Interim Report For The
Upper Mississippi River - Illinois Waterway
System Navigation Study

Effects of Waves on the Early Growth of *Vallisneria americana*

June 1999

US Army Corps
of Engineers

Rock Island District
St. Louis District
St. Paul District
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Effects of Waves on the Early Growth of *Vallisneria americana*

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Preface

The work reported herein was conducted as part of the Upper Mississippi River - Illinois Waterway (UMR-IWW) System Navigation Study. The information generated for this interim effort will be considered as part of the plan formulation process for the System Navigation Study.

The UMR-IWW System Navigation Study is being conducted by the U.S. Army Engineer Districts of Rock Island, St. Louis, and St. Paul under the authority of Section 216 of the Flood Control Act of 1970. Commercial navigation traffic is increasing and, in consideration of existing system lock constraints, will result in traffic delays that will continue to grow in the future. The system navigation study scope is to examine the feasibility of navigation improvements to the Upper Mississippi River and Illinois Waterway to reduce delays to commercial navigation traffic. The study will determine the location and appropriate sequencing of potential navigation improvements on the system, prioritizing the improvements for the 50-year planning horizon from 2000 through 2050. The final product of the System Navigation Study is a Feasibility Report, which is the decision document for processing to Congress.

The Principal Investigator for this report was Dr. Robert D. Doyle, Ecosystem Processes and Effects Branch (EPEB), Environmental Processes and Effects Division (EPED), Environmental Laboratory (EL), U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS, a complex of five laboratories of the Engineer Research and Development Center (ERDC). Dr. Doyle prepared this report and was responsible for experimental design, data analysis, and interpretation. The study was conducted at the WES Lewisville Aquatic Ecosystem Research Facility in Lewisville, TX. Technical assistance was provided by Mr. Matthew Francis, WES contractor.

This investigation was performed under the general supervision of Dr. John Harrison (retired), Director, EL; Dr. Richard E. Price, Chief, EPED; and Dr. Robert Kennedy, Acting Chief, EPEB.
At the time of publication of this report, Commander of ERDC was COL Robin R. Cababa, EN. Acting Director of ERDC was Dr. E. Lewis Link, Jr. This report was prepared and published at the WES complex of ERDC.

This report should be cited as follows


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1 Introduction

Effects of Waves on Aquatic Plants

Wave energy may control the distribution of aquatic plants in shallow-water environments by both direct and indirect means (Kimber and Barko 1994). In fact, wave activity is considered one of the strongest factors influencing the horizontal zonation of plants within the littoral zone of lakes (Hutchinson 1975; Spence 1982). Observational or anecdotal evidence on the influence of waves on the distribution of aquatic plants has been commonly reported in the literature (Spence 1982; Keddy 1983, 1985; Jupp and Spence 1977; Kautsky 1987). Chambers (1987) provides quantitative documentation relating the minimum colonization depth of various species to wave energy. In other cases, the natural distribution of plants in relation to observed wave energy provides evidence of wave impacts. For example, the maximum biomass of *Potamogeton pectinatus* was related to the degree of wave exposure, being three times higher in protected versus wave-exposed sites within the Baltic Sea (Kautsky 1987). Keddy (1985) demonstrates that the frequency distribution of some plant species is maximal at an intermediate level of wave exposure.

In environments subject to frequent and large wave action, the upslope limit of the plant communities distribution may be directly regulated by the waves (Chambers 1987). Direct effects of waves on plant communities include damage or uprooting of established plants, reduced survival of developing tubers or seedlings, and negative impacts on seedbanks because of washout or burial.

Damage to mature macrophytes usually occurs during periods of unusually large-wave or current activity associated with storm events (Kimber and Barko 1994), since the species composition and vertical zonation of the plant community is usually adapted to more common conditions. However, human disturbances, such as recreational boat traffic, can also create waves that impact macrophytes. For example, wave action, caused mainly by recreational boat traffic, was observed to negatively affect plant growth in an in situ experiment with a breakwater (Vermaat and de Bruyne 1993).

