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Evaluation of the Growth of *Vallisneria americana* Michx. in Relation to Sediment Nutrient Availability

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ABSTRACT

Rogers, S. J., D. G. McFarland, and J. W. Barko. Evaluation of the growth of *Vallisneria americana* Michx. in relation to sediment nutrient availability. *Lake and Reserv. Manage.* 11 (1):57-66.

A recent (1988-1991) decline of *Vallisneria americana* Michx. (wildcelery) in Lake Onalaska, Wisconsin, prompted coordinated laboratory and field studies to evaluate the capacity of different sediments in the lake to support *Vallisneria* growth. Two sites were selected that formerly supported *Vallisneria* beds but differed in hydrologic patterns and sediment characteristics. Sediment from Site 1 (the protected site) was predominantly fine-textured, with a silt-clay particle fraction of 77 percent; sediment from Site 2 (the unprotected/open water site) contained 79 percent coarse-grained sand. In the laboratory study, production and morphology of *Vallisneria* were examined on nonamended sediments from each site and on the same sediments amended by additions of N and P. In the field study, *Vallisneria* tubers were planted at the two sites and harvested after 12 weeks of growth to compare morphology and tissue nutrient concentrations. In order to account for local temperature and light conditions, surface water temperature, Secchi depth, and light attenuation were monitored on a weekly basis. Laboratory study results revealed that increased N availability (by N addition) generally increased total biomass production and plant height, and to a lesser extent, tuber and seed pod production. Additions of P had little overall positive effect on *Vallisneria* growth. Where growth was limited, N concentrations in aboveground plant tissues were below the critical N level established for this species. However, in all treatments of the study, aboveground tissue P concentrations were adequate for growth. In the field study, *Vallisneria* grew well at both sites and apparently was not limited by N or P. The only significant difference in growth between the two study sites was in maximum plant height (greater at site 2), probably a response by *Vallisneria* to differences in ambient light conditions between the two sites. Marked differences between field and greenhouse study results suggest that growth of *Vallisneria* on intrinsically infertile sediments may depend on a continuous N supply to the sediments, most likely via sedimentation. Present (1992) conditions in Lake Onalaska are suitable for growth; thus, reestablishment of *Vallisneria* in the lake is likely, as long as conditions remain unchanged.

Key Words: *Vallisneria*, Lake Onalaska, Upper Mississippi River, sediment fertility, nitrogen, phosphorus, growth, biomass production.

A recent (1988-1991) decline of the submersed macrophyte *Vallisneria americana* Michx. (wildcelery) in Lake Onalaska, Wisconsin, has prompted interest in conditions that may influence its recovery. Lake Onalaska (Figure 1), a relatively large (2,835 ha) backwater system located in navigation Pool 7 of the Upper Mississippi River (UMR), is shallow (mean depth = 1.3 m) and has supported abundant aquatic vegetation since it was formed by impoundment in 1937 (Green 1960). In the mid-1980s, *Vallisneria* dominated the greater than 1200 ha of submersed vegetation within the lake (C. Korschgen, Northern Prairie Research Center, La Crosse, WI, personal communication). However, following a three-year drought (1987-1989), *Vallisneria* declined dramatically to less than 121 ha.

There has been interest in restoring *Vallisneria* in Lake Onalaska by means of massive transplantation efforts. *Vallisneria* can help to improve water quality by stabilizing mucky sediments, filtering out suspended particulates, and taking up nutrients that can otherwise support nuisance algal growth (Korschgen and Green 1988; Korschgen 1990; Barko et al. 1991a). Nearly all parts of this macrophyte, especially tubers and rootstocks, can be eaten by a variety of aquatic animals and migrating waterfowl (Haller 1974; Korschgen et al. 1988). Additionally, its leaves provide habitat and shelter for invertebrate communities and spawning sport fish (Muencher 1944; Haller 1974; Poe et al. 1986). Because of the ecological importance of *Vallisneria* in this UMR pool (Korschgen and Green 1988), the potential for this species to become

reestablished needs to be evaluated.

One of several factors potentially contributing to the decline of *Vallisneria* in association with drought conditions is change in sediment nutrient availability (Rogers 1994). In order to sustain macrophyte growth from year to year in aquatic systems, nutrient supplies in sediments need to be replenished by sedimentation and other means, as they become depleted due to diffusional losses and plant uptake (Barko et al. 1988, 1991a). Altered patterns and magnitudes of sediment accretion in Lake Onalaska, which likely occurred during the drought, may have influenced the balance between nutrient losses and replenishment. Thus, it is important to evaluate nutritional conditions in lake sediments before attempting restoration efforts.

The investigation reported here focused specifically on the growth of *Vallisneria* in relation to sediment nutrient availability. The objective of the investigation was to determine the availability of nitrogen (N) and phosphorus (P) for the growth of *Vallisneria* in Lake Onalaska at present (1992). These two elements, in particular N, are the most probable among sediment-derived nutrients to result in macrophyte growth limitation due to deficiency (Barko et al. 1991a).

The investigation consisted of coordinated laboratory and field studies. Laboratory studies were conducted in a greenhouse to determine potential nutrient limitation in *Vallisneria* grown on different sediments from Lake Onalaska under optimal conditions of water temperature and irradiance (Barko et al. 1982). Field studies were conducted in Lake Onalaska to evaluate the growth of this species on the same sediments *in situ* under conditions in which the influences of water temperature, irradiance, and other factors (not reproducible in the laboratory) might interactively affect growth (Barko et al. 1991b).

