 1 |
| 24 | 23 Sept. | 6 | 18 | 4 | 22 | 17 |
| 24 | 13 Oct. | 12 | 5 | 8 | 13 | 10 |
| Mean[c] | | 0.354*a* | | | | |
| | | **9% light (63% shade)** | | | | |
| 12 | 30 June | 0 | 3 | 0 | 3 | 3 |
| 12 | 27 July | 4 | 2 | 2 | 4 | 2 |
| 12 | 15 Aug. | 2 | 4 | 2 | 6 | 3 |
| 12 | 29 Aug. | 9 | 5 | 1 | 6 | 3 |
| 24 | 23 Sept. | 4 | 12 | 1 | 13 | 10 |
| 24 | 13 Oct. | 4 | 15 | 1 | 16 | 12 |
| Mean[c] | | 0.240*a* | | | | |
| | | **5% light (80% shade)** | | | | |
| 12 | 30 June | 0 | 2 | 0 | 2 | 2 |
| 12 | 27 July | 3 | 4 | 1 | 5 | 4 |
| 12 | 15 Aug. | 3 | 3 | 1 | 4 | 4 |
| 12 | 29 Aug. | 5 | 4 | 0 | 4 | 4 |
| 24 | 23 Sept. | 12 | 12 | 5 | 17 | 7 |
| 24 | 13 Oct. | 5 | 7 | 5 | 12 | 7 |
| Mean[c] | | 0.292*a* | | | | |
| | | **2% light (92% shade)** | | | | |
| 12 | 30 June | 1 | 2 | 0 | 2 | 1 |
| 12 | 27 July | 4 | 1 | 2 | 3 | 1 |
| 12 | 15 Aug. | 2 | 2 | 1 | 3 | 3 |
| 12 | 29 Aug. | 2 | 0 | 0 | 0 | 0 |
| 24 | 23 Sept. | 5 | 8 | 2 | 10 | 7 |
| 24 | 13 Oct. | 3 | 2 | 0 | 2 | 2 |
| Mean[c] | | 0.177*b* | | | | |

**Note:** The percent of terrestrial light is that received at the sediment surface, averaged over the period May 13 to October 13.

[a]Numbers of seedlings found in each treatment, counted in each bucket on June 24.

[b]On each harvest date after the initial census, seedlings were counted in harvested buckets of both sediment treatments.

[c]Mean: percentage of buckets with seedlings of all species. Means with the same letter are not significantly different (Student's *t*-test, $P = 0.05$).

were found only at depths less than 1.5, and *Elodea* seedlings were found only at depths less than 1.0 m. *Pontederia* seedlings appeared to be restricted to emergent community locations: six of the seven sites where *Pontederia* seedlings were found were in *Typha*, *Sagittaria*, or *Pontederia* beds. *Sagittaria* seedlings were not restricted to the same degree: beds of emergents were present at only 5 of the 12 sites where seedlings were found. The number of species was high in three regions of the lake: the shallow emergent beds fringing inflows at Sommer's chute, sites north of Sommer's chute receiving inflows from the Mississippi River and the Black River, and shallow sites along the eastern shore of the lake.

**Table 4.** *Vallisneria* seedling survival and bud production as a function of light availability, September 23 census.

| Treatment | *N* | Mean[a] | % seedlings with buds |
|---|---|---|---|
| 25% light (open cell) | 12 | 1.000*a* | 33.3 |
| 9% light (63% shade) | 12 | 0.583*ab* | 25.0 |
| 5% light (80% shade) | 12 | 0.250*b* | 0 |
| 2% light (92% shade) | 12 | 0.167*b* | 0 |

[a]The mean represents the fraction of total buckets that contained seedlings. Means with the same letter are not significantly different (Student's *t*-test, $P = 0.05$).

### Light requirements for seed germination

Seeds germinated in all treatments in the greenhouse study (Table 2). The percentage of germination was not different among any of the light treatments but was significantly higher in the dark treatment. Seeds from the same source also germinated in all treatments in the outdoor pond experiment conducted the following spring with stored seeds. The percentage of germination ranged from 19% in the 63% shade treatment to 49% in the 80% shade treatment, and there was no significant effect of shading on seedling germination.

