ELSEVIER

Aquatic Botany 58 (1997) 1–9

Aquatic botany

Effects of irradiance on growth and winter bud production by *Vallisneria americana* and consequences to its abundance and distribution

C.E. Korschgen *, W.L. Green, K.P. Kenow

U.S. Department of the Interior, Geological Survey, Upper Mississippi Science Center, P.O. Box 818, La Crosse WI 54602-0818, USA

Accepted 13 March 1997

Abstract

Number, total biomass, and individual mass of winter buds of *Vallisneria americana* was significantly related to the depth of the 1% of surface irradiance (Z) and the photosynthetic photon irradiance calculated for each shading treatment imposed during this study. Between the range of 23.8 and 111.2 cm depth for the 1% Z, total biomass of winterbuds produced ranged from 0.63 to 0.01 g, counts ranged from 3.5 to 0.1, and mass of individual winterbuds ranged from 0.18 to 0.04 g. Total biomass of winter buds produced was reduced when plants were exposed to a 14-day period without irradiance during the middle of the growing season. Applying the results of the culture experiments to conditions found in Navigation Pool 8 of the Upper Mississippi River suggests that irradiance may indeed limit the distribution and abundance of *Vallisneria americana* by reducing the number and size of winter buds. © 1997 Elsevier Science B.V.

Keywords: *Vallisneria americana*; Wild celery; Irradiance; Mississippi River; Growth; Winterbuds

1. Introduction

During the last two decades, *Vallisneria americana* has become the dominant member of the submersed aquatic plant community in many of the Upper Mississippi River (UMR) navigation pools (Korschgen, unpublished data). This plant provides important food resources for waterfowl (Korschgen et al., 1988), nursery habitat for fish

* Corresponding author. Tel.: 608-7836451; fax: 608-7836066; e-mail: carl_korschgen@nbs.gov.

PII S0304-3770(97)00014-4

(Poe et al., 1986), substrate for invertebrates (Chilton, 1986; Korschgen and Green, 1988), and also has a strong influence on water quality. *Vallisneria* appears to be better adapted to the high turbidity levels of the UMR than many other submersed species. However, under certain riverine conditions the distribution and abundance of *Vallisneria* have been limited (e.g., high water within Pool 8 during the early 1980s and in several pools during the 1988–1989 drought).

Interactions among key environmental factors such as irradiance, water temperature, sediment texture and composition, and inorganic carbon availability influence the productivity, distribution, and species composition of aquatic macrophyte communities (Barko et al., 1986; Barko et al., 1991b). Recent research has shown that sediment concentrations of phosphorus and especially nitrogen have the potential for limiting production of some aquatic plant species such as *Hydrilla verticillata* and *Myriophyllum spicatum* (Barko et al., 1988; Barko et al., 1991a; Barko et al., 1991b). In an experiment with *Vallisneria americana* cultured under an array of irradiance, sediment fertility, and inorganic carbon conditions, irradiance was the most significant factor affecting shoot biomass (Barko et al., 1991b). Changing irradiance attenuation and nutrient concentrations are believed to be responsible for the fluctuations of submersed macrophytes in the tidal Potomac River (Carter and Rybicki, 1986; Carter and Rybicki, 1990). Many other studies have reported that irradiance availability may limit submersed macrophytes in fresh and saline water.

Various components of water turbidity can affect the productivity of submersed aquatic vegetation. Suspended particulates in the water can physically block the penetration of irradiance through the water column, stained or colored waters absorb the various wavelengths of sunlight differentially, and algae can cause mats or blooms that block sunlight or absorb red and blue wavelengths of sunlight used for photosynthesis. Suspended solids may be harmful to submersed aquatic vegetation when deposited on leaf surfaces by reducing light transmission to photosynthetically active leaf surfaces and possibly altering gas and nutrient exchange.

