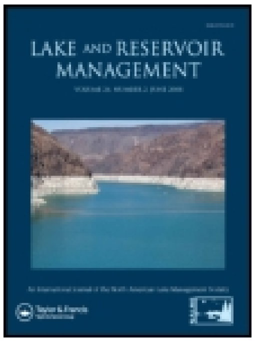

Lake and Reservoir Management

ISSN: 1040-2381 (Print) 2151-5530 (Online) Journal homepage: www.tandfonline.com/journals/ulrm20

Impacts of Water Column Turbidity on the Survival and Growth of *Vallisneria americana* Winterbuds and Seedlings

Robert D. Doyle & R. Michael Smart

To cite this article: Robert D. Doyle & R. Michael Smart (2001) Impacts of Water Column Turbidity on the Survival and Growth of *Vallisneria americana* Winterbuds and Seedlings, Lake and Reservoir Management, 17:1, 17-28, DOI: 10.1080/07438140109353970

To link to this article: https://doi.org/10.1080/07438140109353970

Published online: 29 Jan 2009.

Submit your article to this journal

Article views: 361

View related articles

Citing articles: 2 View citing articles

Full Terms & Conditions of access and use can be found at
https://www.tandfonline.com/action/journalInformation?journalCode=ulrm20

Journal of Lake and Reservoir Management 17(1):17-28, 2001
© Copyright by the North American Lake Management Society 2001

Impacts of Water Column Turbidity on the Survival and Growth of *Vallisneria americana* Winterbuds and Seedlings

Robert D. Doyle
University of North Texas
Department of Biological Sciences
Institute of Applied Sciences
P.O. Box 310559, Denton, TX 76203-0559, USA
Tel: 940-369-7708, Fax: 940-565-4297; Email: rdoyle@unt.edu

R. Michael Smart
U.S. Army Engineer Research and Development Center,
Lewisville Aquatic Ecosystem Research Facility
RR#3, Box 446, Lewisville, TX 75056, USA

ABSTRACT

Doyle, R. D. and R. M. Smart. 2001. Impacts of water column turbidity on the survival an growth of *Vallisneria americana* winterbuds and seedlings. Lake and Reserv. Manage. 17(1):17-28.

Survival and growth of *Vallisneria americana* winterbuds was significantly related to both initial winterbud size and to the water column turbidity under which the plants were grown. Larger winterbuds showed better survival and better growth than did smaller ones. Turbidity likewise significantly impacted the survival and growth of the plants. Over the turbidity range of 0.2-45 NTU (53-7% total incident light), the plants were shown to have progressively poorer survival and to produce fewer rosettes and total number of leaves. *Vallisneria americana* seedlings were likewise influenced by turbidity. Under high turbidity conditions the seedlings had significantly higher mortality, while surviving plants produced fewer rosettes and accumulated less biomass than seedlings grown under low turbidity conditions. In addition, under turbid conditions the seedlings had to invest proportionally more energy into above-ground tissues.

Key Words: turbidity, light, aquatic macrophytes, *Vallisneria americana*, winterbud.

Long-term survival of an aquatic plant population depends on the reproductive success of the "parent" population. Since individual plants of the northern ecotype of *Vallisneria americana* Michx. die at the end of each growing season (Korschgen and Green 1988, Titus and Hoover 1991) continued survival of the population depends on production and survival of asexual (winterbud) or sexual (seed) propagules. This process is fraught with potential bottlenecks including propagule production (induction and maturation) and propagule fate (dispersal, germination, and establishment) which may limit reproductive success (Titus and Hoover 1991). Reproductive failure has been noted as numerous communities of established macrophytes have experienced dramatic losses during the past two decades (e.g., Bulthuis 1983, Orth and Moore 1983). While the declines are sometimes related to episodic diseases (e.g., den Hartog 1987), they are more commonly attributed to changes in light climate (Scheffer 1998). Under reduced light conditions, submersed plants compensate by both morphological and physiological changes (Barko and Smart 1981, Barko and Filbin 1983, Goldsborough and Kemp 1988, Dennison and Alberte 1982, Tanner et al. 1993).

The depth to which aquatic plants can grow is generally restricted by light availability (Duarte 1991, Vant et. al. 1986, Dennison 1987, and Gallegos 1994) which in turn is related to levels of algae or suspended particles in the water column (Scheffer 1998). Changes in either variable impacts both quantity and quality of underwater light (Wetzel 1983). Increased nutrients limit light by promoting the growth of phytoplankton (e.g., Jupp and Spence 1977) or periphyton (Sand-Jensen and Søndergaard 1981). Under eutrophic conditions, phytoplankton usually dominate and most submersed aquatic macrophytes are lost (Duarte 1995, Phillips et al. 1978). Under levels of intermediate fertility, shallow lakes often exhibit alternating states and exist either in a clear state with abundant aquatic vegetation, or in a turbid state where vegetation is sparse (Scheffer 1998, Scheffer et al. 1993, Blindow et al. 1993). Suspended non-algal particles in the water column may also impact light availability. In some cases non-algal turbidity may be related to disturbances within the watershed resulting in increased turbidity and significant declines in the plant population (e.g., Giesen et al. 1990).

Whatever the loss mechanism, once the plants are gone from a given locale, increased sediment resuspension may place significant constraints on recovery. For example, Engel and Nichols (1994) report that in the early 1970's the macrophyte community of Rice Lake (Wisconsin, USA) was mostly eliminated by periods of unusually high water which resulted in poor light conditions. Even after water levels returned to normal, wind resuspension of sediments resulted in unusually turbid conditions that prevented recovery. More than a decade later, the lake continues to be turbid and has very few macrophytes. Similarly, the lush macrophyte community of Lake Apopka, Florida, was destroyed by a hurricane in 1947. Aquatic plants have never recovered and now a thick blanket of unstable sediment is easily resuspended by winds and keeps the lake very turbid (Scheffer 1998).

In this study we manipulate the turbidity levels over a range commonly reported for natural systems (0.2 to 50 NTU) under controlled greenhouse and laboratory conditions to determine turbidity effects on survival and early growth of *V. americana* winterbuds and seedlings.

Materials and Methods

Maintenance of turbidity

Turbidity in all experiments was maintained by addition of natural sediments to greenhouse tanks. A local sediment (80% clay and 20% silt) was dried, pulverized and sieved through a 1-mm sieve. A slurry was prepared by adding 100 g dry sediment to 500 mL water and sonicating the mixture for 1 to 2 hours. The sonication procedure was found to be essential to keep the clay particles suspended.

The light climate was monitored by measuring turbidity with a turbidimeter (Hach Corp., Loveland, CO) calibrated each day with secondary standards and each month with primary standards. The relationships between turbidity (reported as Nephelometer Turbidity Units - NTU) and total suspended solids (TSS), and between turbidity and the light extinction coefficient were determined by simultaneous measurements of these parameters in the tanks under a wide range of turbidities. TSS could not be measured with the standard glass fiber filter filtration method (APHA 1992) because a significant portion (10 to 25%) of the clay passed through all glass fiber filters tested. Instead, TSS was determined gravimetrically as the difference between total solids and total dissolved solids. Light was measured as photosynthetically active radiation (PAR, 400 to 700 nm) with a LiCor spherical quantum sensor.