Methods and Materials

Laboratory Studies

Studies were conducted May through July 1992 in a greenhouse facility at the U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi. Eight 1200-L fiberglass tanks were filled 83 cm deep with a low-alkalinity culture solution described in Smart and Barko (1985). One liquid circulator per tank provided continuous water circulation and temperature control at $25 \pm 1^\circ\text{C}$. The solution was aerated with humidified air to enhance mixing and air/water CO_2 exchange. Maximum midday photosynthetically active radiation (PAR) levels averaged $450 \mu\text{E m}^{-2}\text{s}^{-1}$ using a neutral density shade fabric over the roof of the

greenhouse that reduced natural irradiance by ~ 75 percent.

Sediments used in the study were collected with a Ponar dredge (Wildlife Supply Company, Saginaw, Michigan) from two sites in Lake Onalaska in regions where *Vallisneria* had occurred previously (Figure 1). Site 1 ("protected"), located in the southeastern corner of the lake, was protected from prevailing summer winds by nearby south and southwest shorelines. Site 2 ("unprotected") was located in the west-central portion of the lake >700 m from islands on the west side of the lake and >3,000 m from the north or south shorelines.

Each sediment was mixed separately and divided into four parts. Three parts of each were treated by differential nutrient amendments: nitrogen (N), phosphorus (P), and nitrogen plus phosphorus (N+P); while the fourth part of each was left as a nonamended control. In the N-alone and N+P amendments, N was provided as $0.71 \text{ g NH}_4\text{Cl L}^{-1}$ (wet sediment); in the P-alone and N+P amendments, P was provided as $0.08 \text{ g KH}_2\text{PO}_4 \text{ L}^{-1}$. These levels of amendment were chosen based on past experience to provide approximately 10 g of biomass production beyond points of endogenous nutrient (N and P) limitation. Sediments were placed to a depth of approximately 8 cm in 24.3- x 24.3- x 10-cm-deep polyethylene containers. Six replicate containers were assigned per tank, with each of eight tanks assigned a different treatment (control)/site combination.

Sediment samples from the two collection sites were analyzed for physical and chemical characteristics. Particle size distribution (texture) determinations were made using the hydrometer method of Patrick (1958). Sediment moisture content and density were evaluated gravimetrically after oven-drying measured volumes of sediment at 105°C for ~ 12 hr. Dried samples were placed in a muffle furnace and combusted at 550°C for estimations of organic matter content from loss of mass following ignition (Allen et al. 1974). Exchangeable ammonium-N was obtained by extraction with 1 M NaCl in a cation exchange procedure modified from Bremner (1965). Extractable P was obtained using $0.030 \text{ N NH}_4\text{F}$ and 0.025 N HCl (after Olsen and Sommers 1982). Both N and P concentrations were determined colorimetrically with a Technicon Autoanalyzer II (Bran + Luebbe Analyzing Technology Inc., Elmsford, New York), employing a molybdate method for P and a salicylate method for N (APHA 1985).

For purposes of propagation, *Vallisneria* tubers were collected from a local source of abundance in Pool 4 of the UMRS during mid-April 1992. A water-pumped dredge was used to dislodge the overwintering tubers. Tubers were stored at approximately 4°C until planting. These propagules were germinated under greenhouse conditions to ensure viability and

uniformity at the initiation of the study. Germinated tubers were planted four per container, with basal ends positioned approximately 3 cm deep in the sediment. Following planting, a thin layer of washed silica sand was placed over the sediment surface to minimize physical mixing with the culture solution.

At the end of a nine-week growth period during the summer of 1992, the plants were harvested, measured for morphological responses, and oven-dried to constant mass at 80°C. Evaluations of plant growth were based on determinations of aboveground (AG) and belowground (BG) biomass, rosette (plant) number and height. As an indication of reproductive potential, tubers and seed pods were counted directly and weighed for separate determinations of tuber and seed pod mass.

Dried AG tissue samples were subsequently ground (<0.7 mm diameter) in a Wiley Mill and digested with sulfuric acid and hydrogen peroxide (Allen et al. 1974). N and P concentrations in the resulting digestates were determined using the same colorimetric procedures described for analysis of these nutrients in sediment extracts (see above). Accumulation of N and P in AG tissues was determined as the product of AG biomass and tissue nutrient concentration, corrected for minor contributions of initial biomass (determined at the time of planting).

Field Studies

In early May, tubers of *Vallisneria* were planted about 5 cm deep by a scuba diver in eight 1-m² plots selected randomly at each of the two sediment collection sites in Lake Onalaska (Figure 1). Depths at both sites averaged 1 m. Tubers were obtained from the same lot as used in the greenhouse studies (above). Each study plot was delineated by a frame placed on the sediment surface and anchored with attached legs. A 1-m² planting grid divided the plots into thirty-six 15- x 15-cm cells. Two tubers per cell were planted in the sediment using the grid as a temporary guide.

