

ABIOTIC INFLUENCES ON THE BIOMASS OF *VALLISNERIA AMERICANA* MICHX. IN THE UPPER MISSISSIPPI RIVER[†]

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ABSTRACT

American wildcelery, *Vallisneria americana* Michx. is an ecologically important component of aquatic communities in the Upper Mississippi River (UMR). We conducted a study in 2002 to determine the association of several abiotic factors on the vegetative growth of *Vallisneria* in Navigation Pool 8 (Pool 8) of the UMR. We measured turbidity, percent light absorbance, surface water ammonium, surface water nitrate, current velocity, conductivity, pH and water depth throughout one growing season at 56 stratified sites based on where *Vallisneria* occurred in previous years. Sediment and aboveground biomass samples were collected during peak growth. Sediment was analysed for organic content, particle size, pore water nitrate and pore water ammonium. *Vallisneria* biomass samples were dried to constant mass. Because some sites were without water for much of the growing season, only data from 52 sites were reported. Biomass was associated with depth, percent light absorbance, turbidity and wind fetch. *Vallisneria* was abundant in the depth range of 0.55 to 1.03 m, in areas receiving at least 38% of surface light and in areas exposed to greater wind fetch (>2000 m). Our results suggest that the primary abiotic variable associated with *Vallisneria americana* in the UMR is light, not nutrients. Published in 2007 by John Wiley & Sons, Ltd.

KEY WORDS: *Vallisneria americana*; American wildcelery; upper Mississippi river; nutrients; light

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INTRODUCTION

American wildcelery, *Vallisneria americana* Michx. (hereafter *Vallisneria*), is an important component of macrophyte communities in the Upper Mississippi River (UMR). The winter buds provide high-energy food for migrating waterfowl (Korschgen and Green, 1988; Schloesser and Manny, 1990). Macroinvertebrates use *Vallisneria* as an attachment site for grazing (Chilton, 1990). Fish use *Vallisneria* as food and shelter from predation, for spawning ground and as cover for larval fish (Schulthorpe, 1967). Like most macrophytes, *Vallisneria* affects dissolved oxygen concentrations (Carpenter and Lodge, 1986), serves as a nutrient source and sink (Barko and Smart, 1981; Saunders and Kalff, 2001), promotes sedimentation and reduces water flow (Carpenter and Lodge, 1986).

Korschgen and Green (1988) provided a comprehensive literature review of the ecology of *Vallisneria*. Water depth and turbidity, hydrostatic pressure, substrate types, water temperature, flow velocity, alkalinity, pH and salinity were among the major factors reported to affect *Vallisneria* productivity. Several studies in the UMR that associated *Vallisneria* productivity with environmental conditions were reported. Kimber *et al.* (1995a) estimated the maximum depth that would support *Vallisneria* in the UMR under the turbid conditions of 1992 was 0.8 m. Kimber *et al.* (1995b) showed that seeds incubated in ponds on sediment collected from Lake Onalaska of the UMR germinated under as little as 2% of full sunlight. However, survival was significantly higher and bud production was restricted to the 9% and 25% light treatments. Rogers *et al.* (1995) suggest that *Vallisneria* growth on intrinsically infertile sediments in the UMR may depend on a continuous nitrogen supply from the sediment and the conditions in Lake Onalaska (1992) were suitable for *Vallisneria* restoration. Korschgen *et al.* (1997) applied results of a

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culture study to Pool 8 of the UMR and suggested that irradiance might indeed limit the distribution and abundance of *Vallisneria*.

The three studies cited above were either conducted in the laboratory, cultured or involved a limited number of field sites. Our approach was to collect environmental data at a large number of biomass-monitoring sites to identify those environmental variables most associated with peak *Vallisneria* shoot biomass. Variables that are typically correlated with macrophyte biomass (Barko *et al.*, 1986; Korschgen and Green, 1988) were chosen. We measured surface water ammonium, surface water nitrate, pore water ammonium, pore water nitrate, sediment moisture, sediment particle size, current velocity, water depth, turbidity, percent light absorbance, pH and conductivity at 56 sites in Pool 8, UMR.