In addition to damaging or uprooting established plants, waves may directly impact the plant community by reducing the survival of developing tubers or seedlings. Foote and Kadlec (1988) report that survival of tubers of alkali bulrush (*Scirpus maritimus*) was significantly improved when protected from wave action. Similarly, the most vulnerable period in the development of wild rice was
observed to be shortly after germination, while seedlings still had submersed leaves and were uprooted by waves (Lee and Stewart 1981). Seagrass communities were also shown to have reduced seedling recruitment under high-energy conditions. After several years of continuous investigations, high-energy sites showed erratic and limited seedling germination but nearly continuous annual seedling recruitment at lower energy areas (Fonseca and Kenworthy 1987).

Although lowered mortality of developing seedlings because of wave activity is sometimes reported (e.g., Lee and Stewart 1981), poor seedling recruitment in wind-swept areas is more commonly attributed to seedbank disturbances. The impacts of waves in these cases occur before seed germination, as waves resuspend and transport seeds out of the littoral zone (Foote and Kadlec 1988; Smith and Kadlec 1985; Schneider and Sharitz 1986). Even if the seeds are not physically transported out of the area, they may be prevented from germinating because of burial. Galinato and van der Valk (1986) report that seeds of most plants tested would not germinate if covered by as little as 1 cm of sediment.

Indirect effects of waves also impact plant communities. Indirect effects of wave activity on macrophyte communities include sediment sorting and sediment resuspension. Wave activity generally washes away finer clays and silts and leaves coarser, less fertile sediments behind (Spence 1982; Wilson and Keddy 1985). These sediments may be less favorable to the development of aquatic plants (Keddy 1985). Wave activity may also resuspend sediments and cause indirect light effects. Turbidity caused by sediment resuspension is one of the more commonly reported impacts of hydraulic disturbance on plant communities. For example, Engel and Nichols (1994) report that in the early 1970s, the macrophyte community of Rice Lake (Wisconsin, USA) was impacted by periods of unusually high water resulting in poor light conditions. Once water levels returned to normal conditions, the plant community was mostly gone, and wave resuspension of sediments resulted in unusually turbid conditions. These turbid conditions appear to have prevented the subsequent regrowth of the plant community. More than a decade later, the lake continues to have high levels of resuspended-sediment turbidity and a very sparse macrophyte community.

The species composition of the plant community is impacted by wave action as well. Plants adapted to high-energy environments appear to have one of two basic approaches to dealing with flow (Kimber and Barko 1994). One strategy is to produce longer leaves that are thin and flexible. These leaves “go with the flow” and avoid breakage by their extreme flexibility. Other plants produce short but stout leaves. Canopy-forming species appear to be selected against by wave action (Stewart et al. 1997), while other species appear to be selected for at intermediate levels of wave disturbance (Keddy 1985).

Wave energy also impacts the morphological development of plants. The morphologic characteristics of plants exposed to wave or high-flow environments differ from plants of the same species grown under more sheltered conditions. For example, tensile strength and extensibility were both significantly different in plants grown under high-energy conditions compared with those grown at lower energy sites (Brewer and Parker 1990).
Most of the data available on the effects of waves on freshwater macrophytes come from observational data or field-transplant experiments; little work has been done under controlled conditions. However, Stewart et al. (1997) conducted experiments on vallisneria (*Vallisneria americana*) and Eurasian watermilfoil (*Myriophyllum spicatum*) under controlled hydrologic conditions. Damage to plants was investigated over a range of wave heights (0.1, 0.2, and 0.3 m) and wave periods (3 and 5 sec). They conclude that under low-ambient flow conditions, damage to plants increases with wave heights greater than 0.1 m. Furthermore, canopy-forming species such as Eurasian watermilfoil were more susceptible to damage than plants such as vallisneria, which have long, ribbon-like leaves arising from a basal rosette.

