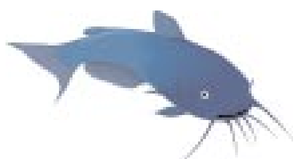
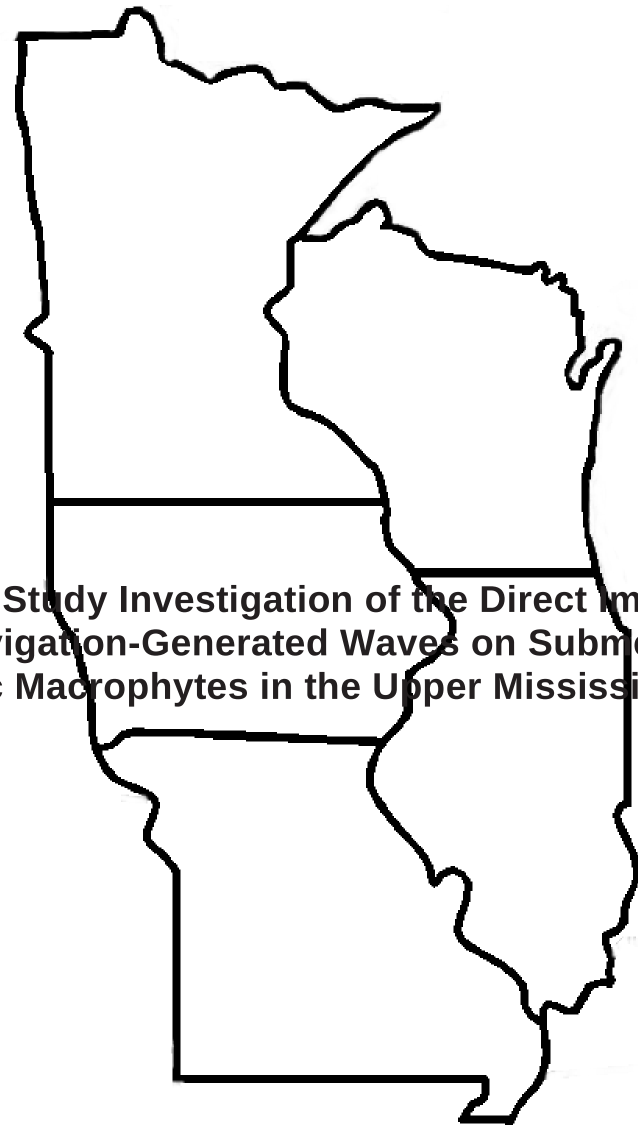
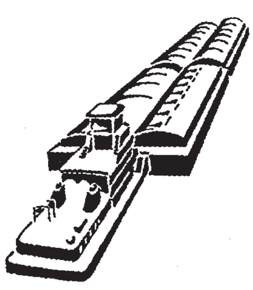
ENV Report 1

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





Flume Study Investigation of the Direct Impacts of Navigation-Generated Waves on Submersed Aquatic Macrophytes in the Upper Mississippi River



September 1997

Rock Island District
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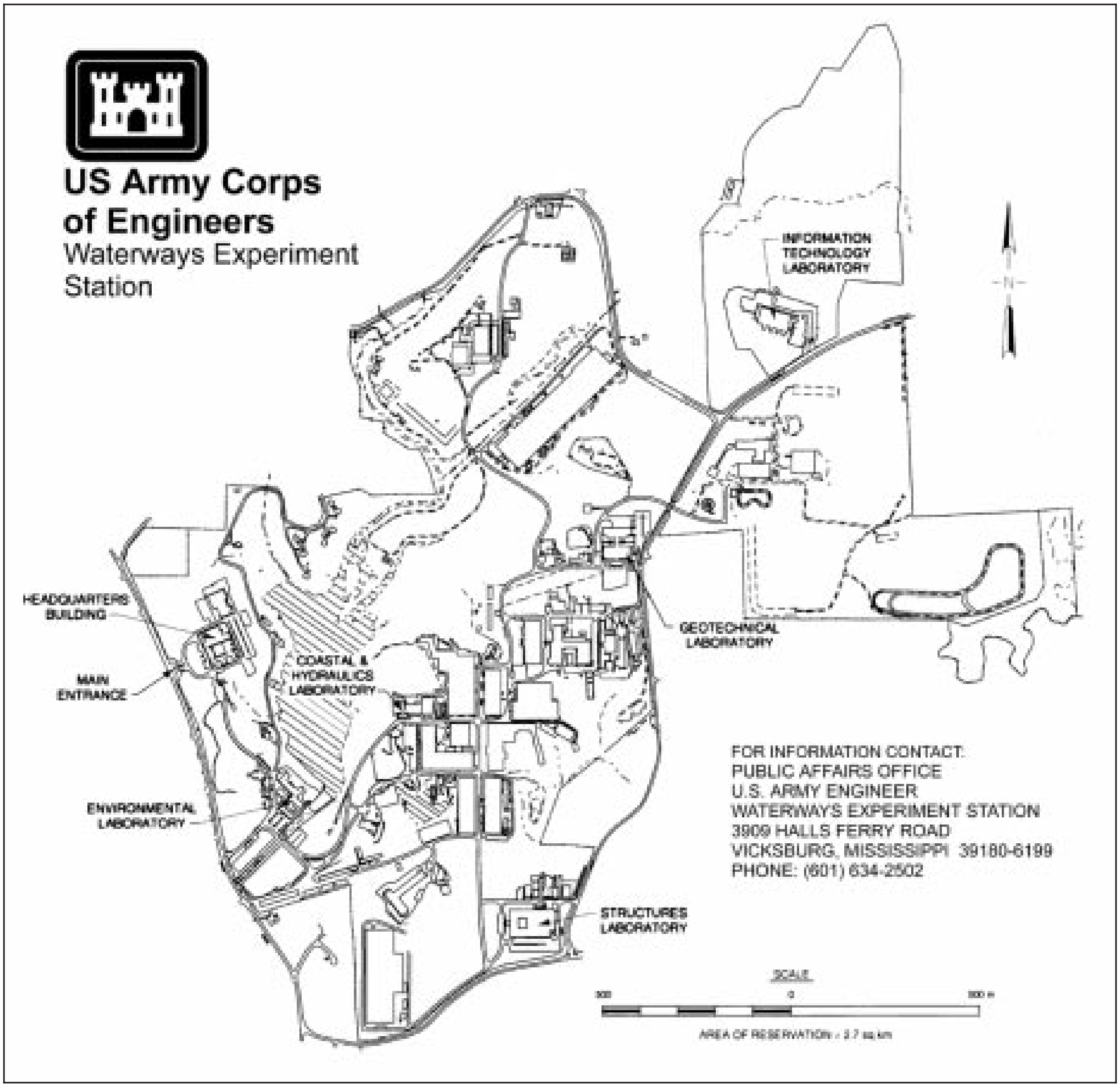

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Preface

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 which will continue to grow into 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 work for this interim effort was conducted as part of Environmental Work Unit 10, Effects of Navigation Traffic on Aquatic Plants, of the Upper Mississippi River-Illinois Waterway System Navigation Study. The work specifically addresses Task I, Resistance to Uprooting and Fragmentation. The study was monitored by Mr. Dan Wilcox, U.S. Army Engineer District, St. Paul, and Mr. Richard Fristik, U.S. Army Engineer District, Rock Island, with technical oversight by Dr. John W. Barko, Director, Center for Aquatic Plant Research and Technology, U.S. Army Engineer Waterways Experiment Station (WES), Vicksburg, MS, and Scientific Technical Director, National Biological Service, Environmental Management Technical Center, Onalaska, WI.

Principal Investigator for this study was Mr. Robert M. Stewart, Ecosystem Processes and Effects Branch (EPEB), Environmental Processess and Effects Division (EPED), Environmental Laboratory (EL), WES. The report was prepared by Mr. Stewart, with contributions from Ms. Dwilette G. McFarland, EPEB, Mr. Donald L. Ward, Coastal Structures Branch (CSB), Navigation and Harbors Division (NHD), Coastal and Hydraulics Laboratory (CHL), WES, and Ms. Sandra K. Martin, Navigation Branch, NHD, CHL. Assistance with plant culture and conduct of the flume study was provided by Messrs. David Reid, AScI Corporation, Vicksburg, MS, and Robby Godwin, WES. Mses. Mary E. McGregor and Sue Fox, AScI Corporation, provided analytical assistance. Mr. Homer Greer, Operations Branch, Instrumentation Services Division (ISD), WES, provided materials and technical assistance for within-flume measurements of tensile loads on test plants, and Mr. David Daily, also of ISD, provided routine technical assistance with flume operation and instrumentation. Technical reviews were provided by Dr. John D. Madsen and Mr. John Skogerboe, EPEB.

This effort was performed under the general supervision of Dr. Richard E. Price, Chief, EPED, and Dr. John Harrison, Director, EL.

At the time of publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Robin R. Cababa, EN.

1 Introduction

Background

The Upper Mississippi River (UMR) is unique among inland freshwater waterways in the United States in that it is an impounded floodplain river, is a Federal inland waterway, and has a Federal fish and wildlife refuge along much of its length. The UMR has been altered for navigation and flood-control purposes over the years, with most extensive changes resulting from construction of a series of 29 lock and dam structures that maintain a 2.75-m navigation channel between St. Louis, MO, and Minneapolis, MN. Impoundment and river regulation has modified the river into a series of navigation pools, with most pools having three distinct zones: (1) the extensively braided tailwater area, (2) the mid-pool marsh area, and (3) the main-pool lentic area (Fremling and Claflin 1984).

Following the 1930s completion of the UMR lock and dam system, aquatic macrophytes began to colonize the newly created shallow-water areas. Emergent plant communities, which were previously widely distributed within the preimpoundment floodplain, quickly colonized the new habitat (Peck and Smart 1986). For submersed species, however, the stable water levels provided by the impoundments created vast new areas suitable for establishment. For these new habitats, water smartweed (*Polygonum amphibium* L.) was often the pioneer colonizer. Records indicate that by the 1960s, submersed communities dominated by pondweeds and vallisneria (*Vallisneria americana* Michx.) had become established (Rogers 1994) reaching peak levels by the early 1980s. Coinciding with multiple years of drought conditions, significant declines in submersed aquatic plants occurred during the late 1980s. The only submersed species not showing significant widespread declines during this period has been Eurasian watermilfoil (also referred to herein as milfoil) (*Myriophyllum spicatum* L.), an exotic species which appears to be forming widespread colonies in areas previously occupied by vallisneria (Rogers 1994).

Reductions in submersed aquatic plants in the UMR are considered significant since they are regarded as a critical component for proper functioning of this multi-use resource. Where established, aquatic macrophyte beds help maintain the integrity of the waterway by reducing shoreline erosion. Emergent and submersed macrophytes also function to improve water quality by reducing suspended solids (Carpenter and Lodge 1986) and nutrients from the water (Kufel and Ozimek 1994). Further, many of the other biological components (e.g., periphyton, arthropods, fish, waterfowl, mammals) utilize aquatic macrophytes for habitat and food (Engel 1985; French 1988; and Killgore, Morgan, and Rybicki 1989).

Given that aquatic macrophytes are a critical component of the UMR system, the Mississippi River - Illinois Waterway Navigation Study has included a series of task areas to determine the potential impacts of navigation traffic on both the integrity of existing plant beds and on the ability of plant species to recolonize previously occupied areas (National Biological Service 1995). These studies were deemed necessary because forces (e.g., waves and currents) generated by navigation traffic are assumed to be of sufficient magnitude and frequency to have both direct and indirect effects on aquatic plants (Kimber and Barko 1994). Direct impacts of navigation traffic are caused directly by hydraulic disturbances produced by passing vessels. Navigation traffic on the UMR system includes commercial towboats and their barges as well as recreational boats. Direct impacts include plant breakage and uprooting caused by waves or altered currents. Direct impacts, for the most part, are likely to be restricted to plant communities within the main channel border. Indirect impacts are defined as those that affect the growth and distribution of the plant communities by impacting their environment. An example of an indirect impact is reduction in photosynthesis rates due to increased water column turbidity levels or to settling out of suspended particles onto photosynthetic surfaces.

Hydraulic Disturbances Generated by Navigation Traffic

As a vessel navigates through a waterway it generates hydraulic disturbances in the form of waves and currents. The dominant hydraulic disturbance features associated with a moving tow are the drawdown, return current, propeller jets, and secondary waves. The size of the vessel with respect to the waterway along with its speed dictate the magnitude of these forces and their effects on the environment (Bhomik, Demissie, and Osakada 1981, Bhomik and Mazumber 1990).

As the vessel displaces water during its forward motion, it causes a drop in the water level alongside the barges known as the drawdown (Figure 1). Drawdown begins near the bow and rebounds near the stern producing a single wave with a duration on the order of 40 to 120 sec, depending on vessel length. Drawdown can cause dewatering of shallow areas along the shoreline during vessel passage, as well as effectively cause a pumping action at the mouth of narrow off-channel inlets to backwaters and side channels. Nearshore dewatering imposed by these drawdowns normally does not extend to depths greater than 0.3 m, and most often is restricted to depths of 0.1 m or less.

