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APPLIED ISSUES

Effects of waves on the early growth of *Vallisneria americana*

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SUMMARY

1. The impacts of 0.15-m waves on the survival and short-term growth and development of young *Vallisneria americana* plants were studied in experimental raceways. Young plants were planted at three depths within both wave and control raceways. Wave events were designed to simulate wave disturbances caused by boat traffic and were generated five or six times each day during the 67-day experimental growth period. The 0.15-m waves generated produced a maximum shear velocity of about 1.4 m s^{-1} as they swept over the plants.
2. All plants survived at all depths in both treatments. However, plants exposed to the waves accumulated significantly less total mass than controls. The total mass accumulation of wave-exposed plants was only 50% of that of undisturbed plants. In addition, the plants experiencing the waves had significantly shorter leaves and produced significantly fewer daughter plants.
3. While plants under both wave and no wave treatments had a similar relative growth rate and both showed a net positive growth over the experimental period, those exposed to frequent wave energy developed more slowly due to continuous leaf loss caused by the waves. Plants exposed to even modest wave energy may spread more slowly and be less resilient to recovery from other forms of disturbance.

Keywords: aquatic macrophyte, hydraulic disturbance, plant establishment, *Vallisneria americana*, waves

Introduction

Effects of waves on aquatic plants

Wave activity is considered one of the strongest factors influencing the horizontal zonation of plants within lakes (Hutchinson, 1975; Spence, 1982) and observations about the influence of waves on the distribution of aquatic plants are often reported (Jupp & Spence, 1977; Spence, 1982; Keddy, 1983, 1985; Kautsky, 1987). Chambers (1987) related the minimum colonization depth of various species to wave energy and showed that the upslope limit for plants may be due to waves. In other cases, the natural distribution of plants in relation to wave energy provides correlational evidence of wave impacts. For example, the maximum biomass of *Potamogeton pectinatus* L. 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) demonstrated that some plant species are most frequent at an intermediate level of wave exposure.

Wave energy may control the distribution of aquatic plants in shallow water by both direct and

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indirect means (Kimber & Barko, 1994). Direct effects of waves on plants include damage or uprooting of established individuals, reduced survival of developing winterbuds or seedlings, and negative impacts on seedbanks due to washout or burial. Wave damage to mature plants usually occurs during periods of turbulence caused by storms (Kimber & Barko, 1994), although human disturbance, such as that caused by boat traffic, can also damage macrophytes. For example, wave action caused mainly by recreational boat traffic, was observed to negatively affect plant growth in an *in situ* experiment (Vermaat & de Bruyne, 1993).

Although less obvious than damage to mature plants, the impact of reducing the survival of developing winterbuds or seedlings may also have major ecological impacts. Foote & Kadlec (1988) reported that survival of the buds of *Scirpus maritimus* L. (alkali bulrush) was very poor when exposed to waves, but improved significantly when they were protected from wave action. Similarly, the most vulnerable period in the development of wild rice (*Zizania aquatica* L.) was shortly after germination, while the seedlings still had submersed leaves and were subject to uprooting by waves (Lee & Stewart, 1981). Seagrass communities also have reduced seedling recruitment under high energy conditions (Fonseca & Kenworthy, 1987).

Poor seedling recruitment in wind-swept areas is often attributed to seedbank disturbance. The impacts of waves in these cases occurred before seed germination, as waves resuspended and transported seeds out of the littoral zone (Smith & Kadlec, 1985; Schneider & Sharitz, 1986; Foote & Kadlec, 1988). Even when the seeds are not physically moved, they may be prevented from germinating if covered by as little as 1 cm of sediment (Galinato & van der Valk, 1986).