Use of clay turbidity has advantages over the use of shade cloth to reduce light because it more closely mimics field conditions. Turbidity results in steep light gradients and shifts in the spectral quality of the light and plant leaves are exposed to substantially improved light conditions as they grow nearer the surface. These real-world conditions are not mimicked by shade cloth.

Winterbud experiment

The winterbud experiment utilized a 2 X 3 factorial design. Each combination of two winterbud size classes (large, small) and three levels of turbidity (low, intermediate, high) was replicated three times in greenhouse tanks at the Lewisville Aquatic Ecosystem Research Facility (LAERF), Lewisville, TX. The opaque fiberglass tanks measured 150 cm in length and 90 cm in width and depth. To ensure that the tanks remained well-mixed and to facilitate gas exchange, compressed air was continuously pumped through two air lifts in each tank. To minimize CO_2 depletion the airstream was amended with CO_2 to an approximate 10 X enrichment (~3500 ppm CO_2). The tanks were filled with pond water treated with alum (10 g $AlSO_4$ per 100 L) to remove soluble P and thereby minimize epiphytic growth. In addition to removing soluble P, alum lowered alkalinity from 120 to 90 mg $\cdot$ L^{-1} as $CaCO_3$ and pH from 8.3 to 8.0. At this pH, soluble Al is undetectable in the water. Water depth was maintained at 73 cm above the pot sediment surface. Water temperature was measured daily and, over the course of the experiment, ranged from 24 to 27 °C.

Winterbuds of *V. americana* were obtained from two sources in April 1996. The winterbuds differed substantially in size and were maintained separate throughout the experiment. The larger winterbuds were purchased from a commercial source (Wildlife Nurseries, INC., Oskosh, WI) and averaged 0.264 g fresh weight per winterbud. The smaller ones were collected by the Environmental Management and Technology Center (EMTC, now USGS Upper Midwest Environmental Science Center) in Onalaska, WI, and averaged only 0.047 g fresh weight per winterbud. Winterbuds from both sources were shipped to LAERF on ice, and were kept refrigerated until mid June, 1996.

The winterbuds were removed from refrigeration and placed in shallow containers in the greenhouse. After 9 days, those which had sprouted were separated for the experiment. Sixty-four winterbuds were randomly selected from each of the two size classes and divided into nine groups of six winterbuds each. Each winterbud was blotted dry and weighed to determine fresh weight. Fresh weight:dry weight ratios and percent ash content were determined for the 10 remaining winterbuds of each size class.

The recently-sprouted winterbuds were grown for eight weeks (June 26 to August 22) under one of three turbidity levels. The sprouted winterbuds were individually planted in 1.0-L plastic pots filled with pond sediment and each of the nine groups was randomly assigned to one of nine greenhouse tanks. The smaller winterbuds were placed at the opposite end of the tank from the larger ones to prevent plant canopy interactions as the plants grew. The nine greenhouse tanks were then assigned to one of three turbidity levels. Each tank contained six pots of each of the two winterbud size classes. The turbidity target levels for the low, intermediate, and high turbidity treatments were <1 NTU (no clay additions), 15 NTU, and 45 NTU respectively. Turbidity was measured daily and adjusted as needed in the 15 and 45 NTU tanks.

All plants were harvested on August 22, and the number of rosettes growing in each pot was determined. The leaves were enumerated and the length of each individual leaf was measured. The leaves were washed to remove debris and epiphytes. Below-ground tissues were separated and washed over a 1 mm sieve to remove sediments and debris. Larger rocks and debris were picked out by hand. Developing winterbuds, if present, were counted and separated from stolons and roots. Plant tissues were dried to constant weight at 60 °C. Ash content was determined for each plant tissue (leaves, roots and stolons, and winterbuds) and used to correct mass measurements. All plant mass values were expressed as ash-free dry weight.

Seedling growth experiment

This experiment was conducted in the lab under artificial lights. Seeds were collected from *V. americana* stock cultures in November, 1996 and maintained refrigerated until January, 1997, when the seed pods were opened to expose the seeds. Storage of *V. americana* seed for 2 to 3 months under refrigerated conditions does not appear to adversely impact seedling germination (Kimber et al. 1995b). Plants in culture had initially been collected from Toledo Bend Reservoir, TX.

The experiment was conducted on germinated and pre-established seedlings. The seeds were germinated in petri dishes containing moist, sterile toweling. Five to seven days after germination, the seedlings were transplanted into small pots (125 mL) filled with heat-sterilized (90 °C for 24 hours) pond sediment. Three seedlings were planted into each pot. The planted pots were placed in a tank filled with alum-treated pond water for 7 days prior to initiation of the experiment to ensure that the seedlings had become established.

After the pre-establishment period, the experiment was set up in experimental tanks. The pots were visually inspected, and the 16 most uniform pots were randomly assigned to one of two experimental tanks (eight pots per tank). Tanks measured 81 cm in length and 56 cm in width and depth. Water depth in the tanks was maintained at 30 cm above the pot surface. The pots were distributed throughout the tank so that neighboring pots were at least 20 cm apart. The turbidity in one of the tanks was then adjusted to 50 NTU. The turbidity of both tanks was checked daily, and the turbid tank was amended as necessary. Air was continually bubbled into both tanks to keep them well-mixed and to provide a continuous source of atmospheric CO_2. Light was provided by bulbs designed to simulate sunlight (Ultramarine Ultralux 6500K bulbs). Daily photoperiod was set to 14h:10h light:dark cycle. Temperature in both tanks averaged 22 °C.

After eight weeks of growth, the plants were harvested. Survival was determined for the three seedlings in each of the pots by counting the number of non-clonal plants in the pot (multiple rosettes attached via stolen = 1 surviving seedling). Total numbers of rosettes were enumerated, and the plant tissue harvested. Plants were separated into above- and below-ground tissues, washed, and dried to constant weight at 60 °C. Tissue weights were corrected for ash content as described above.

Statistical analysis

All statistical analyses were performed using *Statgraphics Plus* (Manugistics, Inc. Rockville, MD). Due to the relatively low number of independent experimental units the level for significance acceptance was $\alpha < 0.1$.

Data for the winterbud experiment were analyzed on a tank population basis. The sum of the six pots of each size class in each tank represents the population response of that size class for that tank. A two-way ANOVA (initial winterbud size and turbidity) was used to analyze the factorial winterbud experiment. Linear regression analysis was used to test for systematic, linear changes in winterbud responses to turbidity.

Statistical comparison of seedling survival and growth between the two turbidity treatments was performed utilizing a t-statistic. Each pot was assumed to be an independent experimental unit (N=8 for each treatment).

Results

Light climate

Although turbidity in the tanks was adjusted almost daily, there was still some fluctuation in turbidity. Typically, values in the tanks with the intermediate and high turbidity treatments dropped by about 20% from one day to the next (Fig. 1).

The relationships between turbidity and light extinction coefficient (Kd), and between turbidity and total suspended solids (TSS) were found to be completely linear over the range of turbidity utilized in this study and related by the following equations:

$$Kd = 0.3 + 0.082(NTU), r^2=0.97 \ (n=23)$$
$$TSS = 0.4 + 1.42(NTU), r^2=0.99 \ (n=6)$$

PAR extinction coefficients corresponded to about 0.3, 1.5 and 4.0 m^{-1} at NTU values of 0.2, 15 and 45, respectively. TSS values for the 15 and 45 NTU tanks were about 21 and 64 $mg \cdot L^{-1}$, respectively.