### Effects of light on seedling growth and bud production

As observed during the earlier seed bank survey, seedlings in this experiment germinated approximately 6 weeks after the experiment was initiated. Seedling germination for all species, observed for all buckets on June 24, was not significantly affected by the three higher light treatments imposed (Table 3) but was significantly lower in the 2% light treatment.

In subsequent harvests, new seedlings appeared that had not been observed in the June 24 census (Table 3), indicating that seeds continued to germinate throughout the summer and especially towards the end of the summer (note September 23 and October 13 harvests). In spite of new recruitment, overall numbers of *Vallisneria* seedlings at the end of the summer were dependent on light availability (Tables 3 and 4). The mean numbers of seedlings from the open and 63% shade treatments (25 and 9% light treatments, respectively) as measured on September 23 were higher than the numbers of seedlings found in the June 24 census for the same light treatments (Table 3) and were also higher than the September 23 harvests of seedlings in the 80 and 92% shade treatments (5 and 2% light availability, respectively). Seedlings that grew in 9 and 25% light availability also produced buds (Table 4); no buds were found in seedlings growing in 5 and 2% light. Bud production by *Vallisneria* seedlings was also observed in the 1990 seed bank study. In both studies, seedlings produced single, short rosettes of four to eight leaves (typical length 5 cm) and after growing to that stage, stored net photosynthate in belowground overwintering buds (mean fresh mass, 0.07 g). *Sagittaria* seedlings, which resemble those of *Vallisneria*, also produced single, short rosettes and buds by the end of the seed-bank study. In addition, *Chara* produced oospores, *Najas* flowered and set seed, and *Zosterella* did not flower but did produce corms.

## Discussion

The seed bank did not reflect the composition of the vegetation within the lake. Extensive beds of *Potamogeton pectinatus* were observed in the lake in 1991 and 1992, but it was the rarest species in the seed bank. Similarly, no seedlings of *Potamogeton richardsonii* and *Potamogeton zosteriformis* were found, even though adult plants have been observed in the lake (Sohmer 1975; personal observation). In a study of Lake Wabamun, Haag (1983) found the species in the adult population were rare in the germinating seed bank and attributed the lack of germination to strong dormancy or a long time requirement for germination.

The number of species was higher in the sandy sediments of areas found either in the northern part of the lake, close to the eastern shore, or near Sommer's chute. Sandy sediments are associated with stronger currents or with greater exposure or wave action (Keddy 1982). Seeds may be carried into these areas, especially the area near Sommer's chute, from the main channel of the Mississippi River or the Black River. Total species distribution patterns also reflected the previous distribution of adult *Vallisneria* beds (C.E. Korschgen, unpublished data), indicating that the beds may trap seeds or other propagules of other species. The lower species diversity in the central and southern portions of Lake Onalaska may be explained by depth limitations for some species. Alternatively, seedlings may be less viable because of sedimentation occurring in the middle of Lake Onalaska (Korschgen et al. 1987*b*). Hartleb et al. (1993) reported that seeds of *M. spicatum* had lower percentages of germination when buried by more than 2 cm of sediment.

In this study, seeds of *Vallisneria* collected in the fall and seeds collected in the fall and stored at 4°C for 7 months both germinated readily and were not affected by light levels. These results are similar to those reported by Muenscher (1936), in which *Vallisneria*, stored either at 1–3°C in the dark or at 18–20°C in diffuse light, germinated regardless of treatment, in contrast with many of the other species examined. This may imply that *Vallisneria* has no inherent dormancy or germination requirements.

Muenscher (1936) also reported that *Vallisneria* had higher rates of germination when protected from direct sunlight. Results showing the insensitivity of *Vallisneria* seed germination to light availability and greater germination in darkness are similar to the responses of *Najas marina* (Forsberg 1965; Agami and Waisel 1984); *N. marina* had greater germination in darkness than at any light level. In contrast, Choudhuri (1966) reported 89% germination of *V. spiralis* seeds in an alternating light–dark regime compared with 10% germination in continuous darkness.