Waves may also impact aquatic plants indirectly. Indirect effects include sediment sorting and sediment resuspension. Sediment sorting takes place when waves wash away finer clays and silts, leaving behind coarser, less fertile sediments (Spence, 1982; Wilson & Keddy, 1985). These sediments may be less favorable for growth (Keddy, 1985). Waves may also resuspend sediments and thus reduce light supply. For example, Engel & Nichols (1994) reported that, in the early 1970s, the macrophyte community of Rice Lake (Wisconsin, USA) was impacted by periods of high water resulting in poor light conditions. Once the water level returned to normal, the plant community was gone and normal wave intensity resuspended sediments, sustaining turbid conditions and excluding plants for at least a decade.

Wave energy also impacts the morphological development of plants. The morphology of plants exposed to waves or high flows differs from that of the same species grown under more sheltered conditions. For example, tensile strength and extensibility were both greater in plants grown under high, rather than low, energy conditions (Brewer & Parker, 1990).

Most information on the effect of waves on freshwater macrophytes comes from observational data or field transplant experiments: little work has been done under more controlled conditions. However, Stewart *et al*. (1997) conducted experiments on *Vallisneria americana* Michaux and *Myriophyllum spicatum* L. under controlled hydrological 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 s). They conclude that, under low ambient flow conditions, damage to plants increases with wave heights above 0.1 m. Furthermore, canopy-forming species, such as *M. spicatum*, were more susceptible to damage than plants such as *V. americana* that have long, ribbon-like leaves arising from a basal rosette.

This paper compares the establishment and early growth of *V. americana* under static and wave-exposed conditions. As a plant that forms long, ribbon-like leaves, *V. americana* typifies plants with a morphology that may be tolerant of high wave energy. The focus was to quantify the direct effects of 0.15-m waves on the survival, growth and morphological development of young *V. americana* plants. The overall objective was to increase predictability in management of aquatic plants by understanding the limits which moderate wave action places on the growth of developing plants.

Methods

Raceway design

Existing raceways at the Lewisville Aquatic Ecosystem Research Facility located in Lewisville, TX, were modified to create static control and experimental wave raceways (Fig. 1). The raceways measured 6 m in length, 0.6 m in depth, and 0.9 m in width. Three planting depths were created at one end of each

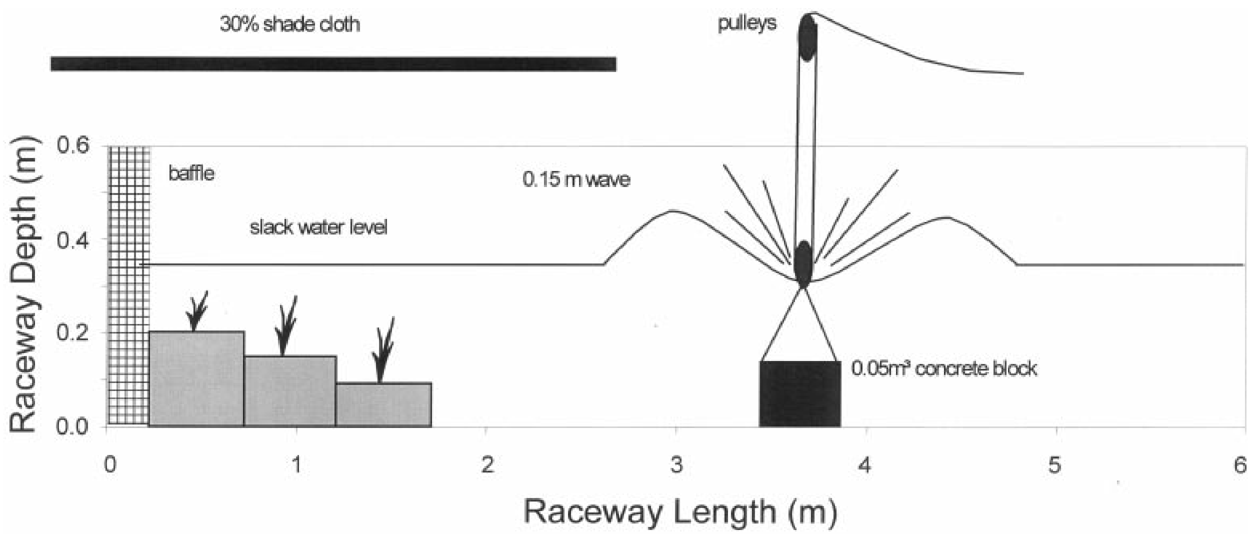

Fig. 1 Design of experimental wave raceway.

raceway to simulate a common shoreline profile. The pockets created by transverse plastic sections were filled with pond sediment covered with a thick layer of coarse sand. The planted end of each raceway was covered with a 30% shade cloth to prevent excessive light and to minimize heating of these shallow water systems.