METHODS

Study site

We conducted our study in Pool 8 of the UMR, which lies approximately 1093 to 1131 km upstream from the confluence of the Ohio River. The pool is located between Navigation Lock and Dam 7 at Dresbach, Minnesota (river km 1131) and Navigation Lock and Dam 8 at Genoa, Wisconsin (river km 1093; Figure 1). The two primary rivers that enter the pool are the La Crosse River, which enters from the east and the Root River, which enters from the west. The pool has five distinct aquatic strata: main channel border areas, impounded areas, backwaters, side channels and the main navigation channel (Wilcox, 1993). Forty-five percent of the pool consists of the impounded area, which is a vast open water area directly upstream of the lock and dam. Side channels and backwater areas are found in the upper two-thirds of the pool. The majority of water flow is restricted to the main channel and side channels and there is only significant flow into the backwaters during flooding events. From 17 June 2002 to 16 September 2002, water in lower Pool 8 was reduced by 0.43 m below the usual low stage at Lock and Dam 8 by the US Army Corps of Engineers. This reduction or 'draw down' was intended to enhance emergent vegetation growth.

Submersed macrophytes are found in all areas except for the main channel. *Vallisneria* is one of the dominant submersed species in the impounded area and is also present in backwater, side channel and main channel border areas (Yin *et al.*, 2000).

Fifty-six study sites (Figure 1) were selected in Pool 8 based on the known occurrence of *Vallisneria* sampled during routine monitoring for the Long Term Resource Monitoring Program (LTRMP, Yin *et al.*, 2000). The LTRMP protocols required that aquatic plants at a site were given a density reading of 0–6 based on the number of plants on a garden rake. The tines of the rake are marked into six equal parts. A density reading of 0 indicated that the particular plant did not exist at the site and a density reading of 6 indicated that the plant was the dominant species. Data from 1998 to 2000 were used to determine the density of *Vallisneria* at a particular site. From the 1789 sites sampled during the 3 years, 8 sites were randomly selected for each density rating. Because *Vallisneria* is typically found in open water areas with some water flow, 35 sites were in the impounded area. The other 21 sites were in main channel border, backwater contiguous and side channel areas. Sites were restricted to the downstream two-thirds of the pool for ease of sampling and access by boat. Sites that exceeded 2.5 m water depth were not sampled.

Experimental design

Sites were sampled every 2 weeks from 20 May 2002 to 16 September 2002. The surface water ammonium, surface water nitrate, current velocity, water depth, turbidity, percent light absorbance, pH and conductivity were measured at each site. A global positioning system unit (Garmin[®], NAD27 datum, average accuracy reading = 5 m) was used for navigation to the sites. Photon irradiance ($\mu\text{m}^2/\text{h}$) was measured at each site with a terrestrial surface sensor (LI-COR, Inc., Lincoln, NE, LI-192SA) and at the top of the plant canopy with an underwater quantum sensor (LI-190SA) and stored on a datalogger (LI-COR, Inc.). Photon irradiance was used to calculate percent light absorbance. Percent light absorbance was the difference in the light from above the surface of the water to the top of the plant canopy. Conductivity and pH were measured with a minisonde 4A (Hydrolab-Hach Company, Loveland, CO), turbidity with a turbidimeter (Model 2100P, Hydrolab-Hach Company)