Average percent light penetrating through the greenhouse roof (65% transmittance) and to the sediment surface of the pots within the tanks over the course of the experiment averaged 53%, 29% and 7% for the low, intermediate, and high turbidity tanks, respectively. Maximum midday PAR levels reaching the sediment surface were approximately 1050, 570,

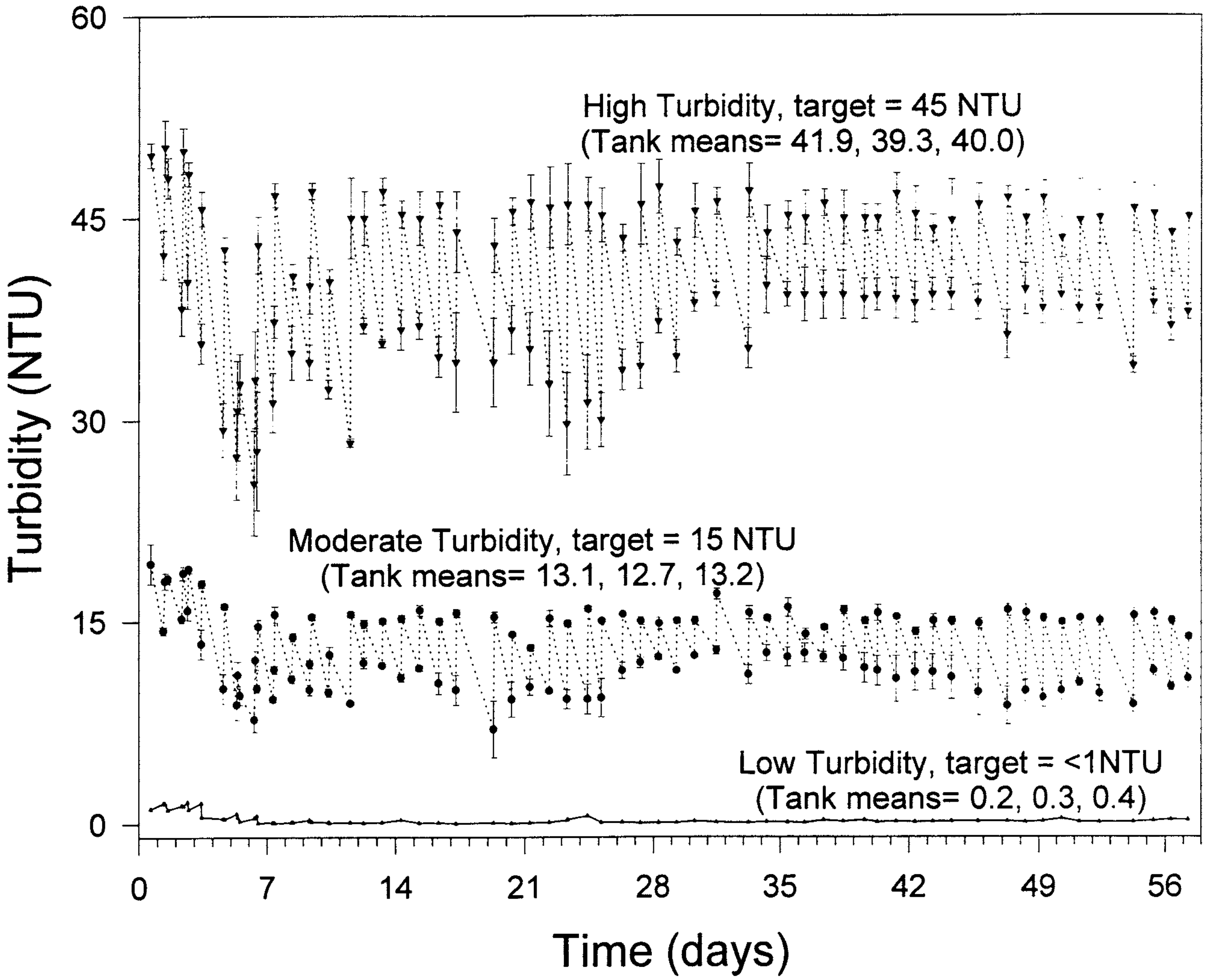

Figure 1.–Turbidity levels throughout the experimental growth period for the greenhouse winterbud experiment. Shown are mean, maximum and minimum turbidity readings for low, intermediate and high turbidity tanks. N=3 tanks for each treatment.

and 140 $\mu E \cdot m^{-2} \cdot s^{-1}$ for the three treatments respectively. Since the integrated daily outdoor PAR at this location during the summer averages about 47 $E \cdot m^{-2} \cdot d^{-1}$ (1992-1994 unpublished data), the tanks were estimated to have received an average of 25.1, 13.4, and 3.4 $E \cdot m^{-2} \cdot d^{-1}$ at the sediment surface in the low, intermediate, and high turbidity tanks, respectively.

Incident light reaching the water surface of the tanks utilized for the seedling experiment was ca.500 $\mu E \cdot m^{-2} \cdot s^{-1}$. Light levels in the high turbidity tank at the sediment surface ranged between 75 to 95 $\mu E \cdot m^{-2} \cdot s^{-1}$, while that of the low turbidity tank ranged from 450 to 490 $\mu E \cdot m^{-2} \cdot s^{-1}$. Over the 14 hour light period, about 4.3 or 23.9 $E \cdot m^{-2} \cdot d^{-1}$ (9% and 51% of average daily outdoor PAR) penetrated to the sediment surface in the high and low turbidity tank, respectively.

Effects of turbidity and initial size on winterbud survival and growth

Both factors (initial winterbud size and turbidity) were found to significantly effect most plant growth parameters measured (Fig. 2). Two way analysis of variance showed no significant interactions between turbidity and initial winterbud size for any parameter measured, indicating that the effects of turbidity were consistent across both winterbud size classes and that the effect of initial winterbud size was similar at all turbidity levels.

Both turbidity and initial winterbud size significantly influenced survival of *V. americana* winterbuds (Fig. 2A). Larger winterbuds had higher survival rates at all turbidity levels than smaller ones. Survival of both size classes of winterbuds was significantly linearly related to turbidity, with survival decreasing with increased turbidity. Survival of small winterbuds under the most turbid conditions was very poor (0 to 17%) but increased to ~50% under clear water conditions. Large *V. americana* winterbuds survived well at both of the lower turbidity levels, but had lower and more variable survival in the three replicate tanks at the highest turbidity where survival ranged from 50 to 83%.

Morphological development was also affected by winterbud size and water turbidity. The number of *V. americana* rosettes produced was related to both turbidity and winterbud size (Fig. 2B). Under the highest turbidity, small winterbuds averaged only 1.3 rosettes per tank (total of 6 pots) while the total increased to 19.7 at the highest light level. Under the highest turbidity the larger winterbuds averaged 16 rosettes per tank and increased to 32 rosettes per tank at the highest light level. The differences seen in rosette production among turbidity treatments was not simply a reflection of poorer survival in the more turbid tanks. As turbidity increased, the average number of rosettes produced by each surviving winterbud declined significantly (Fig. 2C).