The raceways were filled with alum-treated lake water. The water was treated with alum (aluminium sulphate) to reduce the concentration of dissolved phosphorus and to minimize the growth of algae. Alum-treated water was also used as needed to make up for evaporative losses. The water level within the raceway was maintained at 0.35 m, resulting in planting depths of 0.15, 0.20, and 0.25 m.

A wave was generated within the experimental wave raceway by dropping a solid concrete block from a height of approximately 0.4 m above the water surface. The concrete block was 0.8 m in width, 0.4 m in length, and 0.15 m high (Fig. 1) and displaced 0.05 m^3 of water. The block was manually lifted above the water surface with a double pulley arrangement and then allowed to free-fall back into the raceway. The wave generated by this method was 0.15 m in height, near the low end of the range reported for waves caused by boats (Bhowmik, Demissie & Guo, 1982; Bhowmik *et al.*, 1991). Although waves of much greater height are often created by barges, these would probably uproot aquatic plants in shallow water. The intent of this experiment was to determine if smaller waves, not powerful enough to uproot plants, would affect their growth and development. To simulate the disturbance commonly caused by boat traffic, the block was dropped five times within a period of 3 min. This treatment was then repeated five to six times each day during the experimental growth period. Since the disturbance created by the waves lasted about 3–5 min, the cumulative daily exposure was about 20–30 min of intense wave action. Each day the loose leaf debris (if any) within each raceway was collected, dried and weighed.

A common indirect effect of waves is increased turbidity (Kimber & Barko, 1994). Although the surface sediments in this experiment were coarse sand and gravel, there was some minor ($\sim$ 10 NTU) and short-lived (5–10 min) increase in turbidity associated with the waves. 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.

Characterizing the waves

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 0.15 m with less than 0.01-m variability among replicate waves.

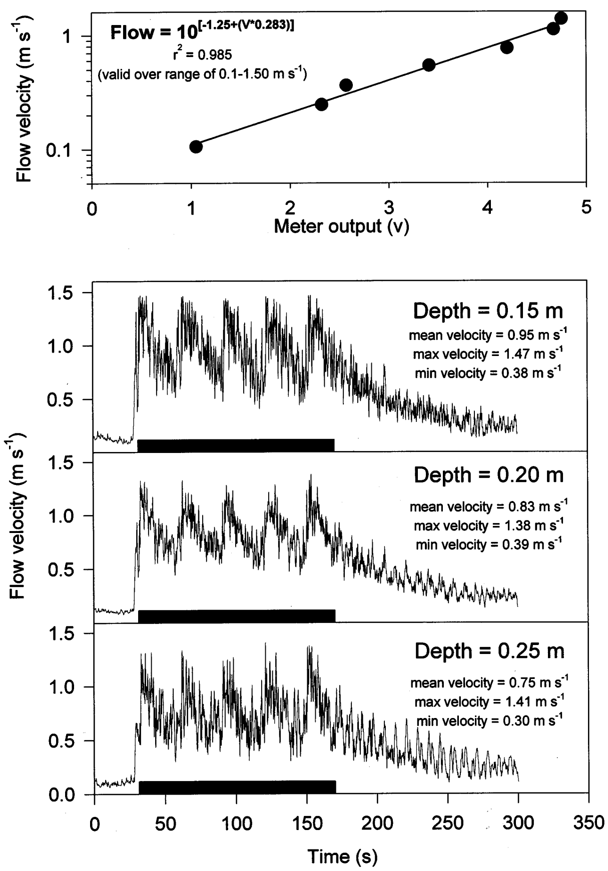

Fig. 2 Top Panel: Calibration of flow velocity sensor over the range of 0.10–1.50 m s^{-1}. Bottom panels: shear flow velocities measured 0.05 m above sediment surface at each of the three planting levels. Black bar indicates period over which velocities were averaged.