**Study Objectives and Scope**

This report compares the establishment and early growth of *Vallisneria americana* (vallisneria) under static and wave-exposed conditions. As a plant that forms long, ribbon-like leaves, vallisneria typifies a plant morphology that may be tolerant of higher energy environments. The focus of the study was to quantify the direct effects of 15-cm (0.15-m) waves on the survival, growth, and morphologic development of young vallisneria plants. The test was conducted in a modified raceway at the Lewisville Aquatic Ecosystem Research Facility (LAERF), Lewisville, TX.
2  Materials and Methods

Raceway Design

Existing concrete raceways at LAERF were modified to create one static-control and one experimental-wave raceway (Figure 1). The raceways measured 6 m in length, 60 cm in depth, and 90 cm in width (12 by 2 by 3 ft). Three planting depths were created at one end of each raceway to simulate common shoreline depths. These levels were created by utilizing appropriate width pieces of recycled plastic lumber wedged across the raceway. The pockets created by the lumber pieces were filled with a layer of pond sediment covered with a thick layer of coarse sand. The planted end of each raceway was covered with a 30-percent shade cloth to prevent excessively high light and to minimize heating of these shallow-water systems.

The raceways were initially filled with alum-treated lake water. The water was treated with alum (aluminum sulfate) to reduce levels of dissolved phosphorus within the water and thereby minimize complications caused by algae growth in these high-light, shallow-water systems. Alum-treated water was also used as needed to make up for evaporative losses. The water level within the raceway was maintained at 35 cm, resulting in planting depths of 15, 20, and 25 cm.

A wave was generated within the experimental wave raceway by dropping a solid concrete block from a height of approximately 40 cm above the water surface. The concrete block was 80 cm in width, 40 cm in length, and 15 cm high (see Figure 1) and displaced 0.05 m$^3$ of water. The block was manually lifted above the water surface with a double pulley arrangement (Figure 1) and then allowed to free-fall back into the raceway. The wave generated by this method was 0.15 m in height. This wave height is near the low end of the range reported for navigation-induced secondary waves (Bhowmik, Demissie, and Guo 1982) and recreational traffic (Bhowmik et al. 1991). Although waves of much greater height are often created by barge and recreational traffic, the larger waves would likely result in uprooting of aquatic plants within the shallow-water zone. The intent of this experiment was to determine if smaller waves, which were not powerful enough to uproot the plants, would affect the growth and development of the plants. To simulate the type of disturbance that might commonly be caused by traffic along a shoreline, the block was dropped five times within the period of 3 min. This treatment was repeated five to six times each day during the experimental growth periods. Since the disturbance created by the waves lasted about 3-5 min, the cumulative daily exposure was about 20-30 min of intense wave...
Figure 1. Design of experimental raceway
action. Each day the loose leaf debris (if any) within each raceway was collected and dried.

A common indirect effect of wave action is increased turbidity within the water column (Kimber and Barko 1994). Although the surface sediments in this experiment were coarse sand and gravel, some minor (~10 NTU) and short-lived (5-10 min) increase in turbidity associated with the waves occurred. Therefore, each time a wave series was made in the wave raceway, the settled sediments in the no-wave control raceway were also stirred up to ensure that the light climates between the two raceways remained similar.

Wave Characterization

Wave height was determined by measuring the maximum upward displacement of water within the raceway associated with the initial wave front propagated by the falling concrete block. Wave height was determined just forward of the first planting level within the raceway. Average wave height measured by this method was 15.0 cm with virtually no variability between replicate waves.

The flow velocity generated by the waves was measured just above the sediment surface of each planting level utilizing a warm bead thermistor flowmeter (LaBarbera and Vogel 1976; MacIntyre 1986). The probe was placed 5 cm above the sediment surface, and output from the flowmeter was recorded at 250-m sec\(^{-1}\) intervals on a computer equipped with a data-acquisition interface. The sensors were constructed of 0.9-mm thermistors (Victory Engineering Corporation), optimized for flow in the range of 5-150 cm sec\(^{-1}\), and temperature compensated at 28 °C. These sensors measure water speed but not direction. Calibration was made over the range of 10-150 cm sec\(^{-1}\) within a 2-cm-diam pipe that was 3 m long (Figure 2).