The availability of irradiance may be the ultimate limiting factor for growth of submersed aquatic plants (Spence, 1982). Research studies on submersed macrophytes suggest that the depth at which intensity of irradiance approximates 1% of the surface irradiance (Z) represents the limit of the biological photic zone (the compensation depth at which photosynthesis and plant respiration are equivalent) (Davis and Brinson, 1980; Barko et al., 1986). In the Potomac River, the depth of 1% Z varied between 1.0 and 2.05 m and no plants were found growing deeper than 2.05 m (Carter et al., 1985). Plant growth under conditions of high turbidity and low irradiance penetration is therefore confined to shallow water.

Although ecological adaptations to nutrients and irradiance appears to determine the distribution of the various submersed plant growth forms, the importance of these environmental factors in controlling growth has yet to be quantified (Chambers and Kalff, 1987). Vegetative persistence of *Vallisneria* within wetlands is determined by two life cycle stages: sprouting of leaves from winter buds (turions) during the spring and production of winter buds at the end of the growing season. The objectives of this study were to determine the irradiance requirements of *Vallisneria americana*, the dominant submersed plant on the UMR, and to relate the findings to riverine conditions.

2. Materials and methods

2.1. Irradiance attenuation

Two culture studies were conducted simultaneously in one 0.04-ha outdoor pond with a minimum depth of 1.0 m. Circular frames constructed of wire mesh and solid black panels of plastic were placed around the sides of the frame to form cylindrical limnocorrals 1 m in diameter. The tops of the limnocorrals were covered with shade cloth. Commercial shade cloths were used to reduce ambient irradiance nominally by 47, 63, 80, 92 and '98%' (by doubling layers of 92 + 80% shade). The accuracy of shade cloth ratings was not important since irradiance was continually recorded within representative limnocorrals. Each treatment was replicated 10 times, and the treatment replicates were randomly positioned within the pond. An electric water pump was used to provide continuous circulation of the water around the limnocorrals, thus preventing thermal stratification within the pond.

Quantum sensors and dataloggers (LI-COR Inc., Lincoln, NE) were used to make and record photometric measurements. Two terrestrial quantum sensors (LI-COR Inc., LI-190SA) were positioned on the sides of the pond to measure irradiance approximately 20 cm above the surface of the water (deck cells). Measurements within the limnocorral were made at two depths in the water by supporting underwater sensors (LI-COR Inc. LI-192SA) on a bracket. These sensors were situated so that the attenuation of the shade cloth (using deck cell readings and water surface readings) and the irradiance extinction coefficient (using the water surface reading and subsurface underwater readings) could be determined for each treatment. No plants were grown in the irradiance-monitored limnocorrals. All sensors were cleaned frequently with a small brush to remove algae growth. Dataloggers were programmed to collect and log the integrated value of irradiance (μmol m^{-2} h^{-1}) in the 400–700-nm waveband. Data were downloaded to a laptop computer once each week.

Readings from terrestrial quantum sensors were averaged to determine the mean hourly photon irradiance. Output files containing readings from the underwater sensors were combined and then merged with the terrestrial readings. Two approaches were used to define the irradiance within each of the limnocorral treatments: (1) calculation of the mean 1% surface irradiance depth (z) and (2) calculation of the photon irradiance received at 50 cm depth for each treatment. Vertical extinction coefficients were calculated for each limnocorral using

$$I_z = I_0 e^{-Kz}$$

(Champ et al., 1980) where I_z = integrated irradiance for underwater sensors at depth z; I_0 = mean integrated irradiance from surface sensors; K = extinction coefficient (natural log/m).

Linear regression was used to determine the 1% Z based upon the extinction coefficients determined for each treatment. This technique permitted prediction of the 1% Z beyond the depth of the pond when the density of the shade cloth was low or irradiance high. Only data between 1100 and 1300 h CST (midday) were used in the calculation of the mean daily depth of 1% Z so that shading effects on the sensors from

the sides of the limnocorrals would be minimized. The photo irradiance over the duration of the experiment was calculated for each treatment, using a general linear models approach. All readings from the sensors were used to calculate photosynthetically active radiation (PAR) at 50 cm, for each hour and date within each treatment. Mean treatment photon irradiances were computed and used to examine relationships with plant growth parameters.