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 & Vogel, 1976; MacIntyre, 1986). The probe was placed 0.05 m above the sediment surface and output from the flowmeter was recorded at 250 ms intervals on a computer equipped with a data acquisition interface. The sensors were constructed of 0.9 mm thermistors (Victory Eng. Corp., Springfield, NJ, U.S.A.), optimized for flow in the range of 0.05–1.50 m s^{-1}, and temperature compensated at 28 °C. These sensors measure water speed but not direction. Calibration was made over the range of 0.10–1.50 m s^{-1} within a 2-cm diameter pipe, which was 3 m long (Fig. 2). These measurements were made only once during the experimental period.

Experimental setup

Young *V. americana* plants were obtained by planting a single winterbud (one apical tip) within a small (125 cm^3) plastic container of sterile pond sediment. These were grown under greenhouse conditions (25 °C, 60% full light) for 4 weeks before the experiment began. After culturing in the greenhouse, the young plants were separated into three groups of 36, 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 young plants 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 twelve plants of each size class were harvested to document initial conditions of the plants. The separation into size classes was done to allow more homogeneous groupings and to provide increased statistical power in comparing impacts of waves during this relatively short experimental growth period.

The light climate and temperature regime were monitored within the raceways. Photosynthetically active radiation (PAR, 400–700 nm) was measured as light quanta (μmol photon m^{-2} s^{-1}) just below the water surface (spherical quantum sensor, Li-Cor model LI-193SA sensor). The measurements were taken between 10:00 and 14:00 h and represent approximate maximum daily irradiance. Water temperature was also monitored periodically utilizing a laboratory thermistor.

Plants were moved to the raceways on 2 June, 1997 and allowed to grow until 7 August, 1997 (67 days). 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, connected along one or more stolons radiating out from the initial plant. Number of *V. americana* rosettes, total stolon length, and maximum leaf length of each rosette were measured. Leaves were separated from the stolons and roots and washed to remove accumulated sediments and epiphytes. Stolons and roots were washed over a 1-mm sieve to remove sediment and debris. Winterbuds and flowers were not present. Plant tissue samples were bagged

Table 1 Mass (g dry weight) and maximum leaf length (m) of plants planted within each level of the raceways at the beginning of the experiment. Value shown are means ± SE, $n = 12$

Planting depth (m)	Leaf mass (g)	Root & stolon mass (g)	Total mass (g)	Max. length (m)
0.15	0.017 ± 0.003	0.014 ± 0.002	0.031 ± 0.004	0.106 ± 0.005
0.20	0.044 ± 0.003	0.030 ± 0.005	0.073 ± 0.006	0.208 ± 0.008
0.25	0.153 ± 0.020	0.067 ± 0.009	0.220 ± 0.024	0.351 ± 0.010

separately and dried at 60 °C in a forced draft oven to constant weight.

Statistical analysis

Statistical analysis utilized a two factor ANOVA [factors = depth (0.15, 0.20, 0.25 m), wave regime (wave, control)] 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. All statistical analysis were performed using *Statgraphics Plus* (Manugistics, Inc. Rockville, MD, USA)

Results

Environmental conditions

Light and temperature during the course of the experiment were within the ranges expected for shallow water plant communities. Maximum daily irradiance during the experiment was approximately 1200–1400 μmol photon m^{-2} s^{-1} (55–65% of full light) while daily temperature averaged 28 °C.