Experimental Setup

Young vallisneria tuberlings were obtained by planting a single tuber (one apical tip) within a small (125-cc) plastic container of sterile pond sediment. These were grown under greenhouse conditions (25 °C, 60-percent light) for 4 weeks prior to initiation of the experimental period. At the end of the greenhouse culture period, the young developing plants were separated into three groups of 36 plants each, based on plant size. Twelve of the smallest size class were planted in the shallowest zone of each raceway (control and wave); twelve of the intermediate size plants were planted within the intermediate depth zone of both raceways; twelve of the largest size plants were planted within the deepest zone of both raceways. The tuberlings were planted by burying the plastic container in the sand/sediment so that the surface of the plastic container was just below the sand surface. The remaining 12 plants of each size class were harvested to document initial conditions of the plants.
The light climate and the temperature regime were monitored within the raceways. Photosynthetically active radiation (PAR, 400-700 nm) was measured as light quanta (μE m⁻² sec⁻¹) just below the water surface utilizing a spherical quantum sensor (Li-Cor model LI-193SA sensor). The measurements were taken between 10 a.m. and 2 p.m. and represent approximate maximum daily irradiances. Water temperature was also monitored periodically utilizing a laboratory thermistor.

Plants were moved to the raceways on June 2, 1997, and allowed to grow until August 7, 1997 (10.5 weeks). At the end of the growth period, each plant was harvested individually. In most cases, the initial plant had grown and consisted of several daughter plants, which were often connected along a single stolon. The number of vallisneria rosettes, total stolon length, and maximum leaf length of each rosette were measured. Aboveground and belowground tissues were separated by cutting the plant stems at the sediment surface. Aboveground tissues were washed to remove accumulated sediments and epiphytes. Belowground tissues were washed over a 1-mm sieve to remove sediment and debris. Tubers and flowers were not present. Plant tissue samples were bagged and dried at 60 °C in a forced-draft oven to constant weight.
Statistical Analysis

Statistical analysis utilized a two-factor analysis of variance (ANOVA) (factors = depth, wave) to test for differences between the two wave treatments across all planting depths. For this analysis, planting depth was a blocking factor and wave treatment the only true main effect variable. In addition, a t-test was used to test for differences in population means between control and wave treatments separately for each planting depth. For both analyses, each plant is considered a single experimental unit.
3 Results

Environmental Conditions

Light and temperature conditions during the course of the experiment were within common ranges for shallow-water plant communities. Maximum daily irradiance experienced by the plants in both the control and wave raceways during the experimental periods was approximately 1,200-1,400 µE m⁻² sec⁻¹ (55-65 percent of full light), while daily temperatures averaged about 28 °C.

Flow velocities recorded at each of the three planting depths within the experimental raceway show that the maximum flow rate generated within the wave flume was about 135-145 cm sec⁻¹ (Figure 3). Mean velocity during the wave events was 95, 83, and 75 cm sec⁻¹ for the 15-, 20-, and 25-cm planting depths, respectively. Following the wave events, the water velocity attenuated to background levels over the ensuing 3-5 min.

Plant Growth Response

The tubers had grown into vigorous plants with well-developed roots and leaves by the beginning of the experimental growth period (Table 1).

<table>
<thead>
<tr>
<th>Planting Depth cm</th>
<th>Aboveground Mass, g dw</th>
<th>Belowground Mass, g dw</th>
<th>Total Mass g dw</th>
<th>Max. Length cm</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>0.017 ± 0.003</td>
<td>0.014 ± 0.002</td>
<td>0.031 ± 0.004</td>
<td>10.6 ± 0.5</td>
</tr>
<tr>
<td>20</td>
<td>0.044 ± 0.003</td>
<td>0.030 ± 0.005</td>
<td>0.073 ± 0.006</td>
<td>20.8 ± 0.8</td>
</tr>
<tr>
<td>25</td>
<td>0.153 ± 0.020</td>
<td>0.067 ± 0.009</td>
<td>0.220 ± 0.024</td>
<td>35.1 ± 1.0</td>
</tr>
</tbody>
</table>