As turbidity increased, the plants produced fewer leaves per tank (Fig. 2D). At the highest turbidity, the larger winterbuds produced an average of about 200 leaves per tank while under clear water conditions the average increased to almost 400. The smaller winterbuds produced fewer leaves per tank. Under the lowest light conditions, the average was only 16 leaves per tank and increased to over 200 leaves per tank at the highest light. For these smaller winterbuds, the difference in leaf production was largely a function of poorer survival as turbidity increased.

Leaf length was also strongly impacted by turbidity (Fig. 2E). Under the most turbid conditions, over half the leaves produced by both winterbud size classes were longer than 60 cm and therefore reached almost to the water surface. Under the highest light conditions, only about 20% of the leaves produced by larger winterbuds were that long, while less than 10% of leaves produced by smaller winterbuds achieved that length.

Initial winterbud size had a substantial impact on total mass produced in each tank (Fig. 2F). Across all turbidity levels, the larger winterbuds produced almost 6X more mass per tank than the smaller winterbuds. This difference was accentuated by poorer survival of the smaller winterbuds, but the total mass produced by each surviving small winterbud was only 50% of that produced by the larger ones (data not shown).

Despite a strong linear relationship between plant number and turbidity (Fig. 2B), total mass of plants produced per tank was not linearly related to turbidity (Fig. 2F). As turbidity increased, the average mass of each individual rosette increased significantly (Fig. 2G). As a consequence, the loss in plant number was offset by an increase in individual plant mass. There was a tendency for more mass production at the intermediate turbidity level than at either high or low turbidity.

Larger winterbuds produced significantly more new winterbuds than smaller ones, but there was no significant linear relationship between turbidity and winterbud production by the plants grown from either large or small winterbuds. This was true for both total winterbud production per tank (Fig. 2H) and winterbud production per surviving winterbud (data not shown). However, when averaged across both winterbud size classes, the intermediate turbidity tanks produced significantly more new winterbuds per tank than either the low or high turbidity tank, reflecting a trend similar to that seen in total plant mass.

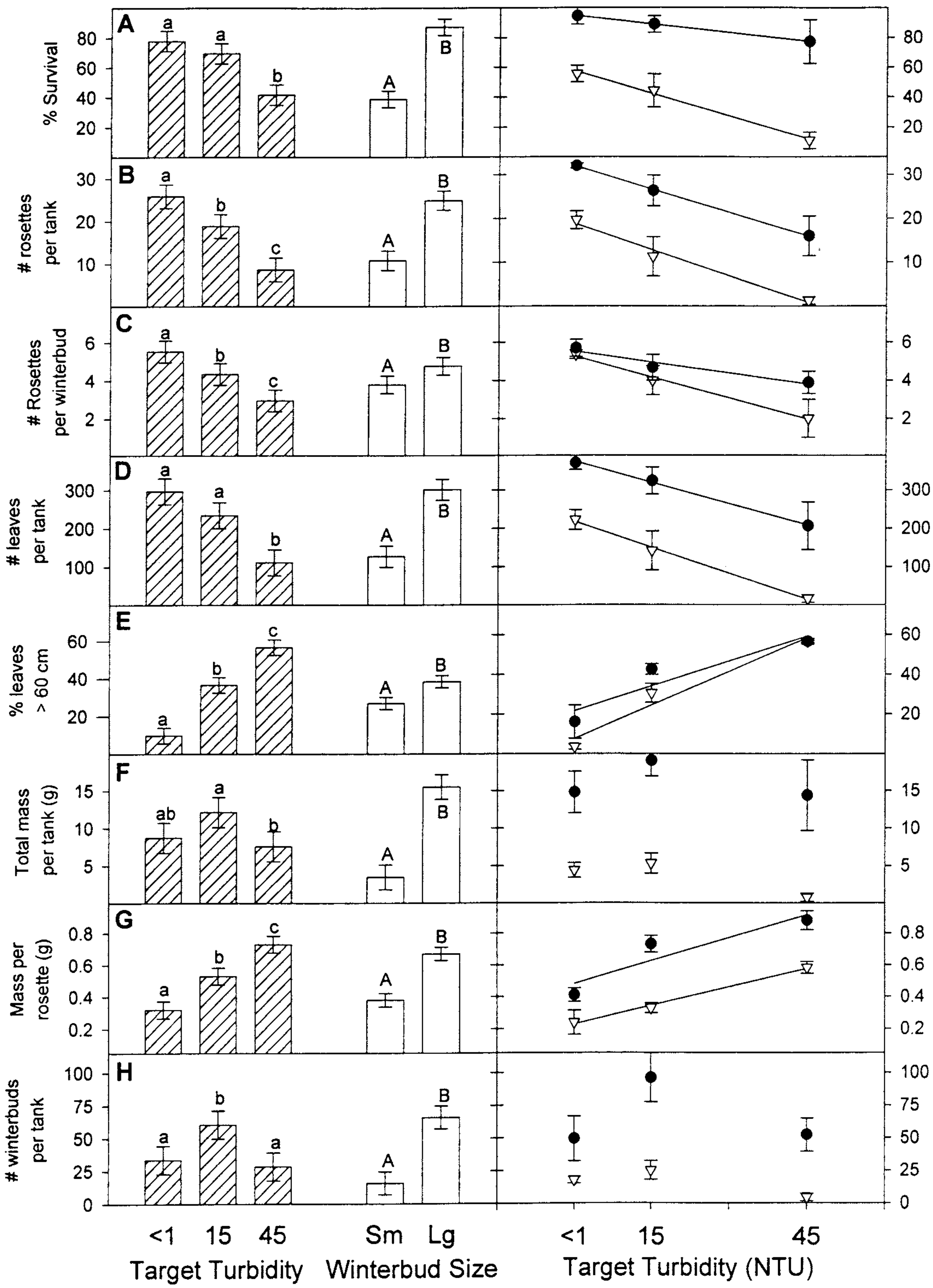

Figure 2.–Survival and selected growth characteristics of two size classes of *Vallisneria americana* winterbuds grown under three turbidity levels. Left panel shows the results of Two- Way ANOVA. Given are means and 90% confidence intervals testing for differences among means. Hatched bars show means of all winterbuds (large and small) grown under each turbidity treatment (n=3 tanks). Open bars show means of all small or large winterbuds (regardless of turbidity level, n=9 tanks). Letters above bars represent significant differences among treatment means (significant Two-Way ANOVAs followed by LSD mean separation test, α<0.10). Right panel shows the average ±se of large (●) or small (▽) winterbuds grown at each of the three turbidity levels (n= 3 tanks). Best fit regression lines are shown where significant linear relationships existed. (a) percent survival of planted winterbuds; (b) total number of rosettes per tank produced at the end of the experimental growth period; (c) average number of rosettes produced by each surviving winterbud; (d) total number of leaves per tank; (e) percent of all leaves within the tank which were longer than 60 cm; (f) total ash-free dry mass per tank; (g) average ash-free dry mass of each rosette produced; (h) total number of new winterbuds produced per tank.

Impact of turbidity on seedling survival and growth

Vallisneria americana seedling survival was significantly higher at the lower turbidity (67 vs. 46%, Fig. 3A). Total number of plants per pot was also much higher (~4 X) in the low turbidity tank (Fig. 3B). In addition to having higher survival, we observed that in all cases, only one seedling in each of the pots in the low turbidity tank had produced additional rosettes. The remaining seedlings in the pots often showed poor growth and did not produce daughter plants. No seedling in the high turbidity tank produced any daughter plants.