2.2. Culture and measurement of *Vallisneria americana*

Winter buds of *Vallisneria americana* were obtained from a commercial source. Winter buds were planted in 4.7 l buckets, one to a bucket. An upland topsoil was used as the substrate in all experiments conducted to promote growth (Smart and Barko, 1985). The topsoil filled about half of the bucket and was covered with a thin layer of sand to reduce resuspension of the sediment. Winter buds were placed near the sediment surface to facilitate emergence. The experiment was conducted between 9 May and 15 October, 1990. Contents of the buckets were screened on 15 October, after senescence of the above ground parts, to determine production of winter buds. The total dry weight biomass of winter buds produced from each planted winter bud was determined by weighing all winter buds from the bucket. The mean mass of winter buds was determined by dividing the biomass by the count (each basal ring was tallied as a winter bud). We used regression analysis to assess the effects of photic depth (1% and photon irradiance) on winter bud biomass, counts, and mean mass.

The second experiment was designed to determine if the timing of a 14-day aphotic period would influence the production of winter buds. Shade cloth treatment 63 was used over all limmnocorral buckets and winterbuds as described above. Fifty limnocorrals, broken down into 5 treatments and one control blocks each with 10 replicates, were dedicated to this experiment and another 10 limnocorrals from the first experiment contained controls. Five 14-day aphotic periods were selected: 7–21 May, 4–18 June, 2–16 July, 30 July–13 August, and 4–18 September. At the designated time the top of the limnocorral was covered for 14 days with a solid black top to eliminate all irradiance. The substrate in which the plants were growing was screened at the same time as the substrate for the first experiment and the winter buds counted and weighed. We used ANOVA techniques to compare winter bud biomass, counts, and mean mass among photic periods.

2.3. Collection of field data

Water samples were collected weekly from May through August at five sites in the lower portion of Navigation Pool 8 during 1983 and 1984. Samples were generally collected between 1000 and 1300 h, chilled on ice, and transported to the laboratory where they were refrigerated. Water samples were analyzed for total suspended solids (nonfilterable residue dried at 103–105°C) (American Public Health Association, 1980). At the same time and sites, a photometer (Kahl Scientific Co., Model 268WA310) was used to collect data on PAR at 10-cm intervals through the water column. The depth of the 1% Z was calculated based upon the regression of the surface reading and the 10-cm

readings through the water column to the bottom. In 1985, water samples were not taken, but irradiance measurements were taken weekly at 25 sites in lower Pool 8. Water depths in Pool 8 were determined during the 1989–92 period by J. Rogala (unpublished data, Environment Management Technical Center, Onalaska, WI) using a boat equipped with a bathymetry system. Depth data were interpolated to provide a generalized depth map for the study area.

3. Results

Winter bud production varied with the different treatment regimes (Table 1). Because of obvious increases in the variances with 1% Z, we weighted by 1/variance in a weighted least squares (WLS) approach for regression analysis (Neter et al., 1990). Using the WLS approach gave approximately the same intercepts and slopes, but the standard errors associated with the estimates were smaller for the weighted analysis. For winter bud biomass and count, the lack of fit F-test (Neter et al., 1990) was significant for both weighted analysis ($F = 12.46$; 3, 44 df; $P = 0.0001$ for biomass and $F = 7.99$; 3, 44 df; $P = 0.0002$ for count respectively) and unweighted analysis ($F = 2.65$; 3, 44 df; $P = 0.0605$ and $F = 7.44$; 3, 44 df; $P = 0.0004$ for biomass and count respectively), indicating that the regression models do not predict the means of the treatment groups well. However, a significant linear relationship existed between the actual values and 1% photic depth for biomass ($r^2 = 0.43$; $P < 0.0001$), winter bud count ($r^2 = 0.61$; $P < 0.0001$), and mean mass of individual winter buds ($r^2 = 0.61$; $P < 0.0001$) using the WLS approach. Similar analyses and results were found for the relationship between the plant parameters and the photon irradiance at 50 cm (Table 1); winter bud biomass ($r^2 = 0.54$; $P < 0.0001$), count ($r^2 = 0.31$; $P = 0.0004$), and mass ($r^2 = 0.53$; $P < 0.0001$).