Note: Values shown are means ± se, n = 12.
The plants were damaged by the wave treatment, although not to the point where any of them were uprooted or washed away. Survival in both raceways was 100 percent. However, throughout the experiment, the plants in the wave raceway were observed to lose several leaves following each wave event, while little leaf material was lost from the plants in the control raceway (Figure 4). Relatively little tissue was lost during the first weeks, but the amount of leaf lost increased towards the end of the experiment when the plants were getting larger.
Figure 4. Mass (g dw) of loose leaf debris collected each day in each of two raceways

The strongest impacts of the wave treatment were on plant mass and leaf length (Table 2).
Table 2
Mean, Standard Error, and Probability that Means are Significantly Different for Various Vallisneria Parameters in Wave and Control Raceways

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Wave</th>
<th>Control</th>
<th>Significance p</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Depth</td>
<td>Mean ± se</td>
<td>Depth</td>
</tr>
<tr>
<td>Total plant mass, g dw</td>
<td>15 cm</td>
<td>0.21 ± 0.03</td>
<td>15 cm</td>
</tr>
<tr>
<td></td>
<td>20 cm</td>
<td>0.32 ± 0.03</td>
<td>20 cm</td>
</tr>
<tr>
<td></td>
<td>25 cm</td>
<td>0.54 ± 0.09</td>
<td>25 cm</td>
</tr>
<tr>
<td></td>
<td>all depths</td>
<td>0.36 ± 0.04</td>
<td>all depths</td>
</tr>
<tr>
<td>Maximum length, cm</td>
<td>15 cm</td>
<td>10.9 ± 1.1</td>
<td>15 cm</td>
</tr>
<tr>
<td></td>
<td>20 cm</td>
<td>15.8 ± 1.7</td>
<td>20 cm</td>
</tr>
<tr>
<td></td>
<td>25 cm</td>
<td>22.6 ± 1.6</td>
<td>25 cm</td>
</tr>
<tr>
<td></td>
<td>all depths</td>
<td>16.4 ± 1.2</td>
<td>all depths</td>
</tr>
<tr>
<td>Total stolon length, cm</td>
<td>15 cm</td>
<td>24.5 ± 3.5</td>
<td>15 cm</td>
</tr>
<tr>
<td></td>
<td>20 cm</td>
<td>24.6 ± 8.1</td>
<td>20 cm</td>
</tr>
<tr>
<td></td>
<td>25 cm</td>
<td>66.3 ± 18.2</td>
<td>25 cm</td>
</tr>
<tr>
<td></td>
<td>all depths</td>
<td>38.5 ± 7.3</td>
<td>all depths</td>
</tr>
<tr>
<td>Number of rooted rosettes</td>
<td>15 cm</td>
<td>7.8 ± 1.0</td>
<td>15 cm</td>
</tr>
<tr>
<td></td>
<td>20 cm</td>
<td>4.7 ± 1.0</td>
<td>20 cm</td>
</tr>
<tr>
<td></td>
<td>25 cm</td>
<td>8.2 ± 1.4</td>
<td>25 cm</td>
</tr>
<tr>
<td></td>
<td>all depths</td>
<td>6.9 ± 0.7</td>
<td>all depths</td>
</tr>
<tr>
<td>AG:BG mass ratio</td>
<td>15 cm</td>
<td>1.84 ± 0.20</td>
<td>15 cm</td>
</tr>
<tr>
<td></td>
<td>20 cm</td>
<td>3.33 ± 0.63</td>
<td>20 cm</td>
</tr>
<tr>
<td></td>
<td>25 cm</td>
<td>2.27 ± 0.17</td>
<td>25 cm</td>
</tr>
<tr>
<td></td>
<td>all depths</td>
<td>2.48 ± 0.25</td>
<td>all depths</td>
</tr>
</tbody>
</table>

Note: Comparison between raceways across all depths made utilizing an ANOVA analysis with depth as a blocking variable (N = 36).