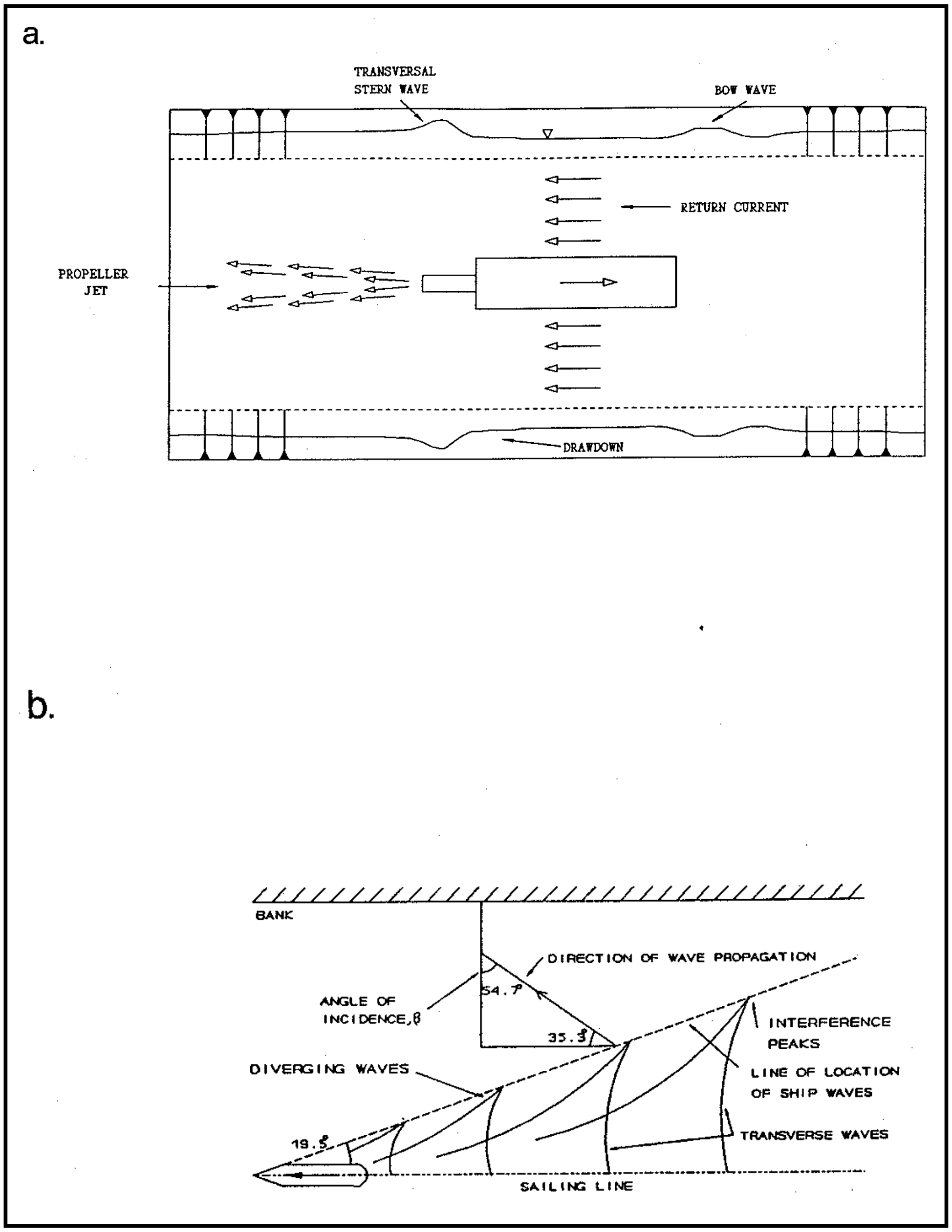

Figure 1. Type of waves and currents generated by commercial navigation traffic: (a) general definition sketch of navigation effects terms, (b) ship wave angles and definition sketch

flow toward the stern parallel to the tow. The maximum return current is produced adjacent to the barges and typically closer to the stern. As vessels move upstream, return currents cause a temporary increase in ambient current velocities. In a tow moving downstream, the return current causes a decrease in ambient current velocities and under certain low flow conditions can create temporary ambient flow reversals.

Currents associated with the propeller jets are highly three-dimensional and cause localized disturbances to the flow. The characteristics of these jets are a function of the hull shape, propeller type and size, and horsepower of the vessel. The thrust, alignment to the bank, and the rudder angles affect the potential flow impingement on the bed or banks. Under normal underway operations, propeller jet effects are limited to the area behind the tow in the navigation lane.

Beginning at the corners of the lead barges, waves diverge from the sides of the tow. As transverse stern waves intersect with this diverging wave, secondary waves are formed which propagate away from the tow at an angle toward the shoreline (Figure 1). These waves are rather consistent in amplitude and have short periods (1 to 5 sec). For high-speed commercial vessels, and particularly for recreational craft, these waves can have significant wave heights and often dominate the hydraulic disturbances produced by the vessel. Transverse waves diminish in magnitude with distance from the stern and have wave periods on the order of 2 to 5 sec.

On the UMR, commercial traffic is characterized by vessels having multiple barge units pushed by towboats with 100 to 7,000 hp and twin screws. The standard barge-tow configuration is made of 9 to 15 jumbo barges (each barge 59.4-m long by 10.7-m wide) configured three barges wide and four or five barges long. The maximum or loaded draft of the tow unit is 2.7 m. Bhomik, Demissie, and Guo (1982) have reported that navigation-generated wave heights of secondary waves are generally less than 0.3 m with a wave period of 1 to 5 sec. Though waves generated by a passing vessel generally last only a few minutes at any one location, the frequency of navigation traffic on the UMR can result in daily cumulative exposures of 30 to 75 min.

Study Objectives and Scope

The primary objective of this study was to investigate the direct damage caused to submersed aquatic plants by different combinations of waves and currents likely to be generated by UMR system navigation traffic. The focus of these tests was restricted to direct effects of navigation-generated secondary waves on aquatic plants along the main channel border. All tests reported herein were conducted in a two-dimensional (2-D) flume facility at the Waterways Experiment Station (WES), Vicksburg, MS. The 2-D system allowed tests to be run for different combinations of current velocities, wave periods, and wave heights, but required that all waves be propagated in the same direction as the ambient current. Further, all tests were performed using plants reared under greenhouse conditions with no ambient current or waves. Therefore, a secondary objective was to compare the tensile strengths of test plants with field-collected plants from the UMR system.

2 Materials and Methods

Test Description

Wave-current (2-D) test flume

Tests were conducted in a 64-m-long by 1.5-m-wide concrete flume with wave and current generating capabilities (Figure 2). The flume (Figure 2a) is 2.0 m deep at the wave generator, from where the bottom rises at a 1:44 (V:H) slope to the test-section depth of 1.5 m. The test section extends to 28.7 m in length, and culminates into a rock wave absorber set at a slope of 1:6. In addition, rubberized matting ("horsehair") was placed at the far end of the test channel to minimize wave reflection back onto the test plants by absorbing wave energy. A 14.6-m-long glass observation area is built into one side of the flume test section.

Monochromatic wave trains were produced within the flume by an electro-hydraulic piston-type wave generator controlled by a computer-generated signal using software developed at WES. Currents were produced by a Gould Model 3410 electric pump plumbed with a 25.4-cm-diam intake pipe of polyvinyl chloride (PVC) and a 20.3-cm-diam PVC exhaust pipe. Plumbing to and from the pump to the flume consisted of a 25.4-cm-diam PVC pipe positioned alongside the flume at floor level. Flume inflow/outflow was routed first through a floor pit at either end of the flume and then through a 20.3-cm-diam PVC pipe that passed through the flume sidewall. These sidewall pipes were connected in series to the larger diameter pipe running alongside the flume to the pump to complete the closed circuit.

To obtain the desired water depth of 0.5 m in the flume, while simultaneously maintaining maximal hydraulic head for reaching higher current velocities, a false bottom was built within the test section of the flume (Figure 2a). Current within the flume is typically adjusted to desired velocities by valves in the large pipe running alongside the flume wall. For this set of tests, however, desired current velocities could not be obtained within the full 1.5-m width of the flume, even though the depth had been effectively reduced by inclusion of the false bottom in the test section. To reduce volume, and thereby increase attained velocities, removeable divider walls were constructed of 3.8-cm-thick plywood that, when positioned, reduced the operating flume width to either 0.76 m or 0.38 m. The divider wall was 1.22 m high by 17.1 m long (Figure 2a).

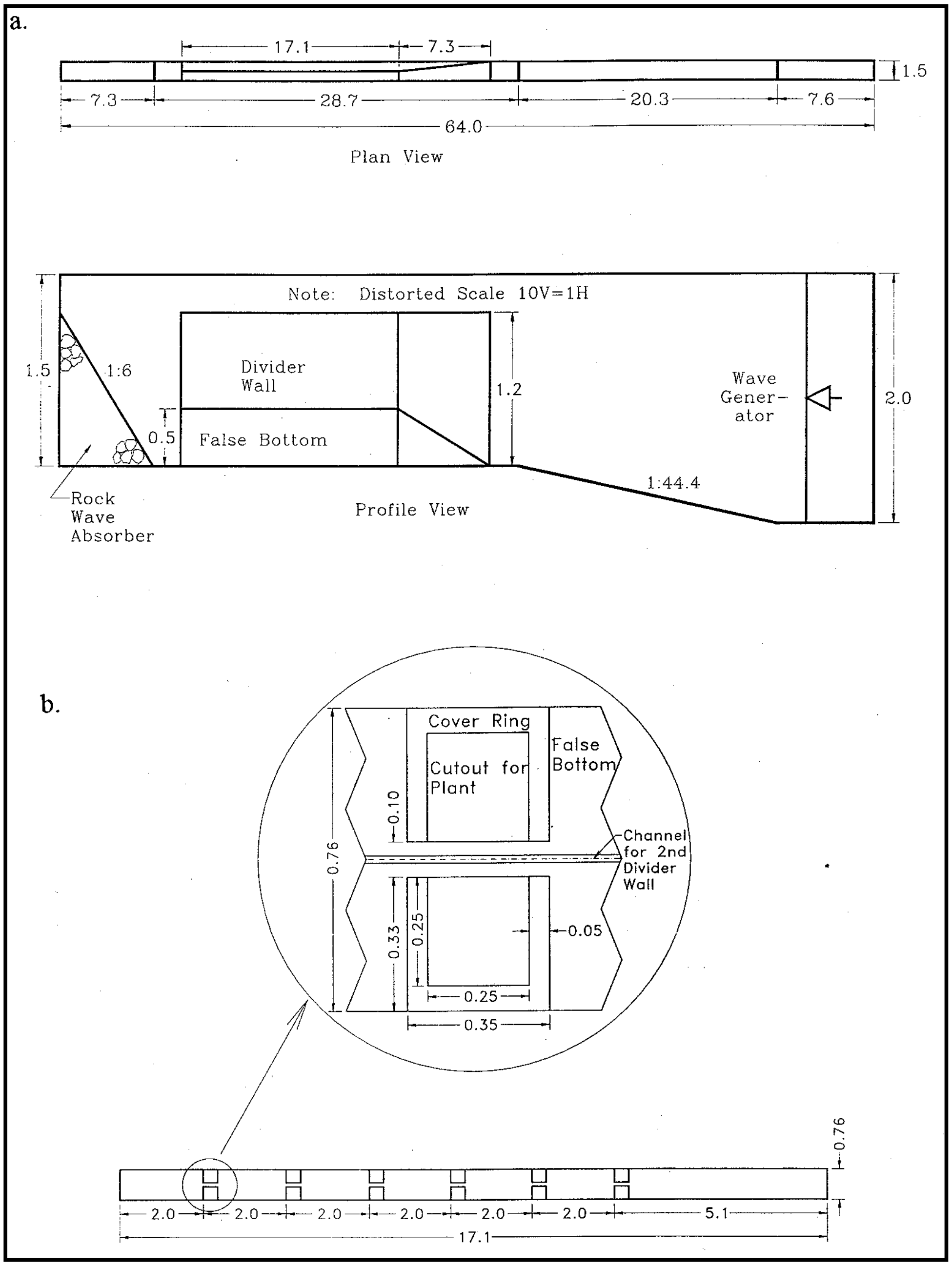

Figure 2. Schematic of flume facility: (a) plan and profile views of the flume structure with secondary walls and false bottom, (b) plan view with enlarged cutout showing positioning and construction of cutouts for placement of plant flats during treatment runs

Twelve rectangular holes approximately 35 cm by 33 cm were cut out of the false bottom for placement of test plant containers (Figure 2b). The size of the holes was such that a test plant container could be positioned flush with the flume false bottom and touching one side of the rectangular hole. The top rims of the test plant containers were then locked in place by fastening a C-shaped plywood ring around the other three sides of the containers (Figure 2b). The twelve holes were positioned in pairs, with 2 m between pairs. A wire screen made of 1.27-cm hardware cloth was positioned behind each pair of holes. Since containers of the same species were never assigned as pairs during a test run, fragments collected on the screens could be sorted by species and properly enumerated.