The impact of turbidity was even more pronounced for total plant mass produced. The plant mass in the pots within the low turbidity tank exceeded that of the pots in the high turbidity tank by about 7 X (Fig. 3C). Finally, the allocation of biomass in the developing seedling differed between the two treatments: above-ground to below-ground ratios in the low turbidity tank averaged only 1.86 but increased to 2.85 in the high turbidity tank (Fig. 3D). Seedlings in the high turbidity tank invested proportionally more energy in developing leaf tissues than those in the low turbidity tank.

Discussion

The findings of this research support a growing body of literature which points to light availability as the key environmental variable controlling the population dynamics of submersed macrophytes, including *V. americana*.

Field experiments with light manipulations have shown that severe shading can result in death of submersed plants while more moderate shading results in significantly decreased growth relative to unshaded control plants (Bulthuis 1983). Similarly,

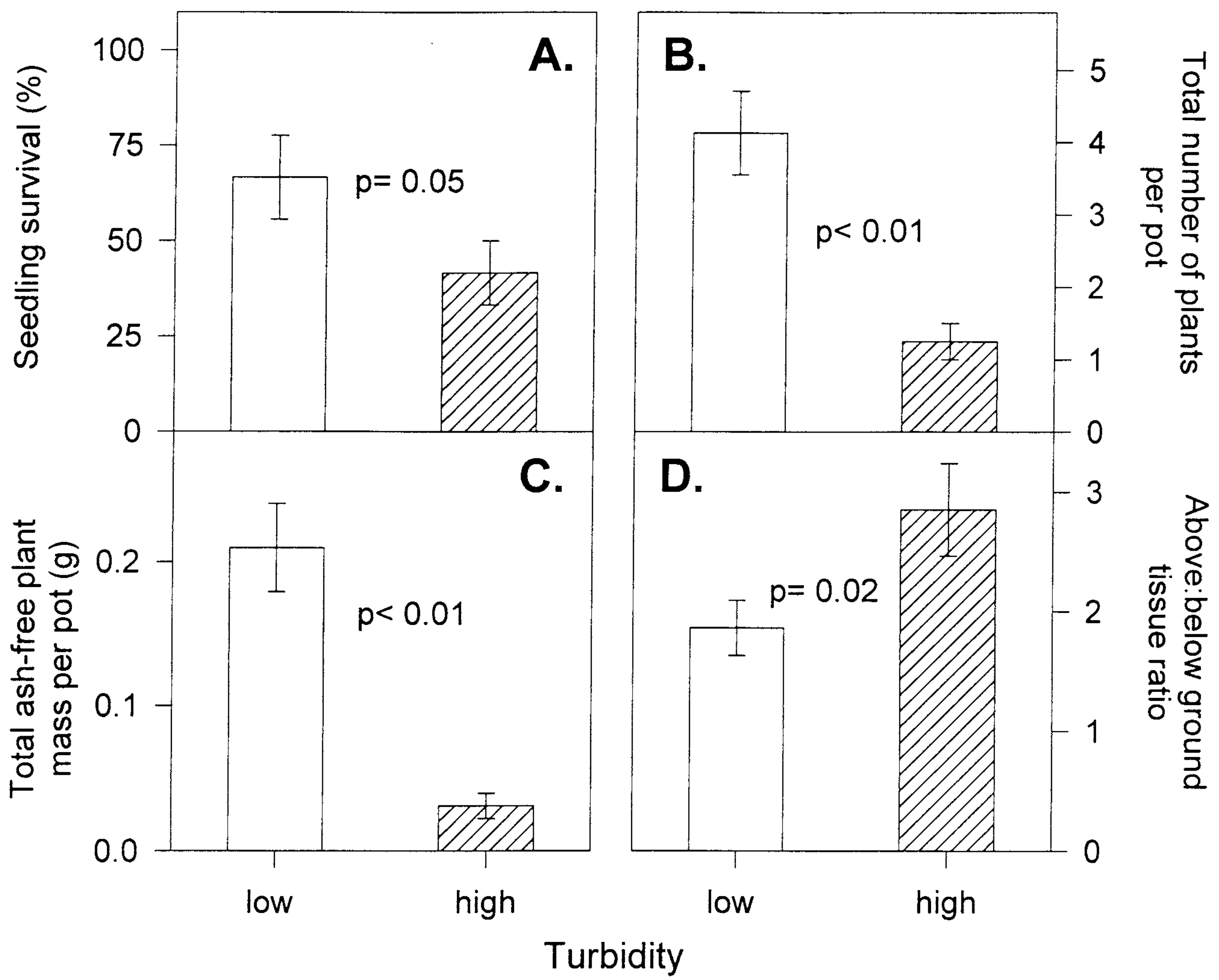

Figure 3.–Comparison of survival and growth of seedlings in low turbidity (open) and high turbidity (hatched bars) water. Given are means ±se (N=8). Significance level refers to *t*-statistic comparing the means.

Egeria densa plants growing under controlled conditions showed declines in relative growth rates and biomass accumulation as levels of suspended clays in the water column increased (Tanner et al. 1993). Transplant experiments have also demonstrated that due to the constraints of turbidity, submersed plant survival is often limited to very shallow depths or sites where light transparency is high (Zimmerman et al. 1995, Carter and Rybicki 1985).

Recent changes in *V. americana* populations in the Upper Mississippi River System (UMRS) have also been attributed to unusual hydrologic conditions (Fischer and Claflin, 1995; Kimber et al. 1995a; and Korschgen et al., 1997). While the exact cause of the decline is debated, there is little disagreement that sediment resuspension and turbidity has negative impacts on *V. americana*. When *V. americana* was cultured under various fertility, inorganic carbon and light regimes, light was determined to be the strongest factor influencing biomass production (Barko et al. 1991). Similarly, changing patterns of submersed macrophytes (including *V. americana*) in the freshwater tidal Potomac River are attributed mostly to light variability (Carter and Rybicki 1990, Carter et al. 1994). Artificial enhancement of light levels resulted in increases in the plant population (Carter et al. 1996). In another experiment, when winterbuds were planted into three water depths in backwater areas of the Mississippi river, only those at the shallowest depth (highest light availability) survived (Kimber et al. 1995a) and the authors calculated that winterbuds would survive depths of only 0.8 m or less. Recently, experimental data have demonstrated that total biomass of winterbuds and the biomass of individual winterbuds was reduced when plants were grown under poor light conditions (Korschgen et al. 1997).

Blanch et al. (1998), in experiments that varied both turbidity (90 to 500 NTU) and planting depth (12.5 to 150 cm), showed that growth of *V. americana* followed a light-saturation pattern. The average daytime light intensity required to balance daily respiratory losses was estimated to be 26 $\mu E \cdot m^{-2} \cdot s^{-1}$ (ca. 1.1 $E \cdot m^{-2} \cdot d^{-1}$), and growth was light saturated at average daily light levels of 60 to 140 $E \cdot m^{-2} \cdot s^{-1}$ (2.6 to 6.0 $E \cdot m^{-2} \cdot d^{-1}$). Plant biomass accumulation and rosette and leaf production likewise followed a light-saturation pattern.