The maximum flow velocity generated by the waves within the wave raceway ranged between 1.38–1.47 m s^{-1}, depending on planting depth (Fig. 2). Mean velocity during the wave events were 0.95, 0.83, and 0.75 m s^{-1} for the 0.15, 0.20, and 0.25-m planting depths, respectively. Following the wave events, the water velocity attenuated to background levels over the ensuing 3–5 min.

Plant growth response

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

During the course of the experiment, these developing plants were damaged by the wave treatment, although not to the point where any were uprooted or washed away. Survival in both raceways was 100%. However, the plants in the wave raceway lost several leaves following each wave event, while little leaf material was lost from control plants (Fig. 3). 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.

The waves significantly impacted both total plant mass accumulation and maximum leaf length at all planting depths (Fig. 4). Total plant mass was significantly higher at all planting depths in the control raceway. Across all three planting depths, the plants in the control raceways accumulated approximately twice the mass of those in the wave raceway. 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 (Fig. 4). At all planting depths the plants in the wave raceway had a maximum leaf length shorter than that in the controls. The

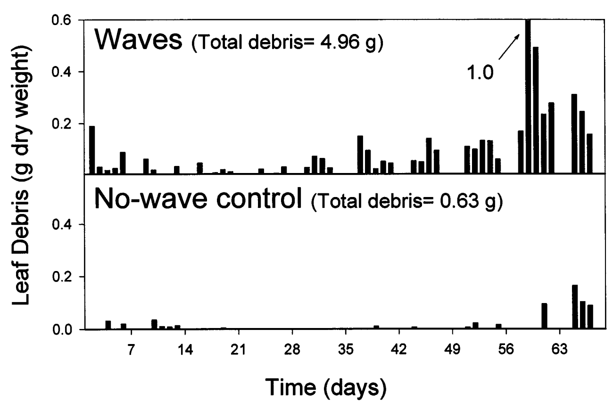

Fig. 3 Mass (g) of floating leaf debris collected each day in each of the two raceways.

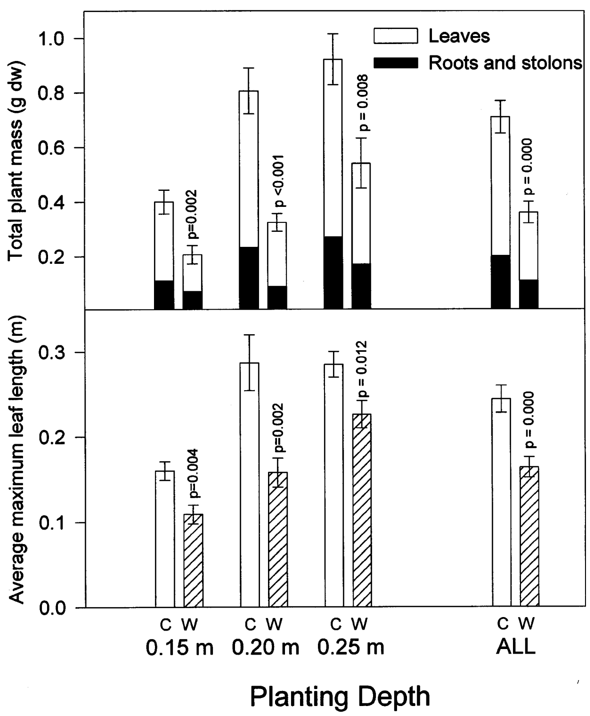

Fig. 4 Total mass (top) or average maximum leaf length (bottom) of *V. americana* after 67 days of growth under experimental conditions. Values shown for each planting depth represent means of 12 individual plants. In the top panel, total bar height represents total plant biomass and error bars are $\pm$SE of total plant mass. The shaded portion of the bar is the mass of roots + stolons, while the open portion is the leaf mass. Bars at the right of the figure are means $\pm$SE for all planting depths ($n = 36$). *P* level of *t*-test (individual planting depths) or two-way analysis of variance (ANOVA) (ALL) are shown beside each pair of bars being compared. C = control raceway, W = wave raceway.