Vallisneria was harvested by hand cutting at the sediment surface in mid-August from four randomly selected plots at each site. The plants were rinsed of loose epiphytic materials, measured for morphological characteristics, and then oven-dried (80°C) to a constant mass. Plant growth was evaluated through determinations of oven-dry biomass, plant (i.e., rosette) heights, number of plants, and the number of flowers per plot. Plant height measurements included average plant height and maximum plant height per plot. Nitrogen (N) and phosphorus (P) concentrations were determined for aboveground tissues following the digestion procedures described above.

In order to account for potential differences in *Vallisneria* growth between sites due to the influences of local temperature and light conditions (Barko and Smart 1981), surface water temperature and Secchi depth were determined approximately weekly. Light attenuation was determined at 10-cm intervals through the water column by simultaneous measurement of underwater photosynthetically active radiation (PAR) with LI-COR quantum sensors (LI-COR, Inc., Lincoln, Nebraska). Measurements were based on an average of five readings. Extinction coefficients were calculated using the Lambert-Beer equation: $I_z = I_0 e^{-kz}$ where I_0 = average light intensity at a given depth, I_z = average irradiance at depth z 0.15 meters below, and k = vertical extinction coefficient. The 10% light depth (Z_{10}), considered here as a conservative lower limit for the depth of macrophyte growth (Barko et al. 1981), was calculated from the extinction coefficient ($Z_{10} = 2.3/k$).

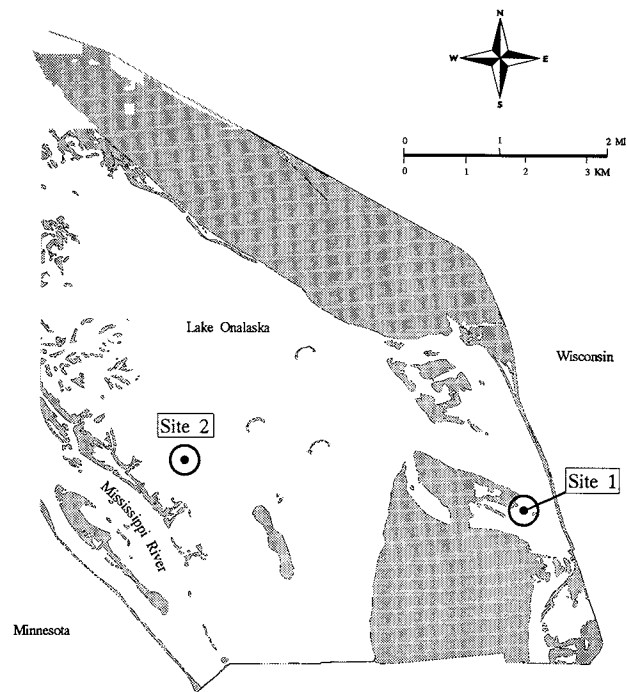


Figure 1.—Location of transplant sites in Lake Onalaska, 1992.

Data Analysis

Laboratory and field data were analyzed using ANOVA and post-ANOVA procedures of the Statistical Analysis System (SAS Institute 1991). Comparisons of means were accomplished using Student's *t*-Test, Duncan's Multiple Range Analysis, and Dunnett's Procedure. Nonparametric (Wilcoxon Rank Sum) tests were used for comparison of plant growth and water quality data between the two sites. Statistical significance is reported at the 5% probability level.

Results

Sediment Composition

Sediments from the two sites used in both the laboratory and the field studies differed substantially in major compositional characteristics (Table 1). Sediment from Site 1 (the protected site) was predominantly fine-textured, with a silt-clay particle fraction exceeding 75 percent. Sediment from Site 2 (the unprotected site) contained a high proportion of coarse-grained sand, and thus possessed greater bulk density and less moisture than sediment from Site 1. Organic matter content was greater in Site 1 than in Site 2 sediment, but in both cases, fell within the lower range reported for sediments from North American lakes (Barko and Smart 1986).

Initial concentrations of extractable nutrients in control and treated sediments used in the laboratory study are presented in Table 2. Comparisons between the two controls showed that sediment from Site 1 had approximately 40 percent less P but nearly 80 percent greater N than sediment from Site 2. N additions to these sediments resulted in approximate six- and ten-fold increases in exchangeable N concentrations in Site 1 and Site 2 sediments, respectively. P-treated sediments showed relatively minor increases in extractable P, indicating that the added P probably sorbed to a sediment fraction other than that affected by our extraction procedure. Concentrations of this nutrient were, however, slightly higher in Site 2 than in Site 1 sediment following P addition.

Laboratory Study Findings

Aboveground (AG) biomass in *Vallisneria* differed significantly between the two control sediments, with approximately 25 percent greater AG biomass obtained on sediment from Site 1 (Figure 2). Relatively low AG biomass occurred on nonamended sediments and on sediments that received the P amendment alone. Increased N availability (in the N and N+P treatments) stimulated AG production to about the same level on sediments from both sites, but the increase in response was greater on sediment from Site 2. While N and N+P additions promoted a 33 percent increase in AG biomass on Site 1 sediment, the respective increase on sediment from Site 2 was 50 percent.