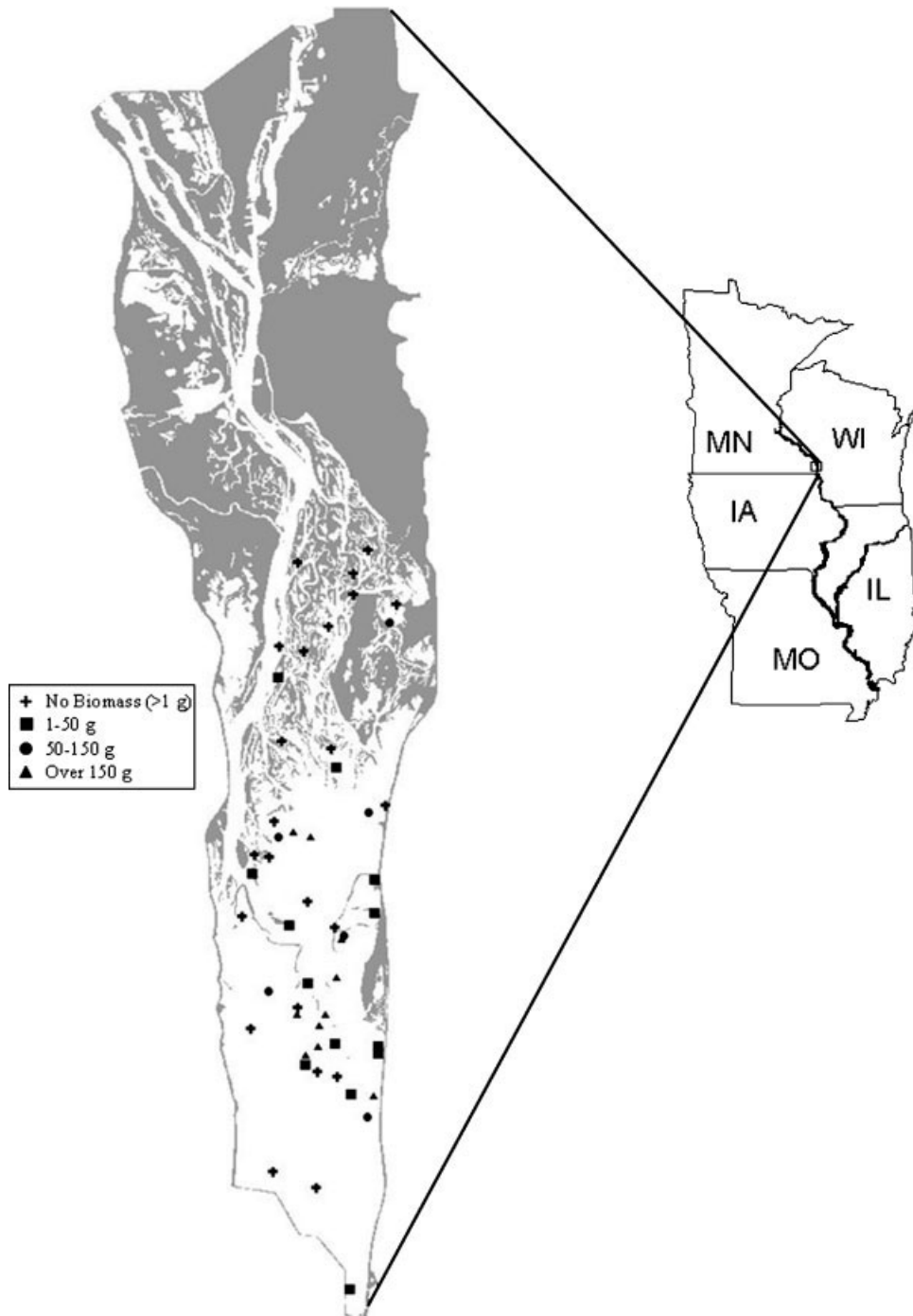


Figure 1. Upper Mississippi River System, highlighting Pool 8. Symbols indicate biomass density at each of the 52 sample sites. IA = Iowa, IL = Illinois, MN = Minnesota, MO = Missouri and WI = Wisconsin.

and current velocity with a velocimeter (Model 2000, Marsh-McBirney, Inc., Frederick, MD). Water samples were collected at 20 cm below the water surface, filtered (0.45- μ m Nalgene[®] filter), acidified with one drop of concentrated sulphuric acid and stored on ice for transport to the laboratory. Samples were analysed for ammonium and nitrate on a continuous-flow autoanalyser (AAII, Bran + Luebbe, Norderstedt, Germany) according to standard methods (APHA *et al.*, 1998).

Wind fetch readings were obtained for each site from a GIS model generated with ARC/INFO[®] (ESRI, Redlands, CA). The model accounted for average wind direction at each site from 15 years of data (Rogala, 1997). Once the wind direction was determined, effective fetch was calculated by dividing the sum of the cosine-weighted distances by the sum of the cosine weights ($L_f = \sum x_i^* \cos \gamma_i / \sum \cos \gamma_i$, where L_f = effective fetch; x_i = distance to land; γ_i = deviation angle).

Vegetation and sediment sampling

In the field, *Vallisneria* shoot biomass and sediment cores were collected in August. Six subsampling areas at each site were numbered clockwise starting at the front right corner of the boat (Yin *et al.*, 2000). Of the six subsampling areas, two quadrats, either one and three or four and six, were taken from one side of the boat and one quadrat, either two or five, was taken on the other side. The decision as to which side received two quadrats was made randomly. A technician placed a 1.5-m \times 0.36-m aluminium quadrat at each subsample area, and manually harvested all aboveground, rooted, macrophyte tissue within the quadrat. Macrophytes were sorted and identified to species with nomenclature following Gleason and Cronquist (1991), placed in plastic bags, labelled and stored on ice for transport to the laboratory. Plant voucher specimens were taken from all sites and stored in the University of Wisconsin-La Crosse herbarium. After macrophytes were harvested, the technician extracted a sediment core from the middle of the quadrat with a 5-cm diameter sediment core sampler (Wildlife Supply Co., Buffalo, NY). The top 15 cm of sediment was extruded, homogenized and stored on ice for transport to the laboratory.