Effects of turbidity and initial size on winterbud survival and growth

The larger winterbuds of *V. americana* showed better survival than the smaller ones. In this study the initial size of the larger winterbuds were 5.6X greater than the smaller ones. The small winterbuds showed little survival under the highest turbidity but survival increased to near 50% at the highest light level. Larger winterbuds showed excellent survival at both the two lower turbidity levels tested, and decreased to only 77% at the highest turbidity level. These results reinforce the findings of Titus and Hoover (1991) who show a general trend for the mortality of *V. americana* winterbuds is higher for smaller propagules.

In addition to higher survival, larger winterbuds of *V. americana* performed significantly better ($p \leq 0.10$) for all measured growth variables than the smaller winterbuds. This finding confirms the speculations of Korschgen et al. (1997) that winterbud size is an indicator of winterbud fitness. When averaged across all light levels, large winterbuds showed better survival, produced more rosettes, produced more mass, made more leaves, and produced a larger quantity of new winterbuds than smaller winterbuds. Spencer (1987) likewise demonstrated that larger *Potamogeton pectinatus* tubers supported higher rates of growth than smaller ones. Likewise, larger *V. americana* winterbuds produced larger rosettes (Hoover, 1984). Presumably, the difference between growth of larger and small propagules is due to the increased resources available to the larger ones. The results of this study support the speculation of Titus and Hoover (1991) that propagule size is likely a useful predictor of survival and early growth of sprouted vegetative propagules.

Results of this study also clearly demonstrate that turbidity influenced *V. americana* winterbud survival and growth. There appear to be few comparable survival data for winterbuds grown under different light conditions in the literature. Korschgen et al. (1997) reports the growth of *V. americana* from winterbuds under light conditions at 0.5 m depth ranging from 0.03 to 1.05 $E \cdot m^{-2} \cdot d^{-1}$ (all substantially lower than those of this study) but report only winterbud production at the end of the growing season. There appear to have been surviving plants at all light levels tested because all showed some winterbud production. Kimber et al. (1995a) give survival and growth data from large winterbuds (1 to 1.5 g FW) suspended at three depths within Lake Onalaska. Winterbuds planted at 1.5 m (ca. 0.1% light = 0.04 $E \cdot m^{-2} \cdot d^{-1}$) depth did not survive. Winterbuds planted at water depths of 1.0 m (ca. 0.4 $E \cdot m^{-2} \cdot d^{-1}$) had some mortality since the number of rosettes at the end of the study was smaller than the number of winterbuds planted. Only at the highest light levels tested (0.5 m depth, daily light 3.6 $E \cdot m^{-2} \cdot d^{-1}$ = 9% of incident light) was survival near 100%.

The number of rosettes produced was significantly affected by turbidity for both size classes of *V. americana* winterbuds. This decline in rosette production was both a function of poor plant survival and fewer rosettes produced by surviving plants at the higher turbidity levels. The impact was particularly strong for the smaller class of winterbuds. At low turbidity, the number of rosettes produced by a surviving winterbud was similar for both large and small winterbuds (5.7 and 5.4, respectively). However, as turbidity increased, the number of rosettes produced by smaller winterbuds declined more sharply than that of larger winterbuds. At the highest turbidity level tested, the smaller winterbuds produced only about half the number of rosettes produced by the larger ones. The number of rosettes produced by a surviving large winterbud ranged from 3 to 5 at the lowest light level up to 5 to 7 at the higher light levels. Kimber et al. (1995a) report that only winterbuds grown at the highest light level tested (3.4 $E \cdot m^{-2} \cdot d^{-1}$) showed a net increase in number of rosettes. Under those conditions, the winterbuds produced an average of 3.7 rosettes per winterbud planted.

Turbidity also influenced the number and length of leaves produced. As turbidity increased in this experiment, the plants produced fewer but longer leaves than under better light conditions. Leaf length and number were also observed to be related to light conditions by Kimber et al. (1995a). She reports that light levels equal to 12.2 $E \cdot m^{-2} \cdot d^{-1}$ each winterbud produced an average of 18.3 leaves which were on average only 25 cm long. At a light level of 2.6 $E \cdot m^{-2} \cdot d^{-1}$, the average number of leaves produced had dropped to 10 while the average leaf length had increased to 38 cm. This decline in number of leaves produced may have important ecological implications given that stolons (which eventually produce additional rosettes or winterbuds) may develop at every third leaf axil in *V. americana* (Wilder 1974).

Surprisingly, the total mass produced per tank was not strongly related to turbidity. In fact, for the larger winterbuds there was no linear relationship between turbidity and the mass of plant tissue produced per tank. The larger winterbuds which did survive the higher turbidity produced fewer, but larger rosettes with fewer but much longer leaves. For the smaller winterbuds, there was much less mass produced at the highest turbidity level as a result of poorer survival.

The finding that mass production per tank is poorly related to light climate is surprising given results from other studies. Carter et al. (1996) report biomass increases of 11 to 38 fold when field populations were provided additional light relative to unlighted controls. Although cumulative daily light data for the field sites are not presented, they report that the artificial lights increased irradiance 17 cm from the light sources (estimated increase of ~7-8 $E \cdot m^{-2} \cdot d^{-1}$) by 40%. That indicates that cumulative daily light of unlighted controls would have been about 12.6 $E \cdot m^{-2} \cdot d^{-1}$, while that of lighted grids would be on the order of 21 $E \cdot m^{-2} \cdot d^{-1}$. These light levels correspond roughly to the levels utilized for the low and intermediate turbidity treatment in this experiment respectively. In the present study, there was no significant difference in total mass produced at different turbidities for the larger winterbuds: small winterbuds produced significantly less mass in the most turbid tanks than at either of the other two light levels.

The different response of mass and number of rosettes obtained in the current study may be better understood when compared to the data presented by Blanch et al. (1998). In those experiments, Relative Growth Rate (RGR) of *V. americana* (a mass-based parameter) was shown to begin to be light-saturated at an average daily irradiance of only 58 $\mu E \cdot m^{-2} \cdot s^{-1}$ (= 2.5 $E \cdot m^{-2} \cdot d^{-1}$), while number of rosettes produced was still increasing at the highest light levels utilized in the experiment (6.1 $E \cdot m^{-2} \cdot d^{-1}$). This indicates that the total mass produced by a population may stabilize at relatively low light levels , but that the allocation of that mass (many smaller plants vs. fewer larger ones) may vary as a function of light up to a much higher level. Since the lowest light level tested in this study was 3.4 $E \cdot m^{-2} \cdot d^{-1}$, we may have been above any potential light impacts on plant mass.

The reduction in number of rosettes produced under more turbid conditions may have implications for the long-term survival of a population. Winterbud production at a given site is clearly related to the development of the parent population (Titus and Hoover 1991), but may be more a function of the number of rosettes and available meristems for winterbud production than absolute plant mass (Korschgen et al. 1997; Titus and Hoover 1991). If so, the impact of reduced light on the mass of plants at that site may be minor, but if fewer rosettes produce fewer winterbuds, the regrowth of that population the following year could be jeopardized by a low number of overwintering propagules. The impacts of low light on tuber growth and subsequent tuber production may also partially explain the observed decline of native plants (including *V. americana*) beneath a canopy of the exotic *Myriophyllum spicatum* (Madsen et al. 1991).

If winterbud size is a function of rosette size, *V. americana* populations may also be poorly equipped to handle *changing* light environments. Under high light environments, *V. americana* produces numerous small rosettes which in turn produce small winterbuds. These small winterbuds would be ill-equipped for surviving low light levels the following spring. On the other hand, if water clarity is always poor, the plants produce fewer, but much larger rosettes which produce fewer, but larger winterbuds. These larger winterbuds would be better equipped survival under turbid conditions.