Belowground (BG) biomass in *Vallisneria* was similar between control sediments and was little affected by the addition of N alone (Figure 2). However, opposing BG responses (reflecting interactive effects of treatment and sediment) resulted with additions of P. Whereas BG production was stimulated with P and

Table 1.—Sediment physical characteristics.*

Parameter	Sediment	
	Site 1	Site 2
Particle Size Distribution, %		
Sand (>50 μ dia.)	23.35 \pm 0.83	79.19 \pm 0.83
Silt (2 to 50 μ dia.)	45.83 \pm 0.83	11.65 \pm 1.67
Clay (<2 μ dia.)	30.83 \pm 0.84	9.16 \pm 0.83
Moisture, %	54.33 \pm 0.03	21.29 \pm 0.03
Organic Matter, %	8.97 \pm 0.06	1.20 \pm 0.01
Dry Weight Density, g/mL	0.64 \pm 0.01	1.54 \pm 0.01

*Values are means and standard errors based on three replicate determinations. Sediments were collected from Site 1 (a protected area) and Site 2 (an open water area) in Lake Onalaska, WI.

N+P additions to Site 1 sediment, the same additions to Site 2 sediment, for unknown reasons, apparently diminished production below ground.

Vallisneria generated about the same number of rosettes on nonamended sediments from the two sites but under those conditions, grew ~ 11 cm taller ($P < 0.01$) on sediment from Site 1 (Figure 3). Rosette number did not respond significantly to any nutrient addition to Site 2 sediment. Yet, additions of N singly and in combination with P to Site 2 sediment resulted in a two-fold increase in rosette height. Similarly, N and N+P additions to Site 1 sediment promoted marked increases in the height of this species, although the number of rosettes in those treatments was significantly

Table 2.—Initial sediment nutrient concentrations.*

Treatment	Extractable Nutrient, mg/g Dry Sediment	
	NH ₄ ^N	PO ₄ ^P
	Site 1	
Control	0.046 \pm 0.007	0.065 \pm 0.011
+ N	0.283 \pm 0.047	0.064 \pm 0.009
+ P	0.060 \pm 0.001	0.092 \pm 0.001
+ N + P	0.338 \pm 0.002	0.090 \pm 0.005
	Site 2	
Control	0.011 \pm 0.001	0.107 \pm 0.001
+ N	0.108 \pm 0.001	0.104 \pm 0.001
+ P	0.011 \pm 0.000	0.115 \pm 0.003
+ N + P	0.115 \pm 0.002	0.111 \pm 0.002

*Values are means and standard errors based on three replicate determinations. Sediments were collected from same sites indicated in Table 1. Amended sediments received separate additions of nitrogen (+N), phosphorus (+P), or nitrogen and phosphorus in combination (+N+P); nonamended sediments were designated as controls.

reduced. On neither sediment was the height of rosettes affected by additions of P alone.

Under nonamended conditions, seed pods produced on Site 1 sediment significantly outnumbered those on Site 2 sediment by nearly 10 to 1 (Figure 4). N and N+P additions to both sediments greatly increased the number of these propagules, while P added singly had no detectable effect. Seed pod mass (Figure 4) was highly and significantly correlated with seed pod number ($r = 0.95$, $P < 0.001$) and both responses related directly to AG biomass (pod mass: $r = 0.81$, $P = 0.0001$; pod number: $r = 0.80$, $P = 0.0001$).

There was no significant difference in tuber numbers between the two control sediments (Figure

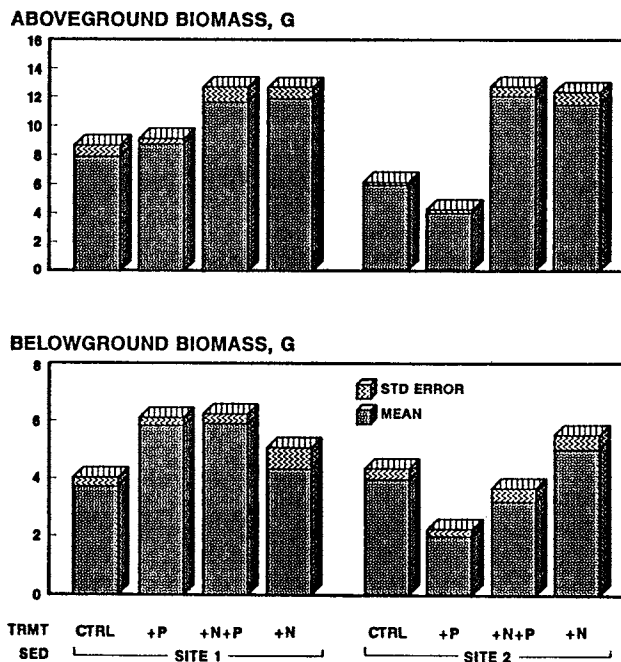


Figure 2.—Effects of sediment (SED) treatment (TRMT) combinations on aboveground and belowground biomass in *Vallisneria*. Values are means and standard errors based on six replicate determinations. Sediments are indicated by location in Lake Onalaska, WI: Site 1 (protected) and Site 2 (unprotected). Treatments are shown as separate additions of nitrogen (+N), phosphorus (+P), and nitrogen and phosphorus in combination (+N+P), or control (Ctrl).