In the laboratory, plants were sorted by species, dried to constant weight in an oven (Model 1406, General Sigma Company, Blue Island, IL) at 80°C, weighed, placed in labelled bags and stored. Only *Vallisneria* biomass was recorded. Within 24 h of collection, sediment samples were centrifuged for analysis of pore water nitrate and pore water ammonium and samples were extracted for exchangeable ammonium associated with the sediment particles (Caffrey and Kemp, 1992). Samples were filtered (Seraclear[®] filter), acidified with 10% sulphuric acid and stored at 4°C. Samples were analysed with a Bran-Luebbe[®] autoanalyser. Sediment samples were also analysed for carbon content by combustion at 550°C (Plumb, 1981) and particle size by the hydrometer method (Patrick, 1958).

Data analysis

Sites were classified as one of three sediment types (Yin *et al.*, 2000): (1) sand, if large particles ($\geq 50 \mu\text{m}$) exceeded 90%, (2) silt/clay, if large particles were $< 50\%$ and (3) sand with silt/clay, otherwise. Daily water depth was calculated based on the elevation of the site and daily river stage data from the US Army Corps of Engineers (St. Paul, MN) gage stations.

Data were analysed for assumptions of normality and homogeneity of variances. Biomass data were converted to g/m^2 and the mean of the three subsampling areas was used for analysis. Shoot biomass data were log transformed to meet the assumption of homogeneity of variances. A value of one was added to the data prior to transformation to ensure that none of the transformed data were undefined.

Data were analysed ($\alpha = 0.05$) for the association of all independent variables (photon irradiance, pH, conductivity, turbidity, current velocity, water depth, surface water ammonium, surface water nitrate, wind fetch, organic carbon content of sediment, pore water ammonium, pore water nitrate and sediment particle size) with peak shoot biomass (dependent variable) using PROC GLM (SAS, 2000). To determine individual associations with peak *Vallisneria* shoot biomass, variables that were measured throughout the growing season were averaged by site and the mean of the subsampling areas was taken for the sediment variables.

RESULTS

Vallisneria occurred in 34 of 56 sites (Figure 1). Five of these sites had $\leq 1 \text{ g}$ dry shoot biomass and were counted as 'no biomass' sites because we were uncertain if the small amount of biomass was actually found in the site or if had floated into the site during collection. Four sites were without water for some of the sampling period and were eliminated from further analyses, resulting in a sample size of 52.

Table I. Mean, minimum and maximum values for the independent variables averaged throughout the growing season ($n = 52$ for all variables except pore water ammonium and pore water nitrate ($n = 43$))

Variable	Mean (SE)	Minimum	Maximum
Conductivity ($\mu\text{S}/\text{cm}$)	348 (2.53)	296	399
Depth (m)	0.74 (0.06)	0.27	2.10
Surface NH_x (mg/L)	0.077 (0.002)	0.059	0.13
Surface NO_x (mg/L)	1.09 (0.06)	0	1.61
pH	8.20 (0.03)	7.28	8.86
Turbidity (NTU)	15 (0.57)	6	27
Current velocity (m/s)	0.091 (0.02)	0	0.56
Wind fetch (m)	1716 (166)	29	3413
Percent light absorbance	67.78 (2.00)	44.82	97.48
Pore water NH_x ($\mu\text{g}/\text{g}$)	2.22 (0.24)	0.09	9.18
Pore water NO_x ($\mu\text{g}/\text{g}$)	0.004 (0.0007)	0	0.023
Extractable NH_x ($\mu\text{g}/\text{g}$)	41.14 (3.98)	1.34	113.94
Extractable NO_x ($\mu\text{g}/\text{g}$)	0.164 (0.026)	0	1.19
% Organic content	2.28 (0.18)	0.29	5.68
% Sand	65 (3.18)	18	97
% Silt	10 (0.80)	2	23
% Clay	25 (2.59)	1	65

Values for mean represent mean ± 1 SE.

NH_x = ammonium + ammonia.

NO_x = nitrate + nitrite.

Biomass was significantly related to percent light absorbance ($F_{(1,51)} = 7.13$, $p = 0.0104$), turbidity ($F_{(1,51)} = 5.88$, $p = 0.0192$), water depth ($F_{(1,51)} = 14.18$, $p = 0.0005$) and wind fetch ($F_{(1,51)} = 12.31$, $p = 0.0010$, model $R^2 = 0.5673$). Shoot biomass decreased with increased turbidity and increased with wind fetch. The most abundant biomass was found in areas with a turbidity reading < 20 nephelometric turbidity units and in areas with a wind fetch ≥ 1500 m. *Vallisneria* was most abundant in the depth range of 0.55 to 1.03 m.