Strong relationships between light and winterbud production (number and mass) are commonly observed (Kimber et al. 1995a, Korschgen et al. 1997). In the present study there was no clear linear relationship between winterbud number and turbidity for either large or small winterbuds on either a per tank or per surviving individual basis. Small winterbuds produced significantly fewer new winterbuds per tank at the lowest light level due to decreased plant survival. Across both winterbud size classes, plants growing in the intermediate turbidity tanks produced significantly more winterbuds per tank than those growing at either turbidity extreme. Surprisingly, there was also no linear relationship between the number of rosettes per tank and the number of winterbuds per tank (data not shown, $p=0.98$ large winterbuds, $p=0.12$ for small winterbuds). Even though there was no linear relationship to turbidity, the impact of initial winterbud size on subsequent winterbud production was quite strong with the larger winterbuds producing as much as 3X more new winterbuds by the end of the growth period. However, it is important to note that the present experiment was not optimized to investigate impacts of turbidity on winterbud production. Plants were harvested only 8 weeks after planting, and winterbud formation was still occurring. The winterbuds harvested were clearly still developing, and perhaps many more would have formed prior to senescence later in the season. Individual winterbud weight ranged between 0.01 to 0.04 g, which is well below the 0.1 g threshold considered essential for winterbud survival (Kimber et al. 1995a).

Impacts of turbidity on V. americana seedlings

Although the importance of seeds to the ecology of *V. americana* is poorly understood, these propagules are clearly able to establish under some field conditions and may be adapted primarily for long-distance colonization of new sites (Titus and Hoover 1991). Even though *V. americana* seedlings are not commonly reported in the field, Kimber et al. (1995b) described the regrowth of *V. americana* populations in areas where plants had not been present for several years and speculate that these may have come from seed. However, even if seeds are present, adequate light is needed for plant establishment. Kimber et al. (1995b) report that although viable *V. americana* seed were collected from sediment samples throughout the Lake Onalaska, WI., survival and subsequent winterbud production took place only at or above 9% of full sun (ca 0.5 m depth).

Despite significant research on seed dormancy and germination (see Titus and Hoover 1991), there is little information in the literature documenting factors related to early growth and establishment. In this study, we show that *V. americana* seedlings were profoundly influenced by turbidity. Under high turbidity conditions the seedlings had significantly higher mortality, produced fewer plants per pot, and accumulated much less biomass than seedlings grown under low turbidity conditions. In addition, the seedlings in the high turbidity tanks had to invest proportionally more energy into above-ground tissues to compensate for the lower light conditions.

The single published report of light requirements for *V americana* seedlings (Kimber et al. 1995b) confirms the importance of light to developing seedlings. Although Kimber et al. (1995b) do not report absolute seedling survival values, they do report the percentage of pots with surviving seedlings (20 seeds planted per pot) over a range of light levels (2 to 25% full light). In the current experiment, all pots grown in the low turbidity tank had seedlings, while 7 of 8 pots in the high turbidity tank also had seedlings (100% and 88% of pots had surviving seedlings). Assuming that total daily available light during the growth period reported by Kimber et al. (1995b) was 39.4 $E \cdot m^{-2} \cdot d^{-1}$ (see Kimber et al. 1995a), the data she presents and the data generated in this experiment begin to provide a picture of seedling survival as a function of light (Fig. 4). The survival data appear to show a sigmoid curve, with survival increasing rapidly in the range of 0 to 5 $E \cdot m^{-2} \cdot d^{-1}$. At levels above 10 $E \cdot m^{-2} \cdot d^{-1}$, survival is excellent, while at levels below 3 $E \cdot m^{-2} \cdot d^{-1}$ there is very high mortality. These findings again support the suppositions of Titus and Hoover (1991) that low stored energy reserves, coupled with low light regimes at the bottom of the water column may pose significant constraints on the establishment of *V. americana* seedlings.

Short-term survival is only part of the picture. Kimber et al. (1995b) demonstrate that at light levels of 2 and 5% light (0.8 and 2.0 $E \cdot m^{-2} \cdot d^{-1}$) there is no winterbud production. Consequently, those plants would not reproduce themselves, and the following year there would be no plants in that area.

We demonstrated that seedlings grown under turbid conditions produce fewer rosettes and much less mass than in clear water conditions. Although we did not allow the experiment to continue sufficiently long to determine winterbud or seed production, biomass is a significant factor for both flowering and winterbud production (Titus and Hoover 1991). It is also important to note that seedlings in the turbid

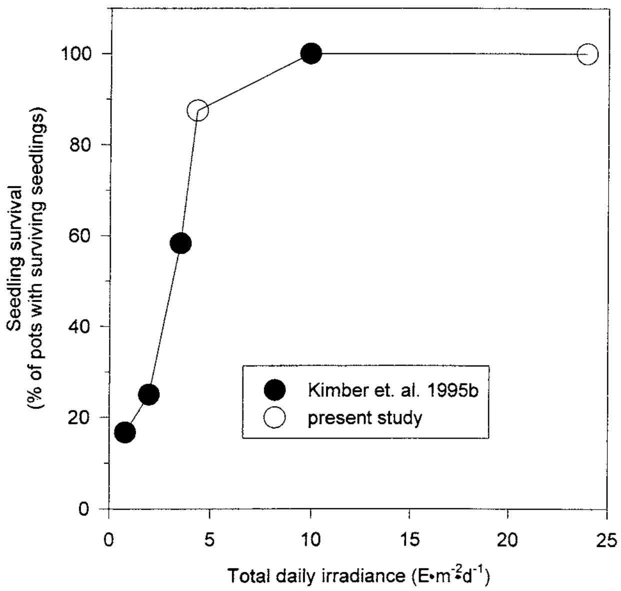

Figure 4.–Seedling survival as a function of average total daily light received. Closed circles are data from Kimber et. al. 1995b, while open circles are data from the current experiment. Survival determined as the percent of pots which had surviving seedlings at the end of the experiment and are not absolute survival values.

tank never produced stolons or daughter plants. Since *V. americana* depends greatly on vegetative growth to colonize nearby sites and to expand the size of the colony, the lack of daughter plant production is likely ecologically significant.

Implications for Vallisneria americana *survival*

High turbidity is a significant problem for *V. americana* growing from seeds or winterbuds. Winterbud survival and growth was demonstrated to be significantly impacted by turbidity. Korschgen et al. (1997) report that the average depth of *V. americana* beds in Pool 8 of the UMRS to be 0.88 m during the 1983 to 1985 period which corresponded to a light level of about 3% surface irradiance. Assuming an average daily surface irradiance similar to the value of 39.4 $E \cdot m^{-2} \cdot d^{-1}$ reported by Kimber et al. (1995a), this would correspond to a daily irradiance of about 1.2 $E \cdot m^{-2} \cdot d^{-1}$ at the sediment surface. Considering that the winterbud population within this region is now apparently dominated by smaller size winterbuds (this location was the source of the smaller winterbuds for the present study), we believe that turbidity may now impose a significant constraint on population recovery. Based on the present study, light levels below 5 $E \cdot m^{-2} \cdot d^{-1}$ can be expected to negatively impact winterbud and seedling survival, and the plants which do survive will produce relatively few rosettes during the growing season.