5). Maximum tuber numbers were approximately the same on sediments from both sites but were attained in different sediment treatments. The addition of N+P promoted greatest tuber production on Site 1 sediment, increasing tuber number by about one-third. On Site 2 sediment, tuber number nearly doubled with the addition of N alone but was unaffected by the addition of both nutrients. P added singly to either sediment had no appreciable effect on the number of tubers produced. On both sediments, tuber mass (Figure 5) was closely related to tuber number ($r = 0.88$, $P < 0.001$) and to BG biomass ($r = 0.93$, $P < 0.001$). Overall, the

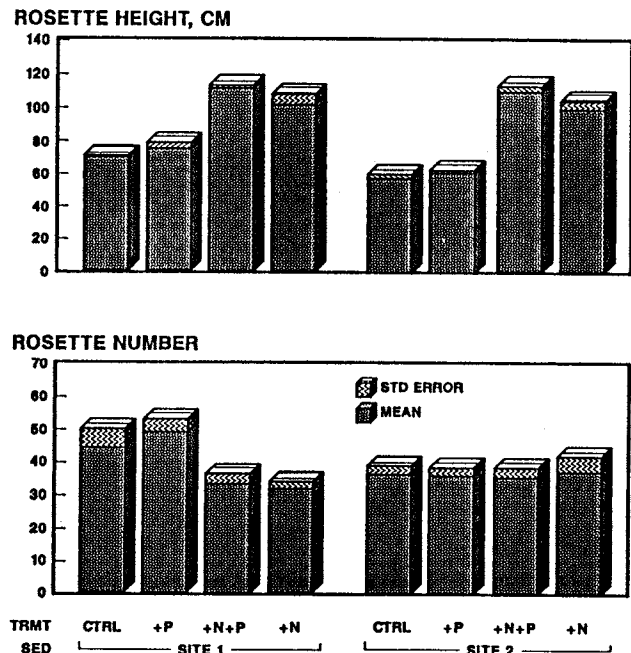


Figure 3.—Effects of sediment treatment combinations on rosette (plant) height and number in *Vallisneria*. Values are means and standard errors based on six replicate determinations. Acronyms same as in Figure 1.

contribution of tuber mass to BG biomass ranged from 64 to 71 percent between Site 1 and Site 2 sediments, respectively.

The accumulation of both N and P in AG plant tissues was strongly related to AG biomass production

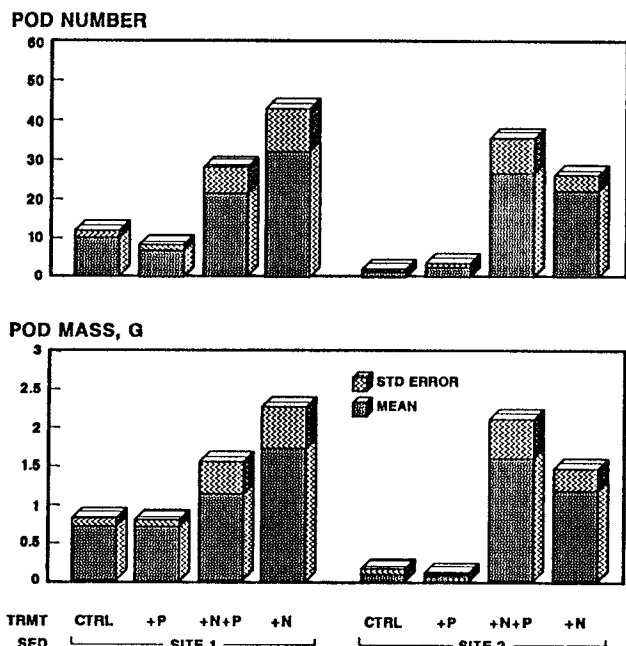


Figure 4.—Effects of sediment treatment combinations on the number and mass of seed pods produced by *Vallisneria*. Values are means and standard errors based on six replicate determinations. Acronyms same as in Figure 1.

(Table 3). When examined for each sediment, relationships between nutrient accumulation and biomass were closer than those between biomass and tissue nutrient concentration. On both sediments, AG biomass correlated closely with concentrations of extractable N but not P, perhaps because the P fraction measured in sediment (see above) was little affected by P addition.

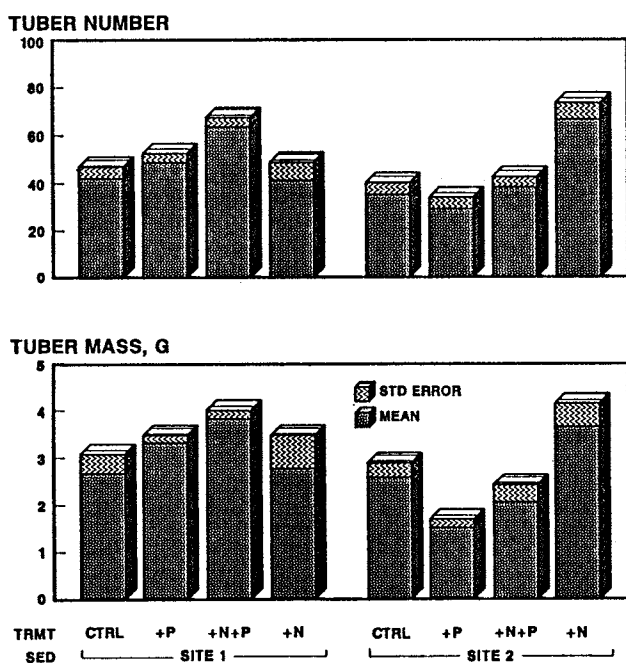


Figure 5.—Effects of sediment treatment combinations on the number and mass of tubers produced by *Vallisneria*. Values are means and standard errors based on six replicate determinations. Acronyms same as in Figure 1.