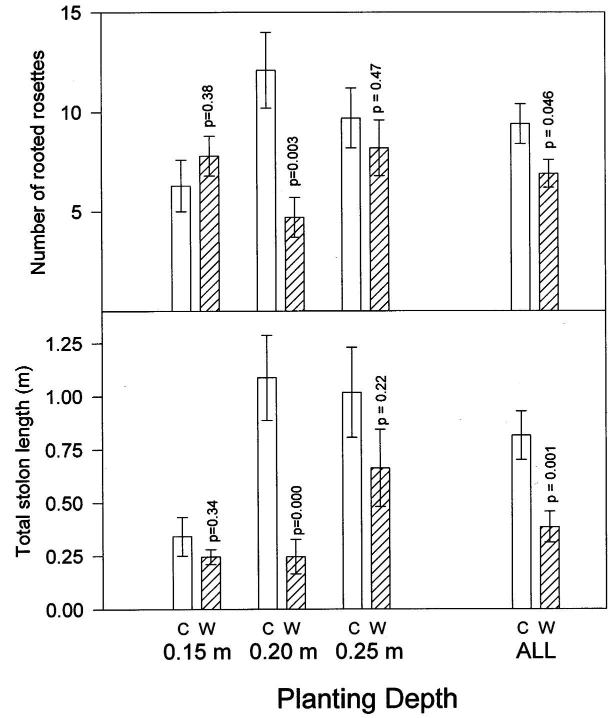

Fig. 5 Number of rooted rosettes (top) or total stolon length (bottom) of *V. americana* after 67 days of growth under experimental conditions. Values shown for each planting depth represent means of 12 individual plants and error bars represent $\pm$SE of the mean. Bars at the right of the figure are means $\pm$SE for all planting depths ($n = 36$). *P* level of *t*-test (individual planting depths) or two-way ANOVA (ALL) are shown beside each pair of bars being compared.

largest differences were observed at the 0.20-m 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 0.16 m, compared to an average of 0.24 m in the control raceway.

In addition to impacting plant mass and leaf length, the wave treatment also affected the total stolon length and number of rosettes produced over the experiment (Fig. 5). Although there was a significant difference between the two treatments when all planting depths were taken together, the effect appeared to be much stronger at the 0.20-m planting depth than at others. 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 when all planting depths were considered. 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 affected the total mass, maximum leaf length, stolon length and number of rosettes per plant, there was a significant difference in relative energy allocation to leaves and roots and stolons only at the shallowest depth. At the 0.15-m planting depth, the leaf to roots + stolon ratio averaged 3.02 ± 0.41 (SE) in the control raceway, but only 1.84 ± 0.20 in the wave raceway ($P = 0.016$, $n = 12$). At the 0.20-m planting depth, the ratio of leaves to roots + stolons in the control raceway was 2.56 ± 0.22 while the ratio in the wave raceway was 3.32 ± 0.63: at the 0.25-m planting depth the ratios were 2.69 ± 0.30 and 2.27 ± 0.17 for the control and wave raceways, respectively.

Discussion

The results obtained from these experiments suggest that the growth of young *V. americana* plants may be slower when exposed to moderate size waves generating shear velocities on the order of 1.4 m s^{-1}. Such wave energies may be commonly produced in shallow waters by recreational watercraft, or in deeper waters by commercial boats.

Unlike the results of field tests reported by Foote & Kadlec (1988), where unprotected plants were often washed away, the waves generated in this experiment were not sufficiently strong to uproot or wash out the plants. Rather, the negative impacts observed were related to damage to the leaves and suppression of vegetative growth. The wave treatment dramatically impacted total mass accumulation and maximum leaf length, and had significant but less dramatic effects on total stolon length and number of rosettes.