Survival, growth, and reproduction of seedlings were significantly greater in treatments with at least 9% of surface light availability over the growing season. These light requirements are the same as those for plants grown from buds (Kimber 1994) and are in agreement with field studies in the Potomac River that indicate that minimal seasonal light availability of 10% is necessary for *Vallisneria* clonal reproduction (Carter and Rybicki 1990). Light levels in Lake Onalaska were monitored during the summer of 1990 (Owens 1993) and indicate that the depth for 10% light availability was less than 0.5 m. In the seed-bank study, three sites were less than 0.5 m and *Vallisneria* occurred at two of those locations. Based on the results of this study, the viable *Vallisneria* seedlings present in shallows should be able to survive and produce overwintering buds. While production of overwintering buds by seedlings of *Vallisneria* may provide a mechanism for re-establishment of populations after disturbance, the extent and frequency to which this occurs is mostly unknown. However, in 1994 we found extensive beds of *Vallisneria* in Lake Onalaska that developed after the lake flooded in 1993 and occurred in locations where plants had been absent the previous 5 years. Plants in these locations could have developed from overwintering buds, if buds were transported with flood waters. Alternatively, populations could have developed from seedlings that germinated and established in the spring of 1994, when there was a period of lower than average rainfall and higher water clarity (J.F. Sullivan, unpublished data). In August 1994 we found plants with seed coats still attached, and it appears that the widespread recolonization of Lake Onalaska was due, at least in part, from seedling establishment.

Another apparent establishment of *Vallisneria* from seed was observed in Toledo Bend Reservoir on the Texas–Louisiana border. This reservoir is populated by the southern ecotype of *Vallisneria*, which is an evergreen perennial and never produces winter buds (Smart and Dorman 1993). Nevertheless, new populations quickly appeared in portions of the reservoir where they had previously not occurred. The presence of several small beds of *Vallisneria*, composed of young, small plants, was observed along northeast-facing shorelines immediately south of a large, well-established population. These beds appear to be in areas and depths where winter storms could windrow seeds and may indicate establishment of populations from seedlings (R. Doyle, personal communication). These observations from Wisconsin and Texas indicate that recolonization from seed banks may be more common than previously thought.

## Acknowledgments

This study was funded by the U.S. National Biological Service, Environmental Management Technical Center, Onalaska, Wis. Jeff Janvrin, Wisconsin Department of Natural Resources, helped collect seed bank cores. John Sullivan, Wisconsin Department of Natural Resources, graciously provided unpublished water quality data. Robert Doyle, Corps of Engineers Lewisville Aquatic Plant Research Program, Lewisville, Tex., kindly provided information on *Vallisneria* populations in the Toledo Bend Reservoir. Jim Majure and his staff at the Geographic Information Systems Laboratory at Iowa State University assisted with contour maps of seedling distribution. An anonymous reviewer provided valuable comments on an earlier draft of this manuscript.

## References

Agami, M., and Waisel, Y. 1984. Germination of *Najas marina* L. Aquat. Bot. **19**: 37–44.

Agami, M., and Waisel, Y. 1988. The role of fish in distribution and germination of seeds of the submerged macrophytes *Najas marina* L. and *Ruppia maritima* L. Oecologia, **76**: 83–88.

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

Carter, V., and Rybicki, N.B. 1990. Light attenuation and submersed macrophyte distribution in the tidal Potomac river and estuary. Estuaries, **13**: 441–452.

Choudhuri, G.N. 1966. Seed germination and flowering in *Vallisneria spiralis*. Northwest Sci. **40**: 31–35.

Davis, F.W. 1985. Historical changes in submerged macrophyte communities of Upper Chesapeake Bay. Ecology, **66**: 981–993.