Field Study Findings

The growth of *Vallisneria* at the two study sites in Lake Onalaska is characterized in Table 4. The difference in mean shoot biomass of *Vallisneria* between the two sites (Site 1 mean = 88.2 g m⁻²; Site 2 mean = 123.4 g m⁻²) was insignificant, owing to high variance. No significant differences were found between the two sites in the number of plants that reached heights >20 cm or the number of plants <20 cm. While mean plant heights were similar between the two sites, plant heights were more variable at Site 2, ranging from 80 to 121 cm compared to 89 to 103 cm at Site 1. Maximum plant heights for *Vallisneria* were significantly different between the two sites, about 26 percent greater at Site 2 than at Site 1. At both sites, *Vallisneria* plants >20 cm in height outnumbered plants <20 cm high by at least 12 to 1. About 20 percent of the plants >20 cm produced flowers. There was no significant difference in the production of male or female flowers between the sites.

Table 3.—Correlation coefficients (*r*) for relationships of aboveground biomass in *Vallisneria* with nutrient uptake (Accumulation and Concentration) in aboveground plant tissues and concentration of extractable nutrients in sediments.^a

Nutrient Pool	Biomass Production	
	Site 1	Site 2
Accumulation in Tissues		
N	0.790 ***	0.956 ***
P	0.892 ***	0.962 ***
Concentration in Tissues		
N	0.565	0.834 ***
P	0.622	0.787 ***
Concentration in Sediment		
N	0.760 ***	0.912 ***
P	0.024	-0.514

^a Sediments are those collected from Sites 1 and 2 in Lake Onalaska, WI, as indicated in Table 1. Asterisks indicate significant correlations at *P* < 0.001.

Analysis of aboveground plant tissues indicated that mean concentrations of N and P from Site 1 were 32.7 mg g⁻¹ (standard error = 0.64 mg g⁻¹, *n* = 3) and 4.40 mg g⁻¹ (standard error = 0.18 mg g⁻¹, *n* = 3), respectively. Mean N concentration at Site 2 was 26.1 mg g⁻¹ (standard error = 1.00 mg g⁻¹, *n* = 3) and mean P concentration was 3.13 mg g⁻¹ (standard error = 0.18 mg g⁻¹, *n* = 3). Mean N concentration in *Vallisneria* was significantly greater at Site 1 than at Site 2. However, tissue P concentrations did not differ significantly between the sites.

Secchi depths were somewhat greater at Site 1, with a seasonal average of 53 cm compared to 45 cm at Site 2 (Figure 6). Temperatures ranged from 16 to 27 °C during the study, averaging 21.7 °C (standard error = 0.81, *n* = 14) at Site 1 and 20.9 °C (standard error = 0.77,

Table 4.—Morphological measurements of *Vallisneria americana* Michx. Plants from transplant sites in Lake Onalaska, 1992.

Growth Characteristics (per m ²)	Site 1	Site 2
Aboveground biomass (g)	88.2 (16.7)	123.4 (7.7)
Number of plants >20 cm	177.2 (26.1)	199.7 (18.3)
Number of plants <20 cm	10.7 (3.1)	7.0 (2.7)
Average plant height (cm)	96.0 (2.8)	98.0 (8.5)
Maximum plant height (cm)	121.5 (1.1)	154.0 (10.4)
Number of male flowers	64.0 (17.0)	59.2 (3.1)
Number of female flowers	66.5 (9.1)	50.5 (11.3)

Means are given with standard errors in parentheses.

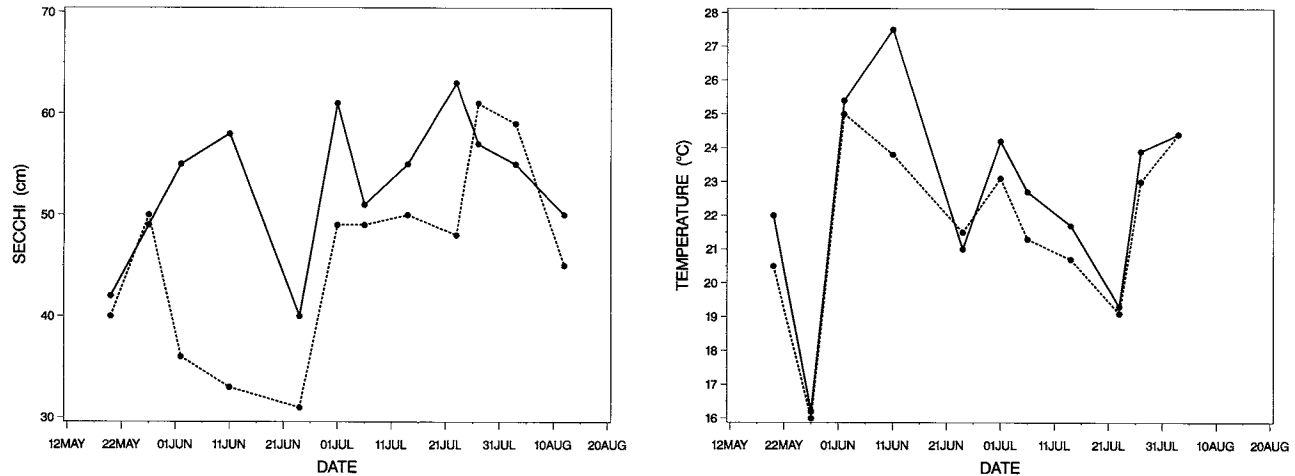


Figure 6—Secchi disk transparency and water temperature at Site 1 and Site 2 in Lake Onalaska, 1992 (Site 1 — Site 2 - - -).