Total plant biomass was significantly affected by the wave treatment (Table 3), with the wave treatment producing plants with only about half the total mass of the plants in the control raceway (Table 4).

Table 3
ANOVA of Plant Biomass

<table>
<thead>
<tr>
<th>Source</th>
<th>D.F.</th>
<th>SS</th>
<th>MS</th>
<th>F-ratio</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>2</td>
<td>2.24877</td>
<td>1.12438</td>
<td>37.83</td>
<td>0.0000</td>
</tr>
<tr>
<td>Depth (blocking)</td>
<td>1</td>
<td>2.22781</td>
<td>2.22781</td>
<td>2.56</td>
<td>0.0274</td>
</tr>
<tr>
<td>Wave</td>
<td>68</td>
<td>4.00415</td>
<td>0.05889</td>
<td>0.3647</td>
<td></td>
</tr>
</tbody>
</table>

Chapter 3 Results
The difference in total biomass between the wave and no-wave treatment was relatively consistent across all planting depths. In each case, the control raceway produced plants with significantly higher mass than the wave raceway (Table 2, Figure 5).

Damage to the plants in the wave raceway is also reflected in the shorter maximum length of plants relative to those in the control raceway (Figure 6, Table 2). At all planting depths, the plants in the wave raceway had maximum leaf lengths that were shorter than those in the control side. The largest differences were observed at the 20-cm planting depth, where the leaves in the control side were almost twice as long as the leaves in the wave raceway. Across all planting depths, the average plant height in the wave raceway was only 67 percent of the height in the control raceway. During harvest, one observed that most of the leaves in the control raceway had intact leaf tips, while most of the leaves of the plants in the wave raceway had frayed or damaged tips.

In addition to impacting plant mass and leaf length, the wave treatment also impacted the total stolon length and number of rosettes produced over the experimental period. Although two treatments differed significantly when all planting depths were taken together, the effect appeared to be much stronger at some depths than at others (Table 2). While the average stolon length was always greater in the control raceway for all depths, the difference was relatively modest at the shallowest planting level and quite pronounced at the intermediate level. Likewise, the number of rosettes per plant was also significantly greater in the control raceway. However, at the shallowest planting depth, the mean in the control raceway was actually slightly smaller than in the wave raceway.

Finally, although the wave treatment dramatically impacted the total mass, maximum leaf length, stolon length, and number of rosettes per plant, relative energy allocation to aboveground and belowground tissues did not differ (AG:BG, Table 2).

### Table 4
Student Newman-Keuls (SNK) Multiple Range Tests for Wave Treatment

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Count, N</th>
<th>Mean, g dw</th>
<th>SNK Least Significant Difference</th>
<th>Homogeneous Groups</th>
</tr>
</thead>
<tbody>
<tr>
<td>Waves</td>
<td>36</td>
<td>0.357</td>
<td>0.107</td>
<td>A</td>
</tr>
<tr>
<td>No waves</td>
<td>36</td>
<td>0.709</td>
<td></td>
<td>B</td>
</tr>
</tbody>
</table>

Note: Groups with different letters were significant at the 99-percent confidence level ($\alpha < 0.01$).
Figure 5. Total mass (g dw) of vallisneria after 10.5 weeks growth under experimental conditions (Values shown represent means ± se (N = 12) of individual plants for belowground (black portion of bar) and aboveground dry weight biomass (open portion of bar). Total bar height represents total plant biomass. For each planting depth, bar on left is control raceway, while bar on right is wave raceway. P level of t-test comparing two means is shown above each pair of bars.)
Figure 6. Average maximum length (cm) of vallisneria leaves after 10.5 weeks growth under experimental conditions (Values shown represent means maximum leaf length ± se of 12 individual plants present at each planting level. For each planting depth, bar on left is control raceway, while bar on right is wave raceway. P level of t-test comparing two means is shown above each pair of bars).
The results obtained from these experiments suggest that 15-cm waves can significantly impact the establishment and growth of vallisneria in shallow waters ($\leq 25$ cm). The waves generated in this experiment were not of sufficient strength to uproot or wash out the plants. Rather, the negative impacts observed were related to damage to the leaves and suppression of vegetative growth.