Wave period and height

The range of wave heights (0.1, 0.2, and 0.3 m) and wave periods (3 and 5 sec) used in this investigation were based on the range of typical wave heights and periods reported for navigation-generated secondary waves in the UMR system (see Chapter 1). Wave settings were monitored by capacitance-type wave gauges located in a three-gauge array directly in front of the wave maker (i.e., gauge number 1-3) plus three gauges (i.e., gauge numbers 4-6) spaced along the 17.1-m test section. Wave heights were calculated using software developed by WES. Data collected by gauges 1-3 were used to ensure repeatability of the wave signals, whereas gauges 4-6 monitored wave conditions affecting the test plants. Wave gauges were removed prior to initiation of each test run to prevent entanglement of plant material on the wave gauge rods.

Wave heights used in this study were $H_{1/3}$, or the average height of the one-third highest wave heights in a time series (also called H_s or significant wave height). During preliminary testing, $H_{1/3}$ and $H_{1/10}$ (average of the one-tenth highest wave heights in a time series) waves generated within the flume were nearly identical. Waves in each test were generated as purely monochromatic (i.e., equal period) wave trains with uniform wave height. However, flume effects, such as sidewall reflectance of wave energy, end flume effects, and shoaling, caused some disruption of the wave train.

Wave-height calibration data were collected in preliminary tests by determining the required wave generator stroke amplitude (cm) needed to create the desired wave heights, as measured by wave gauges 4-6 within the 17.1-m test section of the flume. The wave generator was calibrated prior to each treatment run for that treatment's unique combination of current, wave period, wave height, and operating flume width, which was narrowed from 0.76 m to 0.38 m for high-current velocity treatments. Calibration tests were run for 300 sec for each wave generator stroke setting. Calibration was generally based on recorded output between 60 and 120 sec of the test run. This ensured that the generated wave train had time to reach maximum heights within the test flume section and allowed evaluation of the impacts of end flume reflectance on the wave train over time.

Current velocity

The range of current velocities used in this investigation was selected to evaluate whether current velocities typical of ambient flows along the UMR main channel border can affect the direct effects of navigation-generated secondary waves on submersed plants. Though higher ambient currents sometimes occur along the main channel border, these higher flows could not be generated in the test flume as configured for this study.

Current velocities were measured by a Sonntec acoustic-doppler velocimeter (ADV) at the test section head. Signals from the ADV were displayed directly on a computer monitor using proprietary software from Sonntec. Currents used in this investigation were 0.0 m/sec (no current), 0.10 m/sec, and 0.25 m/sec. To establish the current, the circulating pump was started and allowed to run until the velocity had stabilized. Valves at each end of the circulation pipe allowed velocity control. After the desired current was reached and stabilized, the ADV was removed prior to test wave train initiation to prevent inundation of the meter by the wave action.

Drag measurements

A load cell previously developed by the WES Instrumentation Services Division was made available for measurements of tensile loading stemming from "drag" on plant shoots induced by waves during this study. The load cell had a minimum resolution of approximately 5 g. One end of the load cell and its attached wiring were fastened to the wooden bottom within the flume test section. The attachment was such that allowed the load cell to pivot at an angle projecting along the length of the flume. The wiring from the load cell was attached and run along the interior flume wall so that it exited from the top, from where it was routed to electronic signal processing equipment. The free end of the load cell was fitted with a piece of 6.35-mm-diam surgical tubing approximately 3 cm in length. The bases of intact plant shoots were attached to the surgical tubing. Under conditions of no current or waves, the plant shoot buoyancy was such that it lifted the plant shoot and load cell vertically into an upright position. The pivoting action of the load cell attachment allowed the plant shoot and load cell to maintain orientation in line with either drag forces generated on the plant shoot's base current or passing wave.

Plant Species Selection

This study focuses on Eurasian watermilfoil and vallisneria, two common species of submersed macrophytes in the UMR system. These particular species were selected for study because of their ecological significance to the UMR and because of distinct differences in their growth forms.

Vallisneria is a favorable native species with long, ribbon-like leaves that arise from a basal rosette (Haller and Sutton 1975; Fassett 1975; Godfrey and Wooten 1979). This species grows well at 20 to 32 ^{o}C (Barko, Hardin, and Matthews 1982) and can achieve lengths of 2 m or more depending on water depth (Korschgen and Green 1988). Since vallisneria does not produce a canopy, it typically does not interfere with the use of water resources. Nearly all parts of the plant, especially tubers and rootstocks, are eaten by a variety of aquatic animals and migratory wildfowl (Haller 1974; Korschgen, George, and Green 1988), and its leaves provide habitat and shelter for communities of invertebrates and spawning sport fish (Muencher 1944; Haller 1974; Poe et al. 1986). Established colonies of vallisneria help to improve water quality by filtering out suspended matter, stabilizing sediments, and reducing nutrient concentrations that would otherwise promote algal growth (Korschgen and Green 1988; Korschgen 1990; Barko, Gunnison, and Carpenter 1991; Smart, Barko, and McFarland 1994).

In contrast, Eurasian watermilfoil is an exotic perennial with finely dissected leaves and long, flexible stems (Grace and Wetzel 1978). This species grows rapidly at temperatures from 16 to 35 ^{o}C (Barko and Smart 1981; Smith and Barko 1990), and in a single growing season can achieve lengths in excess of 4 m (Grace and Wetzel 1978; Eggers and Reed 1987). Roots of this species are adventitious, forming on upper portions of the stem prior to autofragmentation and on lower stems buried in sediment (Shannon 1953; Grace and Wetzel 1978; Smith, Barko, and McFarland 1991). As the plant grows, biomass is distributed at or near the water surface, forming a dense mat or canopy of entangled stems and branches. Self-imposed shading beneath the canopy causes a loss of lower leaves on older plants (Adams, Titus, and McCracken 1974). Stolons expand the population locally over a few meters; however, fragments are the predominant means of long distance dispersal and colonization (Kimbel 1982; Madsen, Eichler, and Boylen 1988). Excessive growth of milfoil can be problematic due to the crowding out of native vegetation, and negative impacts on water quality, recreational use, fish and wildlife habitat, and aesthetics (Smith and Barko 1990).

For each species, both 4-week- and 8-week-old plants were tested to provide intraspecific differences in morphology due to developmental stage. From previous experience at WES with greenhouse plant cultures, 8-week-old plants were expected to possess greater biomass, length, and shoot density (i.e., number of shoots per flat) than the 4-week-old plants. In addition, the onset of senescence evidenced by flower and fruit production was expected to occur after 8 weeks in culture. A detailed description of sexual reproduction in milfoil is provided in Grace and Wetzel (1978), and in vallisneria in Kaul (1970).

Plant Culture Techniques

To furnish the large numbers of plants required for flume exposures, an intensive planting effort was initiated in the spring of 1995. Monocultures of vallisneria and milfoil were grown in 1,200-L white fiberglass tanks housed in a greenhouse facility at WES. Tanks were filled 83 cm deep with the low alkalinity culture solution described in Smart and Barko (1985). This solution, prepared with reagent-grade salts and deionized-distilled water, provides major cations (Na^+ = 16.0, K^+ = 6.0, Ca^{+2} = 25.0, and Mg^{+2} = 6.8 mg/L) and anions (Cl^{-1} = 44.2, HCO_3^- = 51.8, and SO_4^{-2} = 26.9 mg/L) but lacks N and P, specifically omitted to minimize algal growth and associated light reductions in the water column. Upon preparation, the solution had a pH of 7.9 and an electrical conductivity of 278 microsiemens/cm (μS/cm). Two air lifts per tank provided filtered-humidified air to enhance air/water CO_2 exchange. Solution temperatures were maintained at 25^o C ($\pm$ 1 ^{o}C) using Remcor circulators plumbed singly to each tank. Temperatures were monitored 2 or 3 times per day with minor thermostat adjustments made as necessary.

Surficial sediment dredged from Brown's Lake at WES provided the rooting medium for the cultures. Sediment from this lake, collected from a site devoid of aquatic vegetation, has been used in WES laboratories for many years to culture a variety of submersed aquatic plants. This fine-textured, inorganic sediment (characterized in McFarland and Barko 1987) has particle size fractions of ≈ 10 percent coarse (> 50 μ diam) and ≈ 90 percent fine (< 50 μ diam) by dry mass. The sediment was amended with ammonium chloride (0.8 g per L wet sediment) while mixing thoroughly in a large-capacity mortar mixer. This chemical amendment was provided to ensure sufficient nitrogen availability for 8 weeks of growth. When mixing was completed, the sediment was poured to a depth of 8 cm in 24.3- by 24.3- by 10.0-cm polyethylene containers. The sediment was then allowed to settle at least two weeks prior to planting. A summary of physical and chemical characteristics of the sediment (after fertilization) as determined by analytical procedures described in Barko et al. (1988) is in Appendix A.

All plants were grown at ≈ 25 percent full sunlight using neutral density shade fabric draped over the greenhouse roof. Maximum midday photosynthetically active radiation (PAR) levels inside the tanks reached ≈ 400 $\mu E/m^2/sec$. At this location (i.e., Vicksburg, MS; 32^o23'N, 90^o52'W), the duration of daylight ranged from 13.4 to 14.3 hr between late April and late July (List 1951).

Eurasian watermilfoil used in the study was clipped 15 cm in length from apices of a continuous WES greenhouse stock. This stock was established from a previous collection in Lake Wingra, WI. Overwintered tubers of vallisneria were obtained commercially from a wildlife nursery in Oshkosh, WI and were sorted prior to planting to ensure size uniformity.

Each species was planted separately at a density of 9 propagules per flat (24.3 by 24.3 by 10 cm deep). The propagules were spaced evenly in the containers, with basal ends of vallisneria buried ≈ 2 cm and milfoil ≈ 4 cm deep in sediment. A thin layer of washed silica sand was placed over the sediment surface to prevent physical mixing with the overlying solution. Immediately after planting, the containers were submersed into prepared culture tanks.

One tank per species was planted each week from late April to late June 1995 (Table 1). Weekly plantings were required to provide plants of two age groups

Table 1
Planting Schedule for Culture Plants

Month	April				May				June				July				August			
Week	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**	**1**	**2**	**3**	**4**
Obtain Propagules			*	*																
M8-1 & V8-1 Culture				P	*	*	*	*	*	*	*	T								
M4-1 & V4-1 Culture								P	*	*	*	T								
M8-2 & V8-2 Culture					P	*	*	*	*	*	*	*	T							
M4-2 & V4-2 Culture									P	*	*	*	T							
M8-3 & V8-3 Culture						P	*	*	*	*	*	*	*	T						
M4-3 & V4-3 Culture										P	*	*	*	T						
M8-4 & V8-4 Culture							P	*	*	*	*	*	*	*	T					
M4-4 & V4-4 Culture											P	*	*	*	T					
M8-5 & V8-5 Culture								P	*	*	*	*	*	*	*	T				
M4-5 & V4-5 Culture												P	*	*	*	T				
M8-6 & V8-6 Culture									P	*	*	*	*	*	*	*	T			

(i.e., 4 and 8 weeks) for weekly exposures for one month (July) in the flume. Seven flats were positioned in each culture tank, allowing six flats for flume exposures and one for pretreatment assessments of biomass, morphology, and tensile strength.

Pretreatment Plant Measurements

Milfoil measurements

After attaining their preselected age in culture, the growth characteristics of the dominant shoots originating from 15 plants from each culture tank were measured. For this, dominant shoots which had been produced by all nine of the original apical plantings of one of the seven culture flats were removed for pretreatment measurements. Additionally, the dominant shoot originating from one of the nine original apical tips was removed from each of the remaining six culture flats, resulting in a total of fifteen shoots for pretreatment measurements. These measurements included length (mm) along main shoot axis, total number of meristems (including all branches), and dominant shoot biomass. Additionally, the 15 dominant shoots were divided into three zones for characterization of mechanical properties. Zone 1 included the portion of the shoot from its base to 40 cm distally. Zone 2 included an indeterminate length of the main shoot between Zone 1 and Zone 3, which consisted of the 40-cm section of the shoot from its apex toward the base. For each of the three zones, the proximal end of each shoot section was attached to a customized gripping fixture attached to a LICOR Model DFGS-10 digital force gauge. The force gauge was mounted horizontally on a table, with the display facing upwards. The shoot section was grasped distally by hand and slowly pulled along a graduated (cm) line originating from the force gauge gripping fixture until breaking. The breakage force (N) was recorded, and the diameter of the shoot section at its breaking point was measured (mm) with a Mitutoya Model CD-6"BS digimatic caliper.

Tensile strength estimates for each shoot section were calculated using the equation:

$$T = B/A,$$

where

T = tensile strength (N/mm^2)
B = breakage force (N)
A = cross-sectional area of the shoot at the breaking point (mm^2).

After all 15 dominant shoots were measured, all shoot material from one flat for each culture tank was dried and weighed for later calculation of mean flat shoot biomass per age group.