There was a significant difference between the means of the biomass of winter buds produced ($F = 3.03$; 5, 54 df; $P = 0.0175$) in relation to the timing of the aphotic period (Table 2). The count and mean mass of winter buds ($F = 1.86$; 5, 54 df; $P = 0.1164$) and ($F = 2.18$; 5, 47 df; $P = 0.0721$, respectively) produced did not vary significantly. There was an obvious trend for suppression of winter bud size when the aphotic period occurred during the middle of the growing season, 2–16 July.

Table 1
Summary of mean (±s.e.) winter bud measurements in relation to mean depth of the 1% Z and the cumulative photosynthetic photon irradiance at 50 cm from 9 May to 15 October, 1990

1% Z (cm)	Photon irradiance (mol m^{-2})	Winter bud measurements		
		biomass (g) per sample	count per sample	mass (g) per winter bud
111.2	168.1	0.63±0.13	3.52±0.60	0.18±0.02
80.3	117.3	0.60±0.10	5.05±0.68	0.12±0.02
55.2	66.2	0.21±0.05	2.30±0.40	0.09±0.02
46.9	30.4	0.06±0.01	1.30±0.37	0.05±0.01
23.8	4.6	0.01±0.01	0.15±0.11	0.04±0.03

Table 2
Summary of mean (±s.e.) winter bud measurements for each aphotic treatment. Within a column, means with the same letter do not differ ($P = 0.05$)

Aphotic period	Winter bud measurements		
	biomass (g) per sample	count per sample	mass (g) per winter bud
7–21 May	0.43±0.13 AB	3.7±1.0 AB	0.14±0.02 A
4–18 June	0.62±0.13 A	5.1±0.9 A	0.11±0.01 AB
2–16 July	0.19±0.06 B	2.2±0.6 B	0.07±0.01 B
30 July –13 August	0.33±0.07 AB	4.0±0.8 AB	0.08±0.01 B
4–18 September	0.27±0.07 B	3.0±0.7 AB	0.09±0.09 AB
None	0.60±0.15 A	5.1±1.1 A	0.13±0.02 A

During the growing seasons of 1983–1985, water quality and irradiance data (PAR) were collected at sample sites in open water portions of Pool 8. The mean 1% photic depths were 112 ± 30 cm ($n = 54$) in 1983, 107 ± 27 cm ($n = 153$) in 1984, and 105 ± 28 cm ($n = 262$) in 1985. The mean suspended solids concentrations at the same sites were 26 ± 12 mg l^{-1} ($n = 52$) in 1983 and 34 ± 15 mg l^{-1} ($n = 162$) in 1984. Fig. 1 illustrates the linear regression between suspended solids and the 1% photic depth based on the 1983 and 1984 data. Measurements of the water depths in *Vallisneria* beds in Pool 8 indicated that the mean depth was 0.88 ± 0.14 m ($n = 554$). This depth represents approximately the 3% surface irradiance depth over the 1983–1985 period.