ACKNOWLEDGMENTS: This research was conducted under the U.S. Army Corps of Engineers Aquatic Plant Control Research Program, Environmental Laboratory, U.S. Army Engineer Research and Development Center. Permission was granted by the Chief of Engineers to publish this information. This work was conducted as part of the Upper Mississippi River-Illinois Waterway (UMR-IWW) System Navigation Study. Technical assistance provided by Ms. Chetta Owens, Mr. Matt Francis, Mr. Ken Banks, Mr. Charles Zipper and Ms. Nece Romines, Lewisville Aquatic Ecosystem Research Facility, Lewisville, TX.

References

APHA. 1992. Standard Methods for the Examination of Water and Wastewater. 18th ed. A. E. Greensger, L. S. Clesceri and A. D. Eaton, ed., Am. Wat. Works Assoc. and Wat. Pollution Control Federation. Washington, DC.

Barko, J. W. and R. M. Smart. 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. Ecol. Monagr. 51:219-235.

Barko, J. W. and G. J. Filbin. 1983. Influences of light and temperature on chlorophyll composition in submersed freshwater macrophytes. Aquat. Bot. 15:249-255.

Barko, J. W., R. M. Smart and D. G. McFarland. 1991. Interactive effects of environmental conditions on the growth of submersed aquatic macrophytes. J. Freshwat. Ecol. 6:199-207.

Blanch, S. J., G. G. Ganf and K. F. Walker. 1998. Growth and recruitment in *Vallisneria americana* as related to average irradiance in the water column. Aquat. Botany. 61:181-205.

Blindow, I., G. Andersson, A. Hargeby and S. Johansson. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. Freshwat. Biol. 30:159-167.

Bulthuis, D. A. 1983. Effects of in situ light reduction on density and growth of the seagrass *Heterozostera tasmanica* (Martens ex Aschers) den Hartog in Western Port, Victoria, Australia. J. Exp. Marine Biol. Ecol. 67:91-103.

Carter, V. and N. B. Rybicki. 1985. The effects of grazers and light penetration on the survival of transplants of *Vallisneria americana* Michx. in the tiday Potomac River, Maryland. Aquat. Bot. 23:197-214.

Carter, V. and N. B. Rykicki. 1990. Light attenuation and submersed macrophyte distribution in the tidal Potomac River and Estuary Estuaries, 13:441-442.

Carter, V., N. B. Rykicki, J. M. Landwehr and M. Turtora. 1994. Role of weather and water quality in population dynamics of submerged macrophytes in the tidal Potomac River. Estuaries 17:417-426.

Carter, V., N. B. Rybicki and M. Turtora. 1996. Effect of increasing photon irradiance on the growth of *Vallisneria americana* in the tidal Potomac River. Aquat. Bot. 54, 337-345.

Dennison, W. C. 1987. Effects of light on seagrass photosynthesis, growth, and depth distribution. Aquat. Bot. 27:15-26.

Dennison, W. C. and R. S. Alberte. 1982. Photosynthetic responses of *Zostera marina* L. (Eelgrass) to in situ manipulations of light intensity. Ecologia (Berl). 55, 137-144.

den Hartog, C. 1987. "Wasting disease" and other dynamic phenomena in Zostera beds. Aquat. Bot. 27:3-14.

Duarte, C. M. 1991. Seagrass depth limits. Aquat. Bot. 40:363-377.

Duarte, C. M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41:87-112.

Engel, S. and S. A. Nichols. 1994. Aquatic macrophyte growth in a turbid windswept lake. J. Freshwat. Ecol. 9:97-109.

Fischer, J. R. and T. O. Claflin. 1995. Declines in aquatic vegetation in navigation pool no. 8, Upper Mississippi River between 1975 and 1991. Regulated Rivers: Res. and Manage. 11:157-165.

Gallegos, C. L. 1994. Refining habitat requirements of submersed aquatic vegetation: role of optical models. Estuaries 17:187-199.

Giesen, W. B. J. T., M. M. van Katwijk and C. den Hartog. 1990. Eelgrass condition and turbidity in the Dutch Wadden Sea. Aquat. Bot. 37:71-85.

Goldsborough, W. J. and M. Kemp. 1988. Light responses of a submersed macrophyte: implications for survival in turbid tidal waters. Ecology 69:1775-1786.

Hoover, D. T. 1984. Reproductive ecology of two submersed macrophytes in varying pH regimes. M.S. Thesis, State University of New Yourk at Binghampton, 87 p. (Cited by Titus and Hoover, 1991).

Jupp, B. P. and D. H. N. Spence. 1977. Limitations on macrophytes in an eutrophic lake, Loch Leven. J. Ecol. 65:175-186.

Kimber, A., J. L. Owens and W. G. Crumpton. 1995a. Light availability and growth of wildcelery (*Vallisneria americana*) in upper Mississippi River backwaters. Regulated Rivers: Res. and Manage. 11:167-174.

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

Korschgen, C. E. and W. L. Green. 1988. American wild celery (*Vallisneria americana*): Ecological considerations for restoration. U.S. Fish and Wildlife Service. Fish and Wildl. Tech. Rep. 19. P. 24.

Korschgen, C. E., W. L. Green and K. P. Kenow. 1997. Effects of irradiance on growth and winter bud production by *Vallisneria americana* and consequences to its abundance and distribution. Aquat. Bot. 58:1-9.

Madsen, J. D., J. W. Sutherland, J. A. Bloomfield, L. W. Eichler and C. W. Boylen. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. Journal of Aquat. Plant Manage. 29:94-99.

Orth, R. J. and K. A. Moore. 1983. Chesapeake Bay: an unprecedented decline in submerged aquatic vegetation. Science 222:51-53.

Phillips, G. L., D. Eminson and B. Moss. 1978. A mechanism to account for macrophyte declines in progressively eutrophicated freshwaters. Aquat. Bot. 4:103-126.

Sand-Jensen, K. and M. Søndergaard. 1981. Phytoplankton and epiphytic development and their shading effect on submerged macrophytes in lakes of different nutrient status. Int. Rev. Gesamten Hydrobiol. 66:529-552.

Scheffer, M. 1998. Ecology of Shallow Lakes. Chapman & Hall, London. 357 p.

Scheffer, M., S. H. Hosper, M-L. Meijer, B. Moss and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecol. and Evol. 8:275-279.

Spencer, D. F. 1987. Tuber size and planting depth influence growth of *Potamogeton pectinatus* L. Am. Midland Natl., 118:77-84.

Tanner, C. C., J. S. Clayton, R. D. S. Wells. 1993. Effects of suspended solids on the establishment and growth of *Egeria densa*. Aquat. Bot. 45:299-310.

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

Vant, W. N., R. J. Davies-Colley, J. S. Clayton and B. T. Coffey. 1986. Macrophyte depth limits in North Island (New Zealand) lakes of differing clarity. Hydrobiologia 137:55-60.

Wetzel, R. G. 1983. Limnology, Second edition. Saunders College Publishing. Philadelphia, PA.

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

Zimmerman, R. C., J. L. Reguzzoni and R. S. Alberte. 1995. Eelgrass (*Zostera marina* L.) transplants in San Francisco Bay: role of light availability on metabolism, growth, and survival. Aquat. Bot. 51:67-86.