Vallisneria measurements

Pretreatment physical measurements were also made for 15 plants in the vallisneria culture tanks. As for milfoil, these measurements were made for primary shoots growing out of the original propagule. For vallisneria, the original propagule was a tuber, and the primary shoot was an entire plant consisting of a basal rosette and numerous leaves. Depending on the plant age (i.e., 4 or 8 weeks), flower pedicels and ramets had also been produced. Plants were removed intact from the culture flats. Roots were clipped at their attachment point to the main rhizome, as were any attached ramets. The plant was then attached basally by the naked root crown to the force gauge, and the leaves and flower pedicels were extended distally along the graduated scale. Physical measurements for each plant included length of longest leaf (cm), number of leaves, number of flower pedicels, length (cm) of flower pedicels, force (N) to break flower pedicels by pulling distally, and diameter (mm) of flower pedicel at breaking point. Tensile strength measurements for the flower pedicels were estimated using the same calculations as described above for milfoil. Tensile strength estimates were not calculated for vallisneria leaves, due to inaccuracy in estimating leaf cross-sectional dimensions (i.e., especially thickness). As for milfoil, estimations were made of the mean shoot biomass of culture flats for the two age groups of plants.

Study Design and Execution

Hydrological treatment combinations

The study incorporated the establishment of 18 treatments (Table 2) based on different combinations of current velocity, wave periods, and wave heights. Plants were exposed to each treatment for 25 min. Each test run (i.e., SPECIES by AGE by TREATMENT) included three replications (n = 3), with each replication consisting of a flat of plants resulting from the growth (i.e., over 4 or 8 weeks) of 9 original apical tips. Pretreatment culture techniques for the test plants are described above.

Test setup and treatment sequencing

On their selected treatment day, planted flats were removed from the culture tank and placed individually into ice chests fitted with a customized foam rubber bottom fashioned to keep the flat stationary during transport. At the flume facility, the flats were removed from the ice chests and placed in the rectangular cutouts in the flume bottom (Figure 2b). Because some entanglement and breakage was unavoidable during flat transport and placement into the flume, plant shoots/leaves were untangled, and broken fragments were removed by gentle hand-teasing under a low velocity current (<0.1 m/sec). This procedure also resulted in the plants being oriented with the current and wave direction prior to treatment initiation. Any fragments coming off the plants during this setup phase were collected and placed in a labeled bag.

Table 2
Hydrological Conditions and Culture Tank Sources of Test Plants for Each Treatment

Treatment ID	Current Velocity, m/sec	Wave Period, sec	Wave Height, m	Plant Source/Culture Tank[1]			
				Milfoil		Vallisneria	
				4 wk	8 wk	4 wk	8 wk
1	0.25	3	0.1	M4-2	M8-2	V4-2	V8-2
2	0.25	3	0.2	M4-2	M8-2	V4-2	V8-2
3	0.25	3	0.3	M4-2	M8-2	V4-2	V8-2
4	0.25	5	0.1	M4-3	M8-3	V4-3	V8-3
5	0.25	5	0.2	M4-3	M8-3	V4-3	V8-3
6	0.25	5	0.3	M4-3	M8-3	V4-3	V8-3
7	0.10	5	0.1	M4-4	M8-4	V4-4	V8-4
8	0.10	5	0.2	M4-4	M8-4	V4-4	V8-4
9	0.10	5	0.3	M4-4	M8-4	V4-4	V8-4
10	0.10	3	0.1	NR[2]	M8-6	NR[2]	V8-6
11	0.10	3	0.2	NR[2]	M8-6	NR[2]	V8-6
12	0.10	3	0.3	NR[2]	M8-6	NR[2]	V8-6
13	0.00	3	0.1	M4-5	M8-5	V4-5	V8-5
14	0.00	3	0.2	M4-5	M8-5	V4-5	V8-5
15	0.00	3	0.3	M4-5	M8-5	V4-5	V8-5
16	0.00	5	0.1	M4-5	M8-5	V4-5	V8-5
17	0.00	5	0.2	M4-5	M8-5	V4-5	V8-5
18	0.00	5	0.3	M4-5	M8-5	V4-5	V8-5

[1] Culture tank is the number after the hyphen.
[2] Not run. Tests were not conducted for 4-week-old plant exposure to Treatment 10, 11, or 12.

Tests were initiated by first establishing the desired current velocity in the flume. For a given current velocity and wave period, three treatment runs were then conducted resulting in sequential exposure of plant flats (n = 3 for each combination of species by age) to the three wave heights (i.e., 0.1, 0.2, and 0.3 m) (Table 2). Each of the wave height exposures was 25 min, after which time wave propagation was terminated, and fragments were collected from the screens before initiation of the next wave height exposure in the series. After collection of fragments from the last wave height exposure (i.e., 0.3 m) in the series, plant flats were removed from the flume. All remaining aboveground plant material was cut at the sediment surface and placed in a labeled bag, along with any plant fragments that had been collected during the test-run setup phase.

Treatment effects measurements

Fragments collected during exposure of a given plant species and age to a treatment (i.e., current velocity by wave period by wave height) were placed into a tray of water. Fragments were counted, characterized as to type (i.e., flower, apical or non-apical stem section (milfoil), or leaf section (vallisneria)), fragment length, fragment diameter at breaking point (milfoil stem or vallisneria pedicel), number of nodes (milfoil stem), and number of meristems (milfoil stem). After enumeration, all fragments for a given treatment replication were placed in a labeled bag for determination of total fragment dry weight.

Data Analysis

Pretreatment measurements

Pretreatment plant measurements were analyzed both by culture tank and by age for a given species. For a given species and age, a one-way analysis of variance (ANOVA) using a general linear models (GLM) procedure was conducted to determine significant differences ($p = 0.05$) in shoot growth between culture tanks, with mean separations ($n = 15$) being provided by a Fisher's Least Significant Difference (LSD) test (SAS 1988). A separate ANOVA was also conducted by age group ($n = 60$ shoots) for each species to determine which parameters were significantly different ($p = 0.05$) between age groups.

Treatment effects comparisons

For both plant species and age groups, fragment damage resulting from each of the test treatments was analyzed by a one-way ANOVA (PROC GLM, SAS 1988). Means separations for the amount of damage resulting from the different treatments were performed using Fischer's LSD test ($p = 0.05$). Parameters used to assess fragment damage were cumulative fragment number and cumulative fragment dry weight per treatment. Based on assumptions of the experimental design, these cumulative values were derived by summing fragment collections across sequential wave height exposures. As an example, and referring to Table 2, analysis of Eurasian watermilfoil exposure to Treatments 1-3 were conducted by comparing fragments from Treatment 1 to the cumulative fragments collected through Treatment 2 and to the cumulative fragments collected through Treatment 3. These summations were deemed necessary since all three wave height treatments for a given velocity and wave period combination were run in a series and were conducted using the same plants. Therefore, fragments broken by the 0.1-m wave treatment were not available for breakage by the 0.2-m wave treatment, and fragments broken by the 0.1- and 0.2-m wave treatment were not available during the 0.3-m treatment.

Mechanical Properties of Field Plants

In August 1995, plant collections were made from Lake Onalaska, WI, to provide tensile strength data of field-grown plants for comparison with tensile strength estimates of test plants used in this flume study. Field collections were made for Eurasian watermilfoil, sago pondweed (*Potamogeton pectinatus* L.), American pondweed (*P. nodosus* Poir.), curly leaf pondweed (*P. crispus* L.), Richardson's pondweed (*P. richardsonii* (A. Benn.) Rydb.), water stargrass (*Heteranthera dubia* Jacq.), and coontail (*Ceratophyllum demersum* L.). From these collections, the breaking force of the basal (Zone 1) and apical sections (Zone 3) of nine shoots of each species were measured. Stem diameters, or other dimensions of cross-sectional area, were measured at the breakage points for later tensile strength calculations.

3 Results

Pretreatment Measurements

Milfoil

Pretreatment measurements of 4- and 8-week-old milfoil test plants are compared in Figure 3. Dominant shoot length (Figure 3a) of test plants was statistically different (F = 11.27, p = 0.0001) among culture tanks, with mean comparisons tests indicating that dominant shoots from each of the 8-week culture tanks were longer than dominant shoots from each of the 4-week culture tanks. Significant differences (F = 69.28, p = 0.0001) were also detected in shoot length for data pooled by age group. Dominant shoot biomass (Figure 3c) was more variable among culture tanks, with differences being only slightly significant (F = 2.10, p = 0.0495). However, when pooled by age group, 8-week-old dominant shoots had significantly more biomass than 4-week-old shoots (F = 11.23, p = 0.0011). Meristems per dominant shoot were significantly different among culture tanks (F = 3.83, p = 0.0009), but differences in pooled data by age group were not significant (F = 1.16, p = 0.284). In addition to significantly larger dominant shoots in 8-week cultures, 8-week cultures were also observed to have more shoots per flat. When pooled by age group, total flat biomass was significantly higher for 8-week plants than for 4-week plants (Figure 3d) (F = 10.05, p = 0.0193).

Shoot-breaking forces and tensile strengths of milfoil test plants are compared in Figure 4. Significant differences in shoot-breaking forces were detected (F = 78.84, p = 0.0001) among different shoot sections (Zone 1-Zone 3) and age groups. For both age groups, breaking forces were significantly higher toward the base of the shoots (Zone 1). Differences in breaking forces were partially explained by differences in shoot diameter, which were observed to be greater in basal sections of the shoots, and with basal sections of 8-week-old shoots being greater than 4-week-old shoots. However, since tensile strength measurements

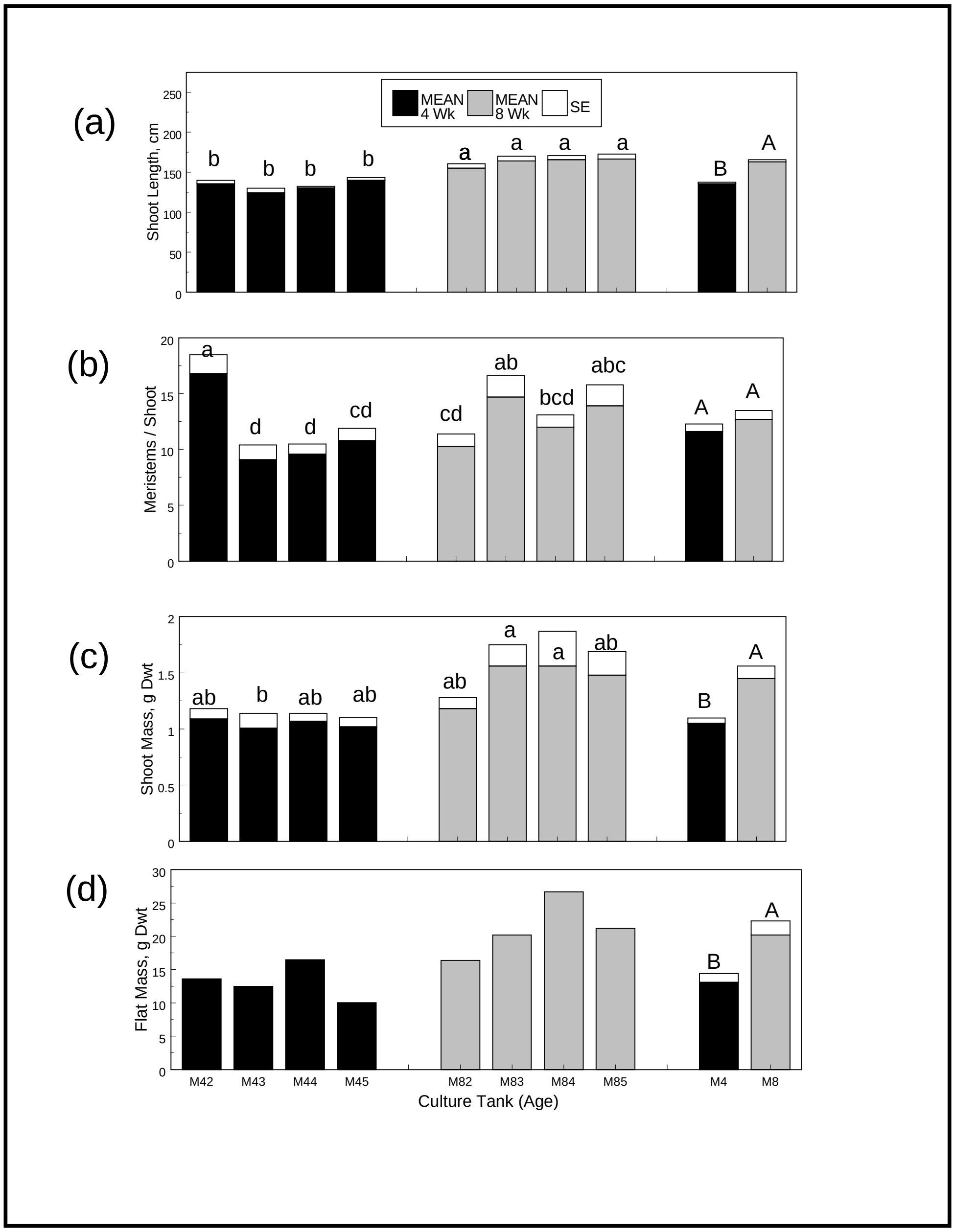

Figure 3. Pretreatment measurements for Eurasian watermilfoil plants: (a) shoot length, (b) meristems/shoot, (c) shoot biomass, (d) total flat biomass. Labels on x-axis indicate culture tank and, therefore, distinguish species and age. Letters above bars show results of means separation tests using Fisher'' least significant difference (LSD) procedure (p = 0.05)

(Figure 4b), which correct for differences in shoot diameter, were also significantly different between age and shoot zone (F = 11.22, p = 0.0001), factors in addition to shoot diameter were apparently involved.