The predictive value of the 1% surface irradiance depth based upon suspended solids (1% $Z = 164 - 1.37 * ss$) was substituted into the regression models for the relationship between biomass and count of winter buds and depth of the 1% Z. These relationships are shown in Fig. 2. When the count of winter buds produced drops below 1 then the population would not expected to be sustained. The irradiance attenuation treatments in

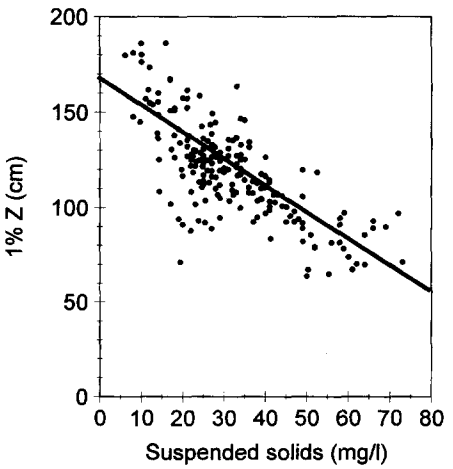

Fig. 1. Relationship between suspended solids and depth of the 1% Z in Navigation Pool 8.

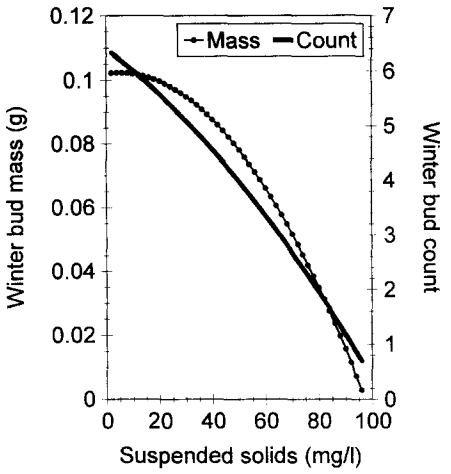

Fig. 2. Estimated relationship between winter bud count per initial plant and mass of winter buds to the concentration of suspended solids (mg/l).

terms of their effects on the 1% Z used during this experiment closely approximated conditions in the UMR.

4. Discussion

We related the plant variables (winter bud biomass and count) measured in this study to suspended solids concentration in Pool 8. Results from this study indicate that the distribution of *Vallisneria* in UMR Navigation Pool 8 is probably influenced by water turbidity. The productivity of *Vallisneria* can be limited by turbid conditions in the fall when winter buds are produced. Irradiance attenuation by suspended solids in the water during the spring can potentially reduce vigor of plants, thereby limiting production of additional rosettes on stolons. Normally, each rosette has the capability of producing winter buds (Korschgen, unpublished data), so a decrease in rosette production may decrease the standing crop of *Vallisneria* winter buds. Reduction in PAR during the middle of the growing season has a pronounced impact on winter bud production, primarily by reducing the size of the winter buds. Winter buds which are smaller produce smaller plants the following spring (Hoover, 1984; Korschgen, unpublished data). In a dynamic riverine system such as the UMR, plants arising from large winter buds will have the best opportunity for survival.

If the photic environment and depth morphology are known for various pools or reaches of the UMR, it may be possible to predict the potential abundance and distribution of *Vallisneria*. A total of 1500 ha of Pool 8 is between 100 and 200 cm in depth. Because of the shallow nature and morphology of this area, moderate increases in the 1% photic depth substantially increase the potential area that *Vallisneria* could colonize. For instance, increasing the mean annual depth of 1% Z from 100 to 150 cm in

Pool 8 could potentially increase the total area suitable for *Vallisneria* beds from 1379 to 2664 ha. Once the size of the beds reached this potential size, they would be expected to reduce the ambient levels of turbidity by changing the hydrology of the pool.

Short term changes in water levels, discharges, and turbidity in the UMR are to be expected. Thus, management plans will have to be formulated on a set of average expected conditions. Habitat rehabilitation and enhancement projects should attempt to limit suspended sediments to < 20 mg l^{-1} so that the annual 1% Z will be between 1–1.5 m in depth. This depth should provide for adequate light energy for successful growth and reproduction and enough potential habitat area for good aquatic plant distribution and diversity. If management plans attempt to exceed conditions for *Vallisneria*, then other submersed plant species should flourish.