Individual plants exposed to 0.15-m waves periodically during the day accumulated substantially less biomass than those not exposed to waves over the 67-day growth period. Across all three planting depths, the average total plant mass for those plants exposed to waves was only 0.36 g, while the average mass of those plants not exposed to waves was twice that amount (0.72 g). These results are similar to those of Vermaat & de Bruyne (1993) who found that, after 30 days of exposure in the field, the development of *P. pectinatus* plants was about twice as high when sheltered from waves produced by recreational boat traffic. Likewise, *P. pectinatus* populations growing naturally under sheltered conditions accumulated over three times the mass of plants growing under wave-exposed conditions (Kautsky, 1987).

Not all water movement is deleterious to submersed macrophytes. In fact, the stimulation of photosynthesis in stirred water relative to stagnant controls has long been known (e.g. Westlake, 1967). Also, seagrass production has been experimentally shown to be stimulated by increasing current flow velocity over a range of 0.02–0.50 m s^{-1} where leaf damage does not occur (Fonseca & Kenworthy, 1987). In the present experiment, however, the waves damaged the leaves resulting in substantial leaf debris over the course of the experiment. In fact, the total amount of accumulated leaf debris in the wave treatment (4.96 g) accounted for about 78% of the total living leaf mass accumulation in the raceway between the beginning and end of the experiment (6.33 g). In contrast, the total mass of leaf debris produced in the control raceway was only 0.63 g and represented only 4% of the total leaf mass accumulation (15.62 g).

The difference in mass accumulation between the plants in the control and wave raceways is mostly explained by the loss of leaves during wave events. The relative growth rates (RGR) of the plants was similar in both raceways when appropriate corrections are made for leaf loss. When corrected for leaf loss, the estimated RGR of the plants in the wave raceway was 26.26 mg g^{-1} d^{-1} while the RGR of the control raceway was only 11% higher at 29.25 mg g^{-1} d^{-1}. In the absence of leaf debris formation, these RGRs would have resulted in mass accumulation of 22.09 g in the wave raceway and 26.84 in the control raceway. These values are unlikely to be significantly different.

However, while the waves do not appear to have affected the RGR of the plants, it did produce shorter plants. Across all depths, the average maximum leaf length of plants exposed to waves was only 67% of the length of those not suffering exposure to waves. During harvest, it was 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 simple damage, however, the change in leaf length may be related to the phenomenon of thigmomorphogenesis. Some terrestrial plants are know to have retarded growth under conditions of mechanical perturbation (e.g. Jaffe, 1976). Although the phenomenon does not appear to have been demonstrated for aquatic plants, a reduction of photosynthetic rate at increased current velocity has been observed (Madsen & Sondergaard, 1983).

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 (0.385 m) was less than half the total length of those not exposed to waves (0.815 m). The total number of daughter plants produced by plants in the wave environment was also significantly lower than in those grown under calm conditions (Fig. 4). Since *V. americana* expands vegetatively primarily by forming new daughter plants along developing underground stolons (Korschgen, 1988), this result indicates a marked reduction in vegetative growth capacity for a population exposed to 0.15-m waves relative to a population growing in less exposed environments.

These results do not indicate that *V. americana* will necessarily be excluded from areas exposed to moderate waves. The success of *Zostera marina* L under various hydrologic energy regimes illustrates this principle. *Z. marina* is a clonal, rosette-forming marine seagrass with many similarities to *V. americana*. Fonseca & Kenworthy (1987) investigated the density, biomass and net productivity of this seagrass under low, moderate and high energy regimes and found the plant to be quite successful in all three energy regimes. They concluded that, while the species may be limited to current velocities of less than 1.5 m s^{-1}, there is a wide range of flow conditions under which it can grow well. In the present experiment, plants growing in the wave raceway showed strong positive growth over the 67-day growth period at all three planting depths. Individual plants in the wave raceway increase in total mass by factors of $6.8\times$, $4.4\times$, and $2.5\times$ for the 0.15, 0.20 and 0.25-m planting depths, respectively, relative to the mass initially planted at the start of the experiment.

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 spread less rapidly and be less resilient in the face of other types of disturbance, such as herbivory, water level fluctuations or poor water quality.

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