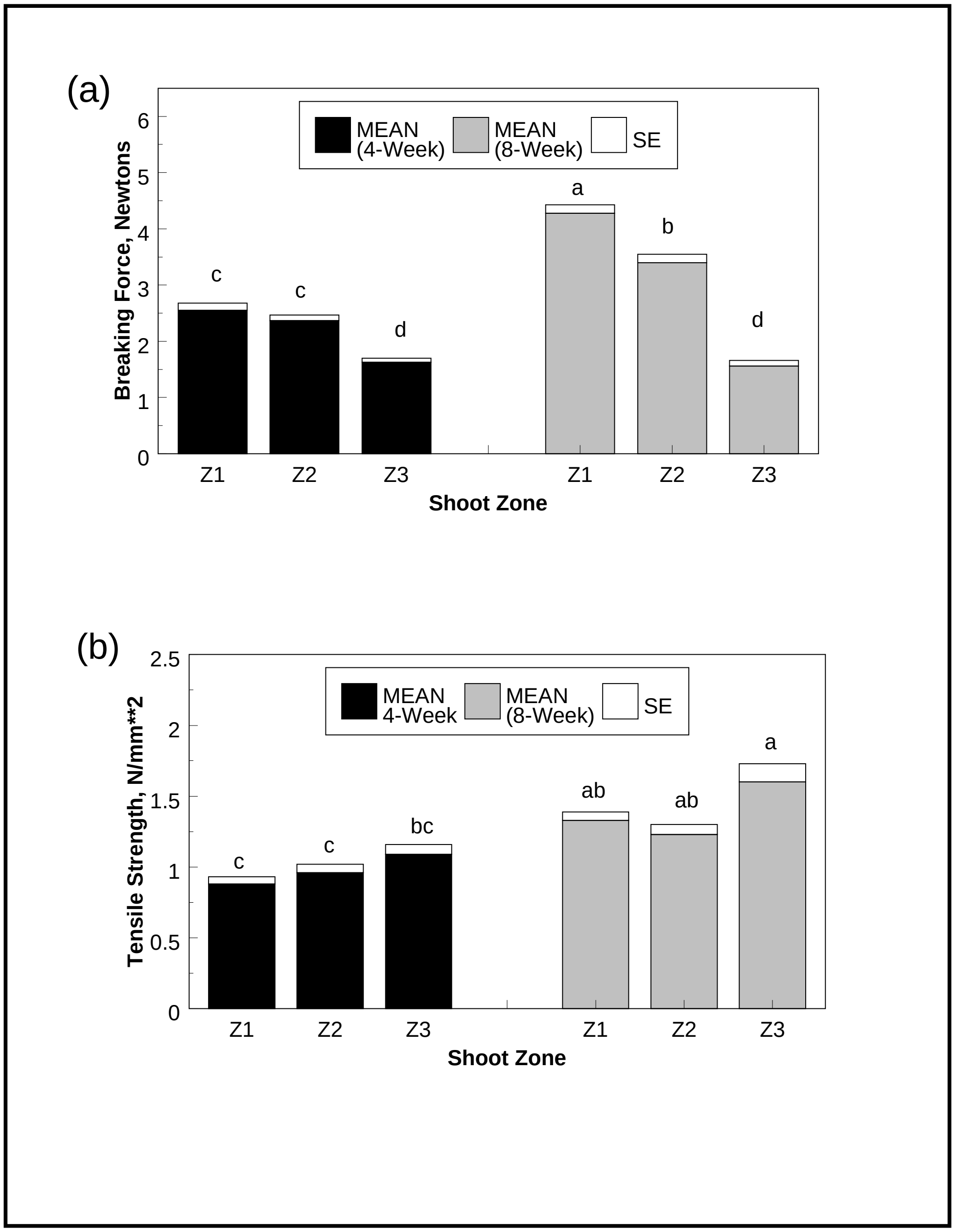

Figure 4. Eurasian watermilfoil shoots: (a) breaking forces and (b) tensile strengths. (Labels on x-axis indicate shoot zones: Z1 = basal section, Z2 = midsection, Z3 = apical section. Letters above bars show results of means separation tests using Fisher's LSD procedure (p = 0.05))

Vallisneria

Mean values for pretreatment growth parameters of vallisneria test plants are shown in Figure 5. Longest leaf measurements (Figure 5a) of dominant shoots were statistically different across culture tanks and age groups ($F = 46.68$, $p = 0.0001$). When pooled by age, 8-week dominant shoots had significantly longer leaves than did 4-week shoots (F = 247.4, p = 0.0001). Significant differences (F = 3.68, p = 0.0013) were also detected in the number of leaves per dominant shoot among the culture tanks (Figure 5b). However, when pooled by age group, number of leaves per dominant shoot were shown to be statistically similar (F = 0.63, p = 0.429). Dominant shoot biomass (Figure 5c) was significantly different among the culture tanks (F = 30.27, p = 0.0001), with 8-week-old shoots having consistently higher biomass than 4-week-old shoots. Pooled shoot biomass data also detected this difference between age groups (F = 145.4, p = 0.0001). As for milfoil, overall flat biomass was significantly higher in 8-week test cultures than in 4-week test cultures (F = 57.2, p = 0.0003) (Figure 5d).

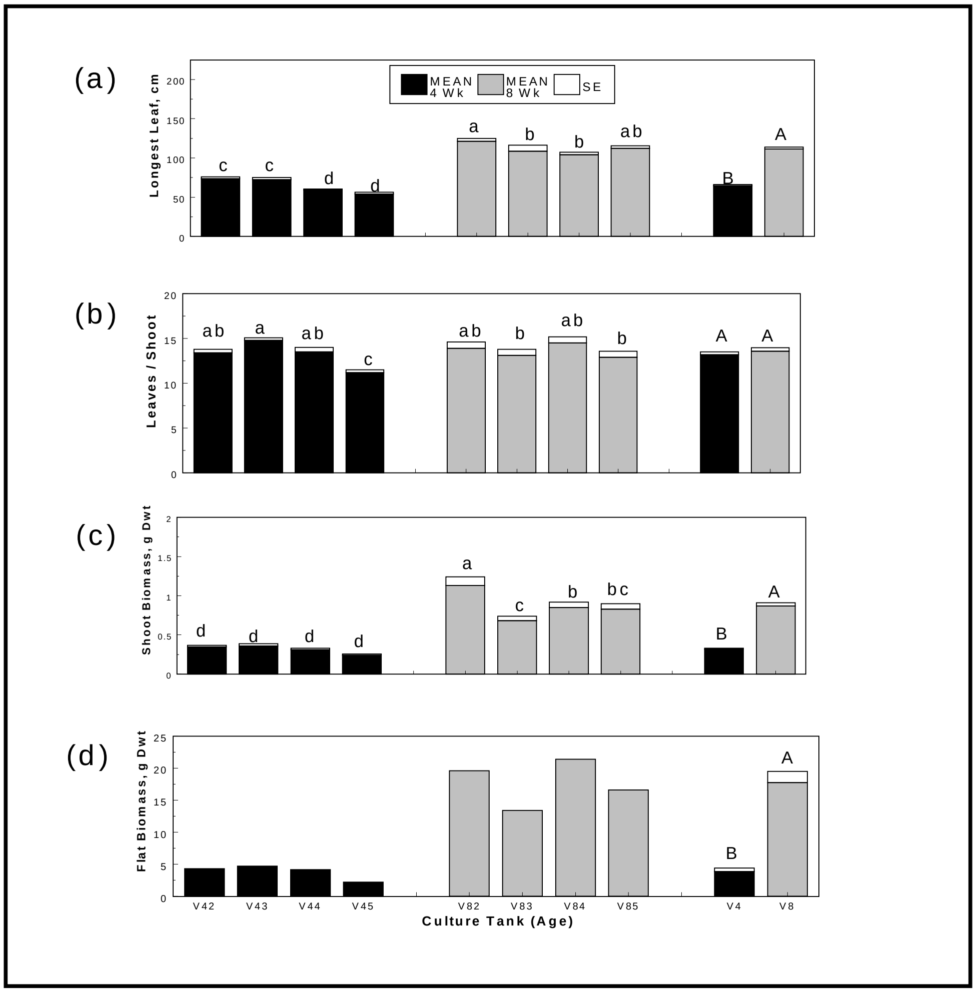

Figure 5 Pretreatment measurements for vallisneria plants. (Labels on x-axis indicate culture tanks and, therefore, distinguish species and age. Letters above bars show results of means separation tests using Fisher's LSD procedure (p = 0.05))

Four-week-old test plants had not begun to develop flowers, while 8-week test plants had a mean of 2.92 flower pedicels per dominant shoot. Overall mean pedicel length was 109.4 cm. Mean force to break flower pedicels and their mean tensile strengths are shown for the 8-week-old culture tanks in Figure 6a. Significant differences ($F = 14.39$, $p = 0.0001$) detected in pedicel breaking forces among the different culture tanks were due to the significantly higher force requirements for pedicels in the V82 culture tank. Statistical differences were not detected in pedicel tensile strengths among the different culture tanks ($F = 0.36$, $p = 0.783$) (Figure 6b), indicating that the higher breaking force of pedicels from the V82 culture tank was a result of greater pedicel diameter.

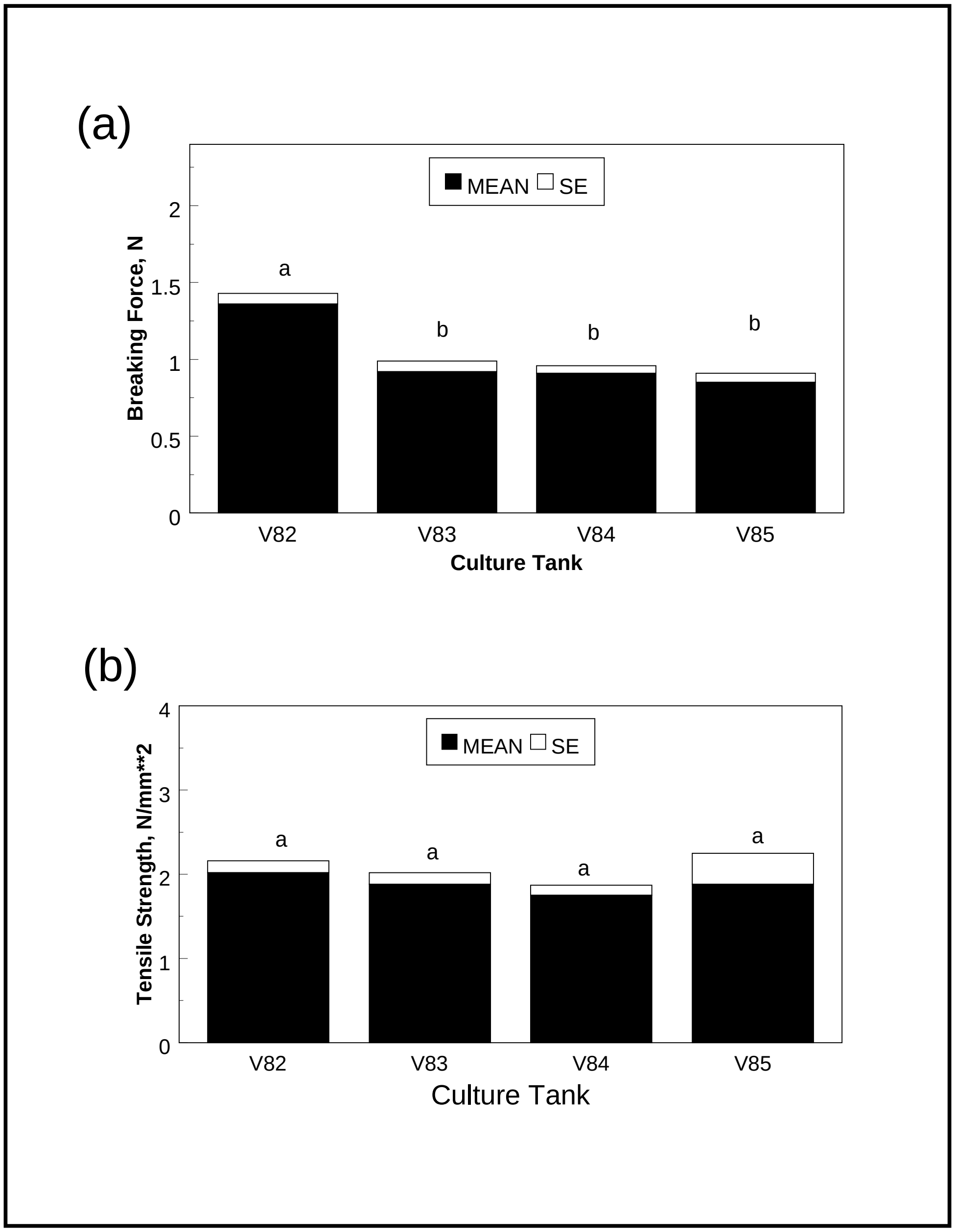

Figure 6. Breaking forces of vallisneria leaves and tensile strengths of vallisneria flower pedicels. (Letters above bars show results of means separation tests using Fisher's LSD procedure ($p = 0.05$))

Damage to Milfoil Plants (Treatment Comparisons)

Cumulative fragment numbers

Mean values for the cumulative number of fragments broken from milfoil plants by each of the hydrological treatments are given in Table 3. Data in the table were analyzed separately by plant age.