Donnermeyer, G.N. 1982. The quantity and nutritive quality of *Vallisneria americana* biomass, in Navigation Pool 9 of the Upper Mississippi River. M.S. thesis, Biology Department, University of Wisconsin, La Crosse, Wis.

Forsberg, C. 1965. Sterile germination of oospores of *Chara* and seeds of *Najas marina*. Physiol. Plant. **18**: 128–137.

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

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

Kaul, R.B. 1978. Morphology of germination and establishment of aquatic seedlings in Alismataceae and Hydrocharitaceae. Aquat. Bot. **5**: 139–147.

Kautsky, L. 1990. Seed and tuber banks of aquatic macrophytes in the Askö area, northern Baltic proper. Holarct. Ecol. **13**: 143–148.

Keddy, P.A. 1982. Quantifying within-lake gradients of wave energy: Interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquat. Bot. **14**: 41–58.

Kimber, A. 1994. Decline and restoration of *Vallisneria americana* from the Upper Mississippi River. Ph.D. dissertation, Iowa State University, Ames, Iowa.

Korschgen, C.E. and Green, W.L. 1988. American wild celery (*Vallisneria americana*): ecological considerations for restoration. U.S. Fish Wildl. Serv. Fish Wildl. Tech. Rep. 19.

Korschgen, C.E., George, L.S., and Green, W.L. 1987*a*. Feeding ecology of canvasbacks staging on Pool 7 of the Upper Mississippi River. *In* Waterfowl in winter. *Edited by* M.W. Weller. University of Minnesota Press, Minneapolis, Minn. pp. 237–249.

Korschgen, C.E., Jackson, G.A., Muessig, L.F., and Southworth, D.C. 1987*b*. Sedimentation in Lake Onalaska, navigation pool 7, upper Mississippi River, since impoundment. Water Resour. Bull. **23**: 221–226.

McAtee, W.L. 1917. Propagation of wild-duck foods. USDA Bull. No. 465.

Muenscher, W.C. 1936. Storage and germination of seeds of aquatic plants. Cornell Univ. Agric. Exp. Stn. Bull. No. 652.

Owens, J.L. 1993. Determination of light availability and primary production in an Upper Mississippi River backwater using a continuous water quality monitor. M.S. thesis, Botany Department, Iowa State University, Ames, Iowa.

Pavlou, S.P., Hines, W.G., and Hom, W. 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. Available from the Columbia National Fishery Research Laboratory Fish and Wildlife Service, U.S. Department of the Interior, Route 1, Columbia, Mo.

Rogers, K.H., and Breen, C.M. 1980. Growth and reproduction of *Potamogeton crispus* in a South African Lake. J. Ecol. **68**: 561–571.

SAS Institute Inc. 1987. SAS/STAT guide for personal computers, version 6 edition. SAS Institute Inc., Cary, N.C.

Sculthorpe, C.D. 1967. The biology of aquatic vascular plants. St. Martin's Press, New York.

Smart, R.M., and Dorman, J.D. 1993. Latitudinal differences in growth strategy of a submersed aquatic plant: ecotypic differentiation in *Vallisneria americana*? Bull. Ecol. Soc. Am. **74**(Suppl.): 439.

Sohmer, S.H. 1975. The vascular flora of transects across navigation pools 7 and 8 on the Upper Mississippi. Wis. Acad. Sci. Arts Lett. **63**: 221–226.

Sullivan, J.F. 1991. Continuous water quality measurements at Weaver Bottoms, pool 5, Mississippi River, during July and August, 1986–1990. Weaver Bottoms Rehabilitation Resource Analysis Program Report, Wisconsin Department of Natural Resources, La Crosse, Wis.

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

van der Valk, A.G., and Davis, C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. Ecology, **59**: 322–335.

van Wijk, R.J. 1989. Ecological studies on *Potamogeton pectinatus* L. III. Reproductive strategies and germination ecology. Aquat. Bot. **33**: 271–299.

Wilder, G.J. 1974. Symmetry and development of pistillate *Vallisneria americana* (Hydrocharitaceae). Am. J. Bot. **61**: 846–866.