$n = 15$) at Site 2 (Figure 6). Seasonal means for temperatures were not significantly different between the two sites.

Mean extinction coefficients were not significantly different between the two sites over the entire period (mean = 3.5, standard error = 0.36, $n = 12$ at Site 1; mean

= 3.1, standard error = 0.15, $n = 12$ at Site 2). However, for most of June and July, extinction coefficients were significantly lower and 10 percent light depths were deeper at Site 1 (Figure 7).

Discussion

Results of the laboratory study suggest that increased N supply to Lake Onalaska sediments can promote growth of *Vallisneria americana* Michx., resulting in significant increases in AG biomass, propagule formation (especially seed pod production), and rosette height. Furthermore, these positive responses to sediment-N additions suggest potential N-limitation of this species on sediments at both study sites. In contrast, additions of P to sediment had little positive effect overall on *Vallisneria* growth. Previous laboratory and field studies have shown that, in many cases, submersed macrophyte production increases with N rather than with P additions to sediment (Anderson and Kalff 1986; Duarte and Kalff 1988; Moeller et al. 1988). In a recent review, Barko et al. (1991a) suggest that submersed macrophytes may be less frequently limited by P than by N due to relatively larger pools of P in most lake sediments.

Examination of tissue nutrient concentrations provide additional evidence that growth of *Vallisneria* in the laboratory study was limited by N. Gerloff and Kromholz (1966) determined that for *Vallisneria americana*, the critical (i.e., growth-limiting) N concentration is approximately 1.3 percent and the comparable P concentration is 0.13 percent. Where production was limited in the laboratory study, i.e., on nonamended sediment and on sediment amended with P only, tissue N concentrations were well below the established N level for this species. However, based on

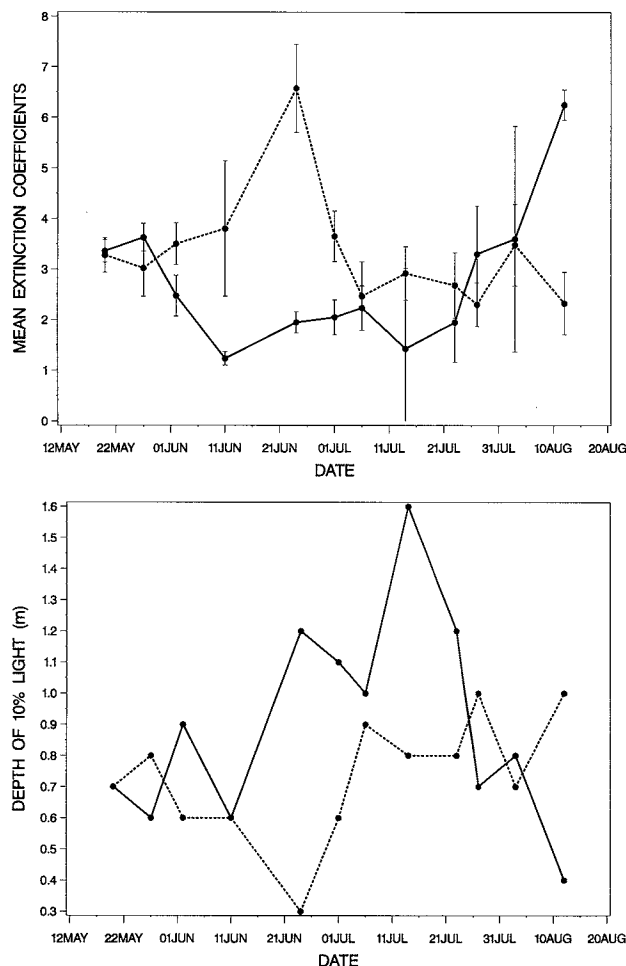


Figure 7.—Mean light extinction coefficients and 10% depth of light penetration at Site 1 and Site 2, Lake Onalaska, 1992 (Site 1 — Site 2 - - -)

comparisons with the suggested critical P concentration for *Vallisneria*, the concentrations of tissue P in all treatments were adequate for growth.

Analyses of the composition of the two nonamended sediments suggest that sediment from Site 2 may have been less suitable for growth than sediment from Site 1, because the former was fundamentally coarse-textured (Barko and Smart 1986). Typically, sediments containing a substantial sand-particle fraction (as sediment from Site 2) exhibit low (especially N) fertility and consequently limit submersed macrophyte production (Bruner and Batterson 1984; Barko and Smart 1986). Conversely, relatively fine-textured sediments (similar to sediment from Site 1) are usually more fertile. In the present study, growth responses of *Vallisneria* under nonamended conditions in the laboratory mirrored these sediment differences.