Individual plants exposed to 15-cm waves periodically during the day accumulated substantially less biomass than those not exposed to waves over the 10.5-week growth period (Table 2). Across all three planting depths, the average total plant mass for those plants exposed to waves was only 0.36 g dw, while the average mass of those plants not exposed to waves was almost twice that amount (0.72 g dw).

The waves were observed to damage the plants quite significantly (Figure 4). In fact, over the course of the experiment, the total amount of leaf tissue lost by the plants in the wave treatment (4.96 g dw) equaled about 78 percent of the total leaf mass accumulation in the raceway between the beginning and end of the experiment (6.33 g dw). In contrast, the total mass of leaf tissue lost by the control plants was only 0.63 g dw and represented only about 4 percent of the total leaf mass accumulation in the control tank (15.62 g).

However, the difference in mass accumulation cannot be entirely explained by the loss of leaves during wave events. Assuming that the sum of the leaf debris plus the live leaf accumulation during the experiment represents the total leaf production for the raceway, the plants in the high-energy raceway lost 44 percent of the total leaf production. Only 4 percent of the leaf production in the control raceway was lost during the experiment. Even so, the total leaf production of plants in the wave treatment was only 11.29 g dw, compared with 16.25 g dw produced in the control raceway.

The waves also resulted in shorter plants, as might be expected with the damage caused to the leaves. Across all depths, the average maximum leaf length of plants exposed to waves was only 67 percent of the length of those not suffering exposure to waves.

The waves also impacted the clonal reproductive potential of the plants, resulting in shorter total stolon length and fewer rosettes per plant produced over the experimental growth period. The total stolon length of the plants in the wave raceway (38.5 cm) was less than half the total length of those not exposed to waves (81.5 cm). Not surprisingly, the total number of daughter plants produced
by plants in the wave environment was also significantly lower than those grown under calm conditions (Table 2). Since vallisneria expands vegetatively primarily by forming new daughter plants along developing underground stolons, this result indicates a marked reduction in vegetative growth capacity of a population exposed to 15-cm waves relative to a population growing in less exposed environments.

These results do not indicate that vallisneria will be excluded from areas exposed to moderate size waves. In fact, plants growing in the wave tank showed strong positive growth over the 10.5-week growth period at all three planting depths. Individual plants increase in total mass by factors of 6.8 X, 4.4 X, and 2.5 X for the 15-, 20-, and 25-cm planting depths, respectively, relative to the mass initially planted at the start of the experiment (compare Table 1 to Table 2). However, the results do suggest that plants growing in an area exposed to waves accumulate mass less rapidly than those in more quiescent environments. As a consequence, these populations may be less resilient to recover from other types of disturbances such as herbivory, water-level fluctuations, or poor water quality.
References


The impacts of 15-cm waves on the survival and short-term growth and development of *Vallisneria americana* plants growing from tubers was investigated in artificial raceways. Twelve recently sprouted tubers were planted at each of three depths (15, 20, and 25 cm) within both wave and control raceways. Wave events designed to simulate wave disturbances caused by traffic along a shoreline were created five or six times each day during the 10.5-week experimental growth period. A wave event consisted of five 15-cm waves generated within the raceway within a 3-min period. The waves generated a maximum velocity of about 140 cm sec\(^{-1}\) as they swept over the plants. All plants survived at all depths in both treatments. However, individual plants exposed to the wave regime accumulated significantly less mass than controls. On average, the total mass accumulated was only 50 percent of that of undisturbed plants. In addition, the plants experiencing the waves had significantly shorter leaves and produced significantly fewer daughter plants. While plants under both wave and no-wave treatments had a net positive growth over the experimental period, those exposed to frequent wave energy developed more slowly and may be less resilient to recovery from other forms of disturbance.
9. (Concluded).

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