Table 3
Cumulative Numbers[1] of Fragments Broken from Eurasian Watermilfoil Plants Exposed to Each of the Hydrological Treatments

Plant Age, Weeks	Current Velocity m/sec	Wave Period = 3 sec Wave Height, m 0.1	 0.2	 0.3	Wave Period = 5 sec Wave Height, m 0.1	 0.2	 0.3
4 WEEKS	0.25	8.67 b-e[2] • 2.404[3] (T1)[4]	14.00 abc • 4.726 (T2)	22.33 a • 6.119 (T3)	1.67 def • 0.882 (T4)	9.00 bed • 2.000 (T5)	13.00 bc • 3.005 (T6)
	0.10	NR[5] (T7)	NR (T8)	NR (T9)	3.00 def • 1.000 (T10)	7.00 c-f • 2.517 (T11)	15.67 ab • 4.978 (T12)
	0.00	0.33 ef • 0.333 (T13)	0.67 def • 0.333 (T14)	12.33 bc • 4.055 (T15)	0.00 f • 0.000 (T16)	0.33 ef • 0.333 (T17)	2.33 def • 0.882 (T18)
8 WEEKS	0.25	12.00 def • 3.215 (T1)	14.00 def • 4.933 (T2)	16.67 def • 4.410 (T3)	3.67 f • 0.882 (T4)	8.67 def • 2.404 (T5)	10.67 def • 3.180 (T6)
	0.10	8.67 def • 3.283 (T7)	23.33 cd • 4.333 (T8)	31.67 bc • 5.696 (T9)	12.33 def • 2.333 (T10)	22.33 cde • 4.333 (T11)	38.67 b • 4.807 (T12)
	0.00	8.67 def • 3.930 (T13)	21.33 cde • 8.452 (T14)	55.00 a • 12.767 (T15)	2.00 f • 0.577 (T16)	8.33 ef • 1.764 (T17)	34.00 bc • 7.572 (T18)

[1] Based on assumptions of the experimental design, fragment numbers were summed through the series of wave height exposures. Numeric values are means • standard errors (n = 3). Treatment results for the two age groups were analyzed separately by ANOVA: 4-week-old plants ($F = 5.91$, $p = 0.0001$), 8-week-old plants ($F = 6.75$, $p = 0.0001$).
[2] Means comparisons among different treatments were conducted separately for the two age groups by Fisher• s LSD test, with significant differences not detected ($p = 0.05$) between means having the same letter (4-week LSD = 8.371; 8-week LSD = 14.815).
[3] Values are standard errors of the means.
[4] Treatment numbers are in parentheses (T1 = Treatment 1, T2 = Treatment 2, etc.)
[5] NR = not run.

For 4-week-old plants, Treatment 3 (referred to as T3 in Table 3), which had wave heights of 0.3 m, a 3-sec wave period, and a current velocity of 0.25 m/sec, was the most damaging treatment. Other treatments which produced statistically similar fragment numbers were Treatment 2 (T2) and Treatment 12 (T12). Though high variability and small sample sizes (n = 3) make it difficult to compare treatment effects, the data tend to indicate that under the high current velocities, irregardless of wave period, similar numbers of fragments were generated by each of the three treatments in a given series of the three wave height exposures. In comparison, under the lower current velocity, no significant damage was generated by wave heights less than 0.3 m. For example, Treatments 13 and 14 (T13 and T14, respectively) generated essentially no fragments, while Treatment 15 (T15), the 0.3-m wave height exposure in that series, generated 12.33 fragments.

For 8-week-old plants, fragment production under the 0.25-m/sec treatment series appears similar to the damage to 4-week-old plants by these treatments. In these treatment series (T1-T3 and T4-T6), damage was again initiated at the 0.1-m wave height treatments, and cumulative fragment numbers after the 0.3-m wave height exposures were near those for 4-week-old plants, though they were not compared statistically. For the two treatment series at 0.1-m/sec, fragment production was similar at each wave height, resulting in a linear accumulation of fragments. Cumulative fragment numbers after the 0.3-m wave height exposures at the intermediate current velocity (0.10 m/sec) were higher than those numbers produced by the high current velocity (0.25-m/sec) treatments. Highest cumulative numbers of fragments were generated by the series of 3-sec waves with no current 0.0 m/sec (T13-T15). The majority of fragments generated by this series of treatments, as well as the majority of fragments generated by the other no current (0.00 m/sec) treatment series (T16-T18), were produced during the 0.3-m wave height exposure. Instead of the near linear accumulation of fragments at each wave height exposure as occurred during the 0.10 m/sec series, the 0.3-m wave height treatments of the 0.00 m/sec series produced two- to three-fold more fragments than had been accumulated during exposures to the two lower wave height treatments.

Cumulative fragment biomass

In terms of biomass losses, the series of treatments to long period waves at the high current velocity (T4-T6) was the most damaging to 4-week-old plants, producing a cumulative total of 0.86-grams dry weight biomass (g dwt) after the 0.2-m wave height exposure and 1.49-g dwt biomass after the 0.3-m wave height exposure (Table 4). The next most damaging treatments were the series of 5-sec waves at the intermediate current velocity (T10-T12) and the series of 3-sec waves at no current (T13-T15). Though these latter two series of treatments produced similar cumulative losses, comparison of the cumulative losses after the 0.2-m wave height exposures (i.e., T11 versus T14) indicates that this intermediate wave height was more damaging in the 0.10 m/sec treatment series than in the 0.0 m/sec treatment series. Similarly, exposures to long period waves with heights less than 0.3 m (T16 and T17) were also not damaging.

Table 4
Cumulative Biomass (g Dwt)[1] of Fragments Broken from Eurasian Watermifoil Plants Exposed to Each of the Hydrological Treatments

Plant Age, Weeks	Current Velocity m/sec	Wave Period = 3 sec			Wave Period = 5 sec		
		Wave Height, m			Wave Height, m		
		0.1	0.2	0.3	0.1	0.2	0.3
4 WEEKS	0.25	0.23 def[2] ±0.059[3] (T1)[4]	0.35 e-f ±0.097 (T2)	0.73 b-e ±0.283 (T3)	0.17 ef ±0.140 (T4)	0.86 a-d ±0.139 (T5)	1.49 a ±0.304 (T6)
	0.10	NR[5] (T7)	NR (T8)	NR (T9)	0.09 ef ±0.020 (T10)	0.53 b-f ±0.390 (T11)	1.02 ab ±0.402 (T12)
	0.00	0.01 f ±0.009 (T13)	0.02 f ±0.021 (T14)	0.90 abc ±0.386 (T15)	0.00 f ±0.000 (T16)	0.01 f ±0.012 (T17)	0.49 b-f ±0.330 (T18)
8 WEEKS	0.25	0.84 de ±0.306 (T1)	0.95 de ±0.404 (T2)	1.30 cde ±0.335 (T3)	0.10 e ±0.035 (T4)	0.39 de ±0.144 (T5)	0.43 de ±0.155 (T6)
	0.10	2.18 b-e ±1.458 (T7)	5.01 ab ±2.465 (T8)	6.25 a ±2.617 (T9)	0.46 de ±0.086 (T10)	1.42 cde ±0.409 (T11)	2.49 b-e ±0.779 (T12)
	0.00	0.54 de ±0.202 (T13)	1.56 cde ±0.371 (T14)	4.16 abc ±1.328 (T15)	0.10 e ±0.059 (T16)	0.63 de ±0.374 (T17)	3.01 bcd ±0.938 (T18)

[1] Based on assumptions of the experimental design, fragment mass was summed through the series of wave height exposures. Numeric values are means ± standard errors (n = 3). Treatment results for the two age groups were analyzed separately by ANOVA: 4-week-old plants (F = 6.46, p = 0.0001), 8-week-old plants (F = 3.02, p = 0.0021).
[2] Means comparisons among different treatments were conducted separately for the two age groups by Fisher's LSD test, with significant differences not detected (p = 0.05) between means having the same letter (4-week LSD = 0.6494; 8-week LSD = 2.885).
[3] Values are standard errors of the means.
[4] Treatment numbers are in parentheses (T1 = Treatment 1, T2 = Treatment 2, etc.)
[5] NR = not run.

Cumulative biomass loss from 8-week-old plants was significantly higher in the series of treatments (T7-T10) with short wave periods and the intermediate current velocity (Table 4). Consistent with cumulative fragment numbers, biomass losses were significantly higher in treatments with intermediate and low current velocities than in treatments with high current velocities.

Damage to Vallisneria Plants (Treatment Comparisons)

Cumulative fragment numbers

None of the hydrological treatments with a 0.25-m/sec current velocity produced fragment numbers significantly greater than zero in either 4- or 8-week-old plants (Table 5). In the intermediate and no-current treatment series (i.e., 0.1 and 0.0 m/sec, respectively) of 4-week-old plants, cumulative numbers of fragments were significantly greater than zero following the 0.3-m wave height exposure of the series (i.e., T12, T15, and T18). In the zero current and short (3 sec)

Table 5
Cumulative Numbers[1] of Fragments Broken from Vallisneria Plants Exposed to Each of the Hydrological Treatments

Plant Age, Weeks	Current Velocity m/sec	Wave Period = 3 sec, Wave Height, m: 0.1	0.2	0.3	Wave Period = 5 sec, Wave Height, m: 0.1	0.2	0.3
4 WEEKS	0.25	1.67 d[2] ±1.667[3] (T1)[4]	2.67 d ±1.764 (T2)	3.33 d ±2.404 (T3)	0.33 d ±0.333 (T4)	0.33 d ±0.333 (T5)	0.33 d ±0.333 (T6)
	0.10	NR[5] (T7)	NR (T8)	NR (T9)	0.33 d ±0.333 (T10)	3.67 d ±1.202 (T11)	10.00 c ±3.055 (T12)
	0.00	2.67 d ±1.333 (T13)	10.33 bc ±3.480 (T14)	19.33 a ±4.333 (T15)	0.33 d ±0.333 (T16)	4.33 cd ±2.028 (T17)	16.33 ab ±3.756 (T18)
8 WEEKS	0.25	2.67 fg ±0.882 (T1)	5.67 efg ±2.603 (T2)	9.33 d-g ±3.712 (T3)	0.67 g ±0.667 (T4)	2.67 fg ±1.667 (T5)	6.67 d-g ±2.667 (T6)
	0.10	4.33 fg ±1.202 (T7)	12.33 d-g ±4.702 (T8)	25.33 ab ±5.783 (T9)	9.67 d-g ±0.333 (T10)	26.33 ab ±3.528 (T11)	36.00 a ±5.132 (T12)
	0.00	5.67 efg ±2.848 (T13)	18.33 bcd ±6.227 (T14)	36.67 a ±6.173 (T15)	1.00 g ±0.577 (T16)	16.67 b-e ±2.404 (T17)	37.00 a ±8.718 (T18)

[1] Based on assumptions of the experimental design, fragment numbers were summed through the series of wave height exposures. Numeric values are means ± standard errors (n = 3). Treatment results for the two age groups were analyzed separately by ANOVA: 4-week-old plants (F = 7.78, p > F = 0.0001), 8-week-old plants (F = 9.21, p > F = 0.0001).
[2] Means comparisons among different treatments were conducted separately for the two age groups by Fisher's LSD test, with significant differences not detected (p = 0.05) between means having the same letter (4-week LSD = 6.19; 8-week LSD = 11.69).
[3] Values are standard errors of the means.
[4] Treatment numbers are in parentheses (T1 = Treatment 1, T2 = Treatment 2, etc.)
[5] NR = not run.

wave period treatment series (i.e., T13-T15), significant cumulative numbers of fragments had been collected from 4-week-old plants following the 0.2-m wave height exposure (i.e., T14). Similar trends, but with higher fragment numbers, were observed for 8-week plant exposures, with the exception being that the 0.2-m wave height treatments generated significant numbers of fragments in all but one of these treatment series (i.e., T7-T9).

Cumulative fragment biomass

Significant biomass losses to 4-week-old vallisneria plants were only generated by the two treatment series with no current (Table 6). In these series, both the 0.2-m and the 0.3-m wave heights generated significant damage in the short (3 sec) wave period series (i.e., T13-T15), while only the 0.3-m waves generated significant damage in the long (5 sec) wave period series (T16-T18). In comparison, 8-week-old plants suffered significant biomass losses under the two hydrological treatment series with no current as well as the two treatment series with an intermediate current (Table 6). As with cumulative fragment numbers, biomass losses resulting from the treatments were higher for 8-week-old plants than for 4-week-old plants.

Species, Age, and Wave Period Effects

Cumulative fragment numbers and biomass following the 0.3-m wave height treatments were analyzed separately by current velocity settings (i.e., 0.25 m/sec, 0.10 m/sec, 0.00 m/sec) to provide further clarification of the effects that plant species, plant age, and wave period setting had on the amount of cumulative damage resulting from the sequential exposures to the three wave heights. These analyses were considered necessary since preliminary tests indicated that species and age were significant factors in all comparisons, and that wave period was significant in all comparisons except for numbers of vallisneria fragments.