Quantitative studies need to be conducted to determine if other habitat variables, especially water and sediment nutrient concentrations, are limiting factors for the growth of aquatic plants on the UMR. Other questions which have management significance are (1) what is the influence of winter bud size on the survivability of *Vallisneria* growing in a variety of water regimes, (2) what is the potential of *Vallisneria* to reestablish itself from seeds, and (3) what is the general photic environment for the UMR and tributaries?

Acknowledgements

We are grateful to J. Barko and K. Lubinski for their support of this study. We thank L. Ames, N. Johnson, J. Patterson, M. Schuller, M. Steiner, M. Steingraber, W. Thrune, and L. Wlosinski, for assistance with the study. T. Shaffer and W. Newton provided statistical consultation. J. Barko, S. Rogers, S. Gutreuter, and M. Wise provided helpful suggestions on the manuscript.

References

American Public Health Association, 1980. Standard methods for examination of water and wastewater, 15th ed. Washington, D.C.

Barko, J.W., Adams, M.S., Clesceri, N.L., 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: A review. J. Aquat. Plant Manage. 24, 1–10.

Barko, J.W., Smart, R.M., Chen, R.L., McFarland, D.G., 1988. Interrelationships between the growth of *Hydrilla verticillata* (L. f.) Royle and sediment nutrient availability. Aquat. Bot. 32, 205–216.

Barko, J.W., Gunnison, D., Carpenter, S.R., 1991a. Sediment interactions with submersed macrophyte growth and community dynamics. Aquat. Bot. 41, 41–65.

Barko, J.W., Smart, R.M., McFarland, D.G., 1991b. Interactive effects of environmental conditions on the growth of submersed aquatic macrophytes. J. Freshwater Ecol. 6, 199–207.

Carter, V., Paschal, Jr., J.E., Bartow, N., 1985. Distribution and abundance of submersed aquatic vegetation in the tidal Potomac River and estuary, Maryland and Virginia, May 1978 to November 1981 — A water quality study of the tidal Potomac River and estuary. U.S. Geological Survey, Water Supply Pap. 2234-A, pp. 46.

Carter, V., Rybicki, N., 1986. Resurgence of submersed aquatic macrophytes in the tidal Potomac River, Maryland, VA, and the District of Columbia. Estuaries 9 (4B), 368–375.

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

Chambers, P.A., Kalff, J., 1987. Light and nutrients in the control of aquatic plant community structure. I. In situ experiments. J. Ecol. 75, 611–619.

Champ, M.A., Gould III, G.A., Bozzo, W.E., Ackelson, S.G., Verra, R.C., 1980. Characterization of light interaction and attenuation in Chesapeake Bay, August 1977. In: Kennedy, V.S. (Ed.), Estuarine Perspectives. Academic Press, New York, pp. 263–277.

Chilton, E.W., 1986. Macroinvertebrate communities associated with selected macrophytes in Lake Onalaska: Effects of plant type, predation, and selective feeding, Ph.D. Thesis. Ohio State University, Columbus, pp. 166.

Davis, G.J., Brinson, M.M, 1980. Responses of submersed vascular plant communities to environmental change. FWS/OBS-79/33. pp, 70.

Hoover, D.T., 1984. Reproductive ecology of two submersed macrophytes in varying pH regimes, M.A. Thesis. State University of New York, Binghamton, pp. 87.

Korschgen, C.E., George, L.S., Green, W.L., 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, pp. 237–249.

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

Neter, J., Wasserman W., Kutner, M.H., 1990. Applied linear statistical models: Regression, analysis of variance, and experimental design. Irwin, Homewood, IL, pp. 1181.

Poe, T.P., Hatcher, C.O., Brown, C.L., Schloesser, D.W., 1986. Comparison of species composition and richness of fish assemblages in altered and unaltered littoral habitats. J. Freshwater Ecol. 3, 525–536.

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

Spence, D.N.H., 1982. The zonation of plants in freshwater lakes. Adv. Ecol. Res. 12, 37–125.