There were no significant relationships between exchangeable ammonium and shoot biomass or the other nitrogen compounds and shoot biomass. No significant relationships were found between biomass and the rest of the independent variables. Particle size was not significantly associated with shoot biomass; however, variability in particle size content was low. Thirty-five sites contained $\geq 50\%$ sand and nine sites had $\geq 90\%$ sand. Organic content was low in the study sites, with a maximum value of $< 10\%$ (Table I).

DISCUSSION

Results from this field study suggest peak *Vallisneria* shoot biomass in the UMR is associated with sites with higher light availability. Whereas Nichols (1992) characterized *Vallisneria*'s ability to tolerate turbid water, other studies on *Vallisneria* seedlings grown from tubers and seeds have shown that decreased light attenuation leads to decreased plant growth (Kimber *et al.*, 1995a; Korschgen *et al.*, 1997). Kimber *et al.* (1995b) reported at high turbidity levels ($\geq 99\%$ light absorbance), *Vallisneria* could only grow in depths ≤ 0.8 m in the UMR. In this study, optimal water depth for growth was 0.5–1.1 m. No biomass was found at sites with light absorbance $\geq 80\%$, although *Vallisneria* has been reported to grow at depths with $\leq 0.5\%$ of surface light (Meyer *et al.*, 1943). Others report optimal growth at 0.3–1.5 m (Hunt, 1963) for the Detroit River and 0.3–3.2 m (Nichols, 1999) for Wisconsin lakes. Optimal depth measures for this study could have been affected because of the water elevation reduction in the pool during the growing season.

Although light availability was related to distribution, *Vallisneria* biomass increased with an increase in wind fetch possibly due to lack of competition from other macrophytes. Increased wind typically leads to increased water turbulence, turbidity and sediment resuspension (Bailey and Hamilton, 1997). Increased turbidity may decrease

shoot biomass because of lower light attenuation (Doyle, 2001); however, increased turbulence and water movement can also increase the production of biomass (Schulthorpe, 1967). Submersed plants tend to increase structural tissue (i.e. biomass) when exposed to moving water. Because *Vallisneria* has adapted to grow in areas receiving some turbulent flow, it is able to grow in areas exposed to higher wind fetches unlike most macrophytes that grow better in areas where there is little or no flow (Peck and Smart, 1986).

Nitrogen did not appear to be growth limiting in this study. Ammonium is the preferred nitrogen compound of macrophytes because it can be readily taken up (Wetzel, 2001). The primary nutrient source for *Vallisneria* is typically the sediment (Barko and Smart, 1981), and concentrations of surface water ammonium were low, suggesting that *Vallisneria* did absorb most ammonium through its roots. In a nutrient availability study, Rogers *et al.* (1995) determined that at extractable concentrations of 11 μg nitrogen/g dry weight of sediment, nitrogen is potentially limiting to *Vallisneria* growth in the UMR. In our study, the average extractable ammonium concentration was 38.58 μg N/g dry weight sediment, indicating current ammonium concentrations were not limiting growth. In another study, Barko *et al.* (1991b) determined that increased light attenuation, not sediment nutrient and inorganic carbon additions, increased *Vallisneria* shoot biomass.

Phosphorus was not measured in this study because previous studies have shown that increases of nitrogen rather than phosphorus result in higher macrophyte biomass (Anderson and Kalff, 1986; Rogers *et al.*, 1995). Barko *et al.* (1991a) suggest that phosphorus-limitation rarely occurs because there are large reservoirs of exchangeable phosphorus available in sediment that are adequate for macrophyte growth.

We were unable to find a significant association between substrate type and *Vallisneria* distribution in this study, although previous studies have found that *Vallisneria* is typically associated with substrates that consist mostly of sand with silt/clay (Hunt, 1963; Nichols, 1992). The majority of our sites consisted of this substrate. Only five sites were in backwater contiguous areas where the substrate is typically silt/clay with sand, whereas 34 sites were in the impounded area where the substrate is sand with silt/clay. Further analyses of *Vallisneria* abundance in backwater sites versus impounded sites are needed to determine the significance of substrate type on biomass production. Also, because time limitations forced us to sample during a year when water flow was reduced, additional studies should be done to determine the association of velocity with *Vallisneria* biomass production.

Overall, this study suggests that during the year of study, light, rather than nutrients, was the main abiotic factor associated with the peak *Vallisneria* shoot biomass in Pool 8.

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