Cumulative fragment numbers and types

Cumulative numbers of fragments generated under treatment series incorporating each of the three current velocity settings are shown in Figure 7. Overall analysis of cumulative fragment numbers resulting from the 0.25-m/sec treatment series (Figure 7a) showed a significant treatment effect ($F = 3.93$, $p = 0.011$). In comparisons between the two species, cumulative fragment numbers were numerically higher for milfoil than for vallisneria. However, Fisher's LSD test detected significant differences only between 4-week-old plants, with 4-week-old milfoil plants incurring significantly higher fragment losses under both wave period settings. For vallisneria, numbers of fragments were higher from 8-week-old plants than from 4-week-old plants, but the means separation procedure did not detect significant differences at $p = 0.05$. The data similarly indicate that 3-sec wave periods consistently generated slightly more damage than 5-sec wave periods for treatments with same species and aged plants.

Table 6
Cumulative Biomass (g Dwt)[1] of Fragments Broken from Vallisneria Plants Exposed to Each of the Hydrological Treatments

Plant Age, Weeks	Current Velocity m/sec	Wave Period = 3 sec Wave Height, m 0.1	 0.2	 0.3	Wave Period = 5 sec Wave Height, m 0.1	 0.2	 0.3
4 WEEKS	0.25	0.02 c[2] ±0.018[3] (T1)[4]	0.025 c ±0.017 (T2)	0.028 c ±0.020 (T3)	0.000 c ±0.000 (T4)	0.000 c ±0.000 (T5)	0.000 c ±0.000 (T6)
	0.10	NR[5] (T7)	NR (T8)	NR (T9)	0.002 c ±0.002 (T10)	0.022 c ±0.003 (T11)	0.049 c ±0.010 (T12)
	0.00	0.029 c ±0.018 (T13)	0.125 b ±0.043 (T14)	0.242 a ±0.056 (T15)	0.001 c ±0.001 (T16)	0.035 c ±0.016 (T17)	0.131 b ±0.017 (T18)
8 WEEKS	0.25	0.043 fg ±0.013 (T1)	0.069 fg ±0.022 (T2)	0.097 efg ±0.036 (T3)	0.044 fg ±0.044 (T4)	0.071 fg ±0.063 (T5)	0.120 d-g ±0.060 (T6)
	0.10	0.056 fg ±0.026 (T7)	0.186 c-f ±0.077 (T8)	0.460 a ±0.125 (T9)	0.106 efg ±0.012 (T10)	0.321 abc ±0.058 (T11)	0.409 ab ±0.090 (T12)
	0.00	0.052 fg ±0.028 (T13)	0.279 bcd ±0.058 (T14)	0.379 ab ±0.090 (T15)	0.009 g ±0.009 (T16)	0.122 d-g ±0.028 (T17)	0.263 b-e ±0.058 (T18)

[1] Based on assumptions of the experimental design, fragment mass was summed through the series of wave height exposures. Numeric values are means ± standard errors (n = 3). Treatment results for the two age groups were analyzed separately by ANOVA: 4-week-old plants (F = 7.78, p = 0.0001), 8-week-old plants (F = 10.10, p = 0.0001).
[2] Means comparisons among different treatments were conducted separately for the two age groups by Fisher's LSD test, with significant differences not detected (p = 0.05) between means having the same letter (4-week LSD = 0.0623; 8-week LSD = 0.1688).
[3] Values are standard errors of the means.
[4] Treatment numbers are in parentheses (T1 = Treatment 1, T2 = Treatment 2, etc.)
[5] NR = not run.

Under treatments with a 0.10-m/sec current (Figure 7b), the effects of plant species, age, and wave period on cumulative fragment numbers were also shown to be significant ($F = 5.26$, $p = 0.009$). At this current velocity, means separation tests showed that 8-week-old plants had significantly more fragments than did 4-week-old plants. Differences between species and wave periods were less than under the higher current velocity and were statistically unimportant.

The effects of plant species, age, and wave period were also shown to be significant ($F = 6.01$, $p = 0.002$) under treatments with no ambient current (Figure 7c). Under these treatments, 8-week-old milfoil plants had significantly more fragments than did 4-week-old plants under both wave period settings. Though 8-

week-old vallisneria plants also had numerically larger numbers of fragments than 4-week-old plants, these differences were not shown to be significant by the means separation test. Similarly for vallisneria, no significant effect was detected for wave period. The cumulative numbers of fragments by fragment type for the individual treatment series are listed in Figure 8.

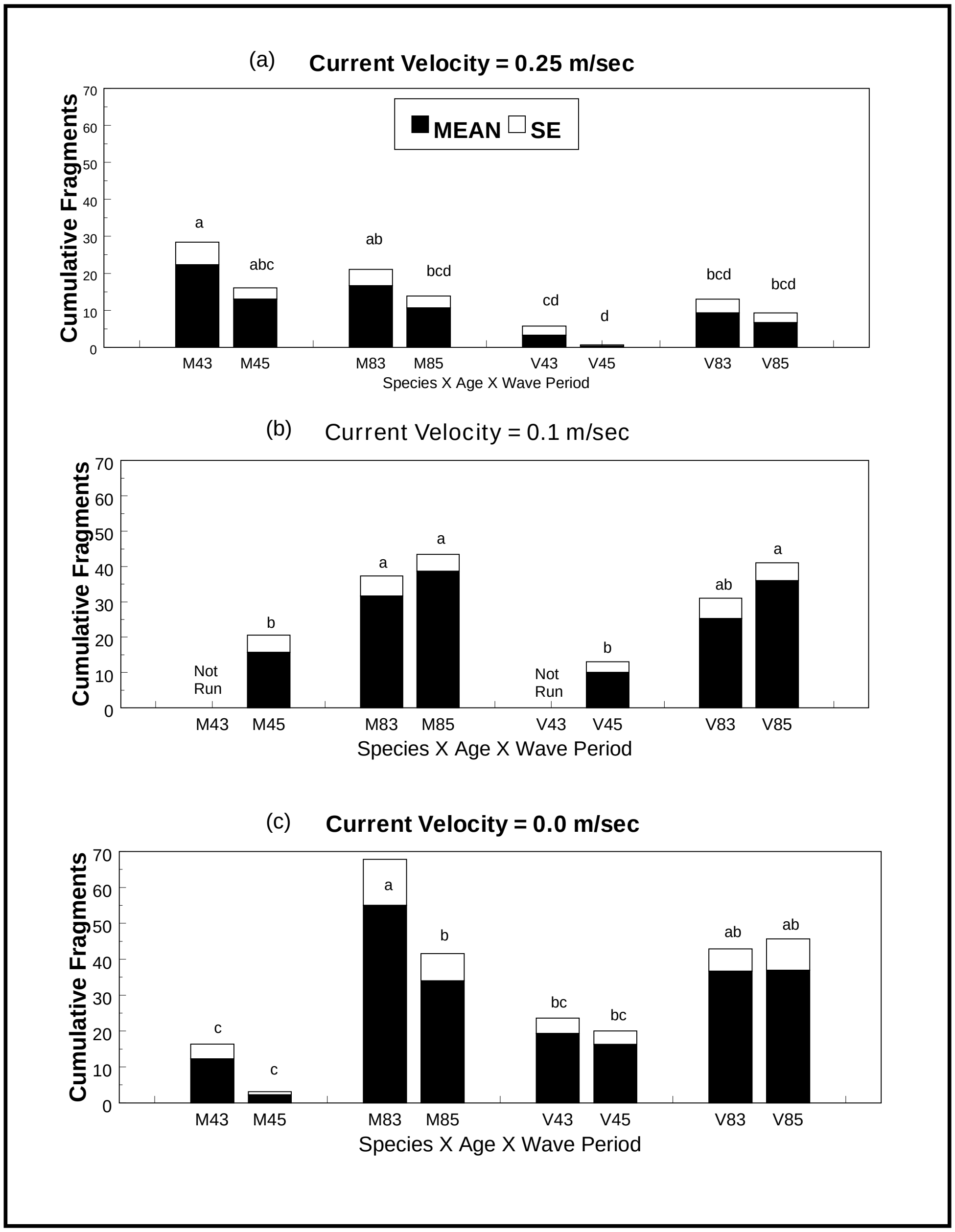

Figure 7 Cumulative numbers of fragments from the different species and age groups resulting from exposures to all three wave height settings under the three different current velocities. (Labels on x-axis indicate species, age (weeks), and wave period (sec). Letters above bars show results of mean separation tests using Fisher's LSD procedures (p = 0.05))

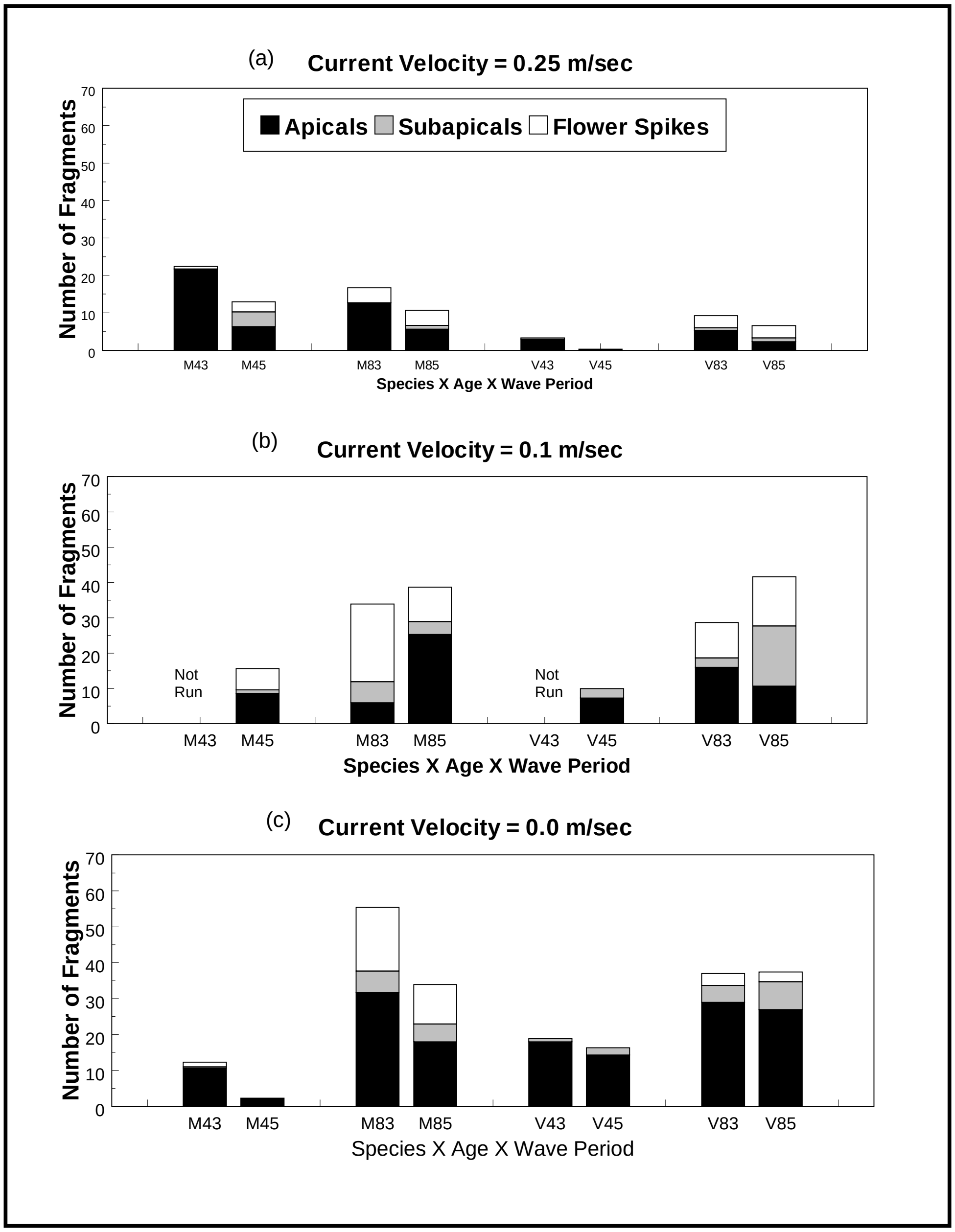

Figure 8. Cumulative numbers of fragments by fragment type for the individual treatment series. (Labels on x-axis indicate species, age (weeks), and wave period (sec))

Cumulative fragment biomass

Cumulative fragment biomass generated under each of the three current velocity settings for treatments incorporating the two plant species, ages, and wave period settings are shown in Figure 9. For the high current velocity treatments (Figure 9a), the overall ANOVA indicated that a highly significant difference existed in the amount of damage to groupings based on plant species, age, and wave period ($F = 8.90$, $p = 0.0002$). Means separations tests further clarified that significant differences existed in three of the four comparisons based on differences in plant species only, with milfoil generally losing more fragment biomass than vallisneria. For vallisneria, no effect of plant age or wave period was detected. For milfoil, significant differences were detected for age and wave period effects, but there was no consistent relationship based on these parameters.