The morphological responses of *Vallisneria* to experimental treatments in the laboratory have important implications for its development on different sediments. On N-rich sediment, *Vallisneria* maximized biomass production and plant height while limiting the number of plants produced. Regulation of density under these conditions could be an advantage in reducing the possibility of self-shading and allowing a greater share of nutrients per plant (Haller and Sutton 1975; Barko et al. 1991b). In contrast, on N-poor sediment, relatively high numbers of plants were sustained at the expense of biomass production and plant height. This growth habit has been observed in other submersed macrophyte species (e.g., *Hydrilla verticillata* [L.f.] Royle and *Potamogeton americanus* L.) as well, and is believed to enable population survival by growing away from unfavorable sediments (McCreary, et al. 1991; McFarland et al. 1992).

While the production of seed pods in the laboratory study was more responsive than was tuber production to N levels in sediment, neither was as dependent as biomass on sediment N supply. From these findings, we suggest that (1) sediment conditions may be a better predictor of biomass than of propagule production in *Vallisneria* and (2) the formation of tubers and seed pods in this species may involve mechanisms beyond those of mineral nutrition alone. Presently, there is very little information in the literature regarding influences of sediment and other environmental factors on reproduction in *Vallisneria americana* Michx. Considering the importance of tubers and seed pods in restoring *Vallisneria* populations in nature (Korschgen and Green 1988), mechanisms involved in the formation of these propagules need to be better understood.

In contrast to the results of the laboratory study, the only significant difference in *Vallisneria* growth between the two study sites in Lake Onalaska was in maximum plant height, which was greater at Site 2. We

suggest that greater maximum plant height at Site 2 was most likely a response by *Vallisneria* to differences in ambient light levels between the two sites, particularly during June and July, when 10 percent light depths were significantly less at Site 2 than at Site 1. This suggestion is supported by results reported for *Vallisneria* by Barko et al. (1982). In that investigation, shoot height for *Vallisneria* increased with decreasing irradiance at temperatures between 20 and 32°C. Water temperature in the present investigation did not differ between sites, and thus most likely did not affect plant height.

Goldsborough and Kemp (1988) suggest that even small increases in plant height may yield increases in available light, especially in turbid systems. The ability to increase height in the water column to adjust to diminished light availability may be important to the survival of *Vallisneria* in the oftentimes turbid waters of the UMRS. However, in the present study the 10 percent depth limit for growth was usually near the bottom, and it is unlikely that biomass production was affected by light.

The results of the laboratory and field studies were contradictory. Whereas *Vallisneria* growth in the laboratory varied significantly between sediment types (fine versus coarse) and was limited by the supply of sediment N, growth in the field was unaffected by sediment type and apparently was not limited by N or P. These results suggest the occurrence of processes in the field that were not duplicated in the laboratory. It is important to note that the laboratory is a closed system with respect to outside inputs (replenishments), and under otherwise optimal conditions of growth, sediment nutrient levels in the laboratory can become depleted (Barko et al. 1988). Thus, results of laboratory studies provide only an indication of the potential influence of sediment nutrient (N and P) levels in the field with no or low-level inputs of these sediment nutrients. Such conditions may have occurred in Lake Onalaska during the period of drought, in conjunction with low river discharge regimes (Gunard et al. 1987-1989) and associated reductions in sediment nutrient transport into plant beds.

These contrasting results suggest that throughout the 1992 growing season in Lake Onalaska, N may have been provided to *Vallisneria* through sedimentation/mineralization, and other processes occurring in the root zone. To most effectively assess the potential for nutrient (N) limitation in Lake Onalaska, information regarding replenishment rates is needed. In nature, nutrients in various forms are transported to lake bottoms by sedimentation (Forsberg 1989; James and Barko 1990), a process which in concert with sediment mixing (e.g., through bioturbation) provides a primary source of nutrients to rooted submersed macrophytes

(Barko et al. 1991a). As demonstrated here in the laboratory, N enrichment of Lake Onalaska sediments increased biomass in *Vallisneria*. Thus, we suggest that sedimentation contributes to the availability of N to *Vallisneria* in Lake Onalaska.

In addition to sediment, groundwater and surface water also constitute potential sources of N to *Vallisneria* in Lake Onalaska. Although we know little about groundwater flow or nutritional composition in the Lake, significant nutrient uptake from groundwater by roots of *Vallisneria* may occur in areas where groundwater inputs are substantial. It is unlikely, however, that surface water contributes much to the nutrition of this plant, because of its reliance on nutrient uptake by roots (Huebert and Gorham 1983) and because of competition with algae and microorganisms for surface water nutrients (Barko et al 1991b). In general, rooted aquatic macrophytes can obtain nutrients exclusively from sediments, even in riverine systems with rapidly flowing water (Chambers et al. 1989). Thus, future investigations of the mineral nutrition of *Vallisneria* in Lake Onalaska should focus on sediments and groundwater.

Two important conclusions can be drawn from this investigation. First, it is apparent (from the laboratory study) that the sediments in Lake Onalaska are intrinsically infertile, particularly those that are coarse textured. Growth of *Vallisneria* (and probably other macrophyte species as well) on these sediments will depend on continuous nutrient supply/renewal, most likely by way of sedimentation. Second, present (1992) conditions in Lake Onalaska are suitable for *Vallisneria* growth. Thus, reestablishment of *Vallisneria* in the lake is likely, as long as conditions remain unchanged.

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