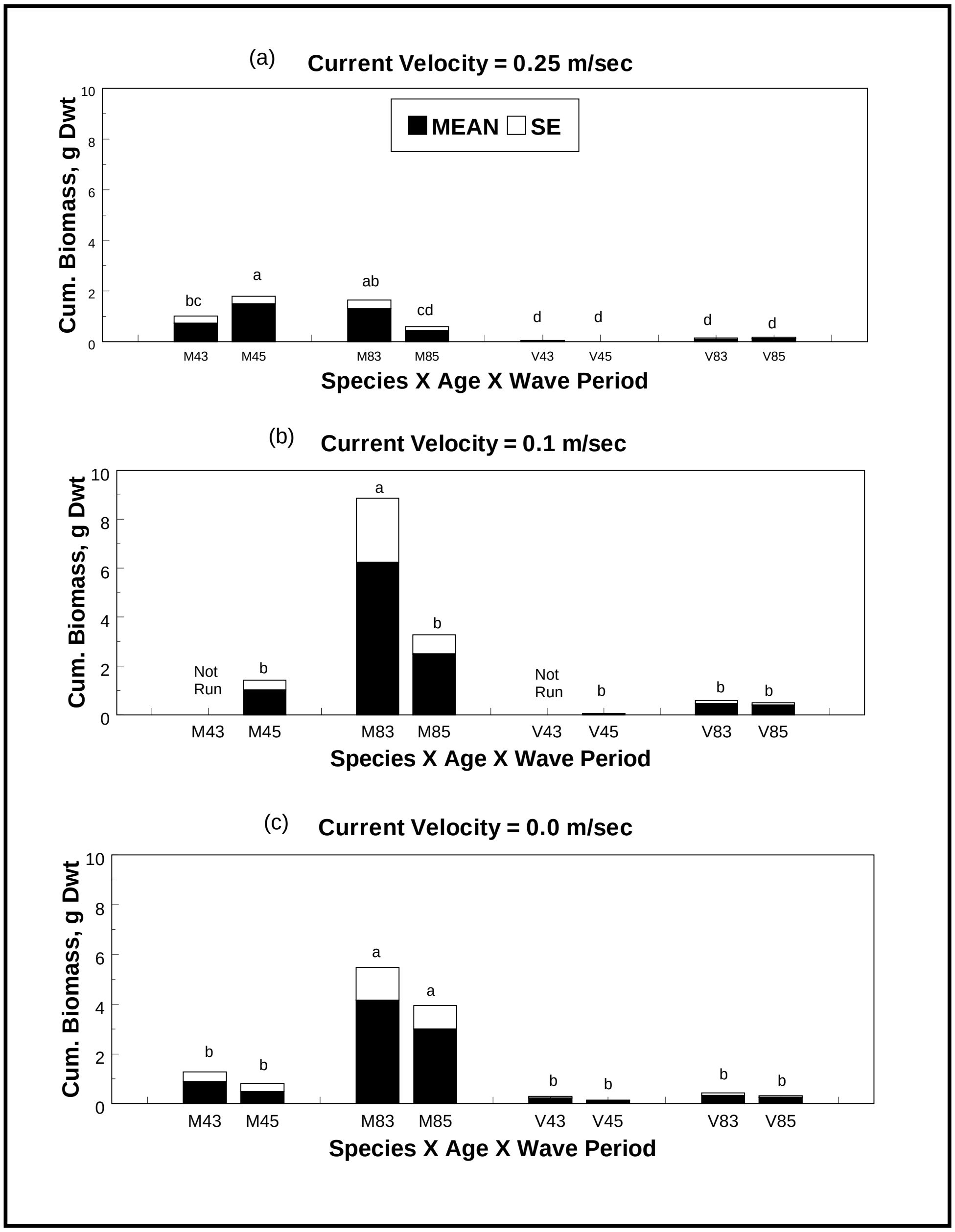

Figure 9. Cumulative biomass of fragments from the different species and age groups resulting from exposure to all three wave height settings under the three different current velocities. (Labels on x-axis indicate species, age (weeks), and wave period (sec). Letters above bars show results of means separation tests using Fisher's LSD procedure (p = 0.05))

For the intermediate 0.10-m/sec current velocity treatments (Figure 9b), a significant group effect was again detected ($F = 4.35$, $p = 0.017$). At this current velocity, 8-week-old milfoil plants exposed under the short (3 sec) wave period lost significantly more biomass than any of the other five groups. Differences between cumulative fragment biomass means for the other groups were not significant.

A significant group effect ($F = 6.35$, $p = 0.001$) was also detected for groups exposed to the no-current treatments (Figure 9c). As with intermediate current velocity treatments, means separation tests again indicated that the difference was the result of the significantly greater amount of biomass loss from 8-week-old milfoil plants. At this test current setting, however, 8-week-old milfoil losses were significantly higher under both wave period settings.

Observations of Test Plant Exposure to Waves

Wave damage to an object depends on the amount of energy within the wave that contacts the object and the ability of the object to withstand the wave energy. Most of the energy within a wave is generated by water circulation around the main wave orbit. The actual force generated within the wave orbit is a function of wave height, wave period, wavelength, and wave celerity (Denny 1988). Wave height not only affects wave force, but also determines how deeply into the water column the wave energy penetrates, with maximum wave forces penetrating to a still-water depth equal to one-half the wave height. Other forces generated by repeating waves are the result of countercurrents in the wave troughs between wave crests (Figure 10).

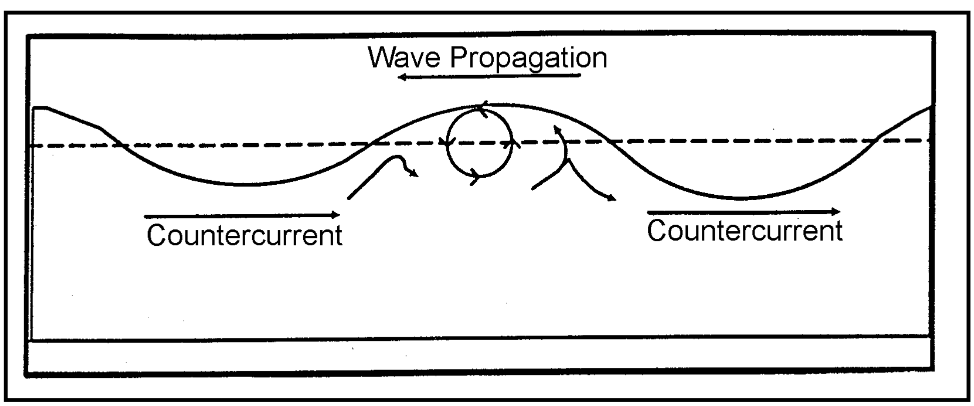

Figure 10. Illustration of the direction of main currents within a repeating wave series

Submersed aquatic plants used in this study are rooted, nonrigid objects whose exposure to wave forces is dependent on the following three factors:

a. The velocity and direction of the ambient current which, among other factors, determines the plant's orientation in relation to the approaching wave.

b. The length of the plant's shoots or leaves, which determines how high into the water column the shoot can extend.

c. The wave height, which determines the maximum depth of wave energy penetration, as well as the amount of wave energy.

Ambient current velocity effects

In all treatments, ambient currents were in the same direction as the direction of passing waves. Major differences in exposure to wave forces occurred as a result of how the ambient current oriented the shoots in relation to the approaching waves. As shown in Figure 11a , the 0.25-m/sec ambient current oriented the 8-week-old milfoil shoots at a 170-deg angle from the source of the approaching waves. This resulted in all of the shoot material being held below the water surface, with the apical tip being approximately 25 cm below the surface. At an ambient current velocity of 0.10 m/sec (Figure 11b), the resulting angle of orientation was reduced to 150 deg, and approximately 50 cm of the shoot apex was floating on the surface. Under treatments with no ambient current (Figure 11c), the angle of orientation was reduced to 90 deg, and two-thirds of the shoot material was on the water surface.

Due to differences in the angle of orientation to approaching waves resulting from the different ambient currents, the exposed plants encountered different wave energy exposures under the different treatments. These differences are visually compared for 0.3-m wave exposures in Figures 12-14, which provide illustrations of the movement patterns of 8-week-old milfoil plants under the three ambient current velocities.

For the high ambient current treatments (T1-T6), wave energy during wave passage caused only minor plant movement patterns (Figure 12 a-d). The only consistent movement pattern was a slight decrease (i.e., < 10 deg) in the angle of orientation, with a slight vertical spreading of apical tips as waves approached, continuing until wave crest passage. Plant shoots were reoriented by the ambient current and oribital wave currents after wave crest passage.

For the intermediate current treatments (T7-T12), plant movement patterns illustrated in Figure 13 (a-d) indicate that ambient current forces were not able to counteract the orbital forces in the passing waves. One of the seemingly most significant differences in plant movement under these treatments occurred as the wave trough passed over shoot material floating on the water surface. During passage of this portion of the wave cycle, floating shoot material was pulled by the countercurrent toward the next approaching wave crest. This “upstream” movement of floating shoot material reoriented the underwater shoot section to near vertical (i.e., approaching a 90-deg angle of orientation). As the wave crest passed, orbital currents on the backside of the wave pulled the shoot material with the wave and reestablished the original orientation. The main effects of this movement pattern were entanglements, which occurred as the shoot was pulled upstream during wave approach, and peak tensile loading, which occurred as the shoot material was returned to its original orientation during wave passage.

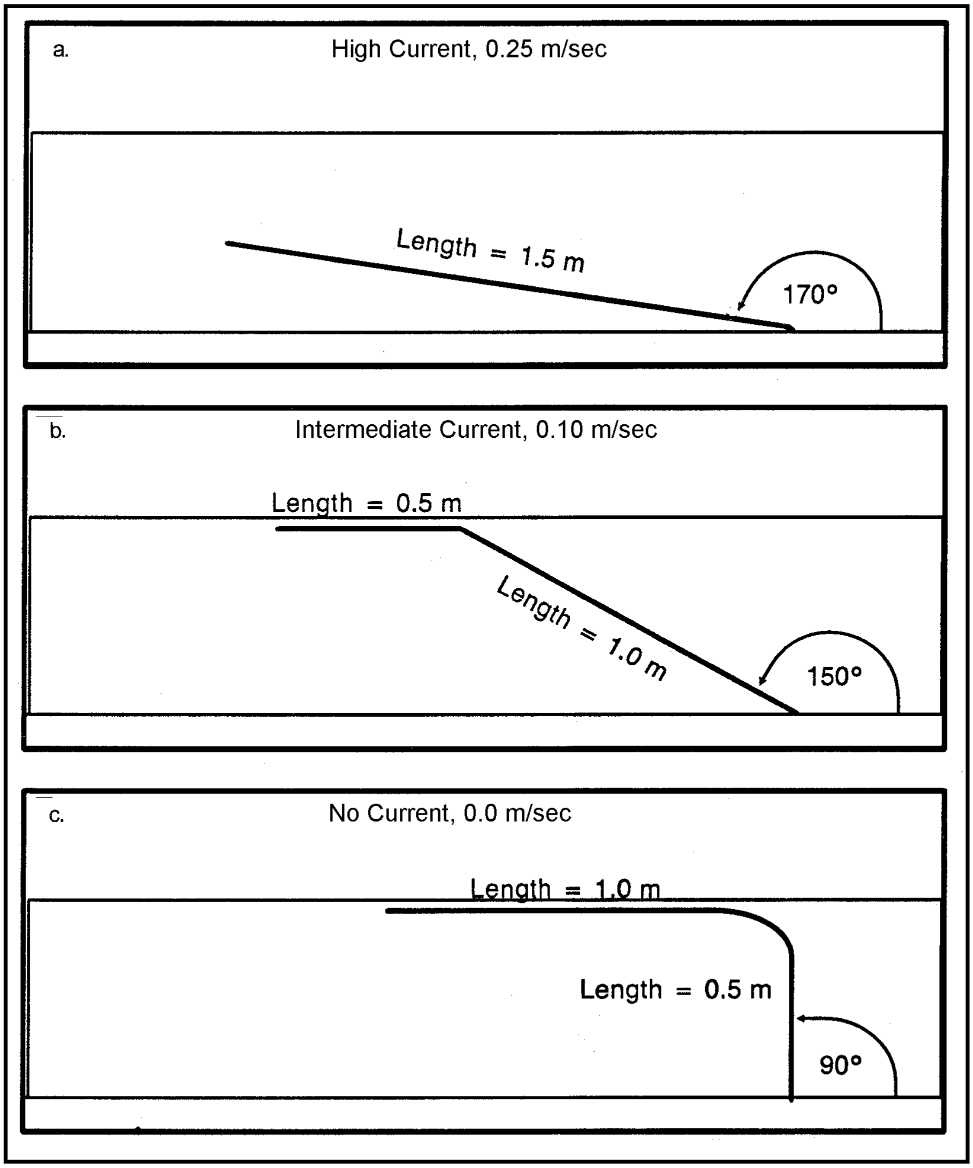

Figure 11. Ilustration of the effects of the three current settings on the orientation of an 8-week-old Eurasian watermilfoil shoot within the flume

Plant movement patterns during wave passage under ambient conditions of no current are illustrated in Figure 14 (a-d). Under these conditions, shoot material was again pulled toward the approaching wave crest by countercurrents in the wave troughs. This movement, in the absence of ambient current, resulted in a reduction in the angle of orientation of the main shoot axis to approximately 65 deg. As with the intermediate ambient current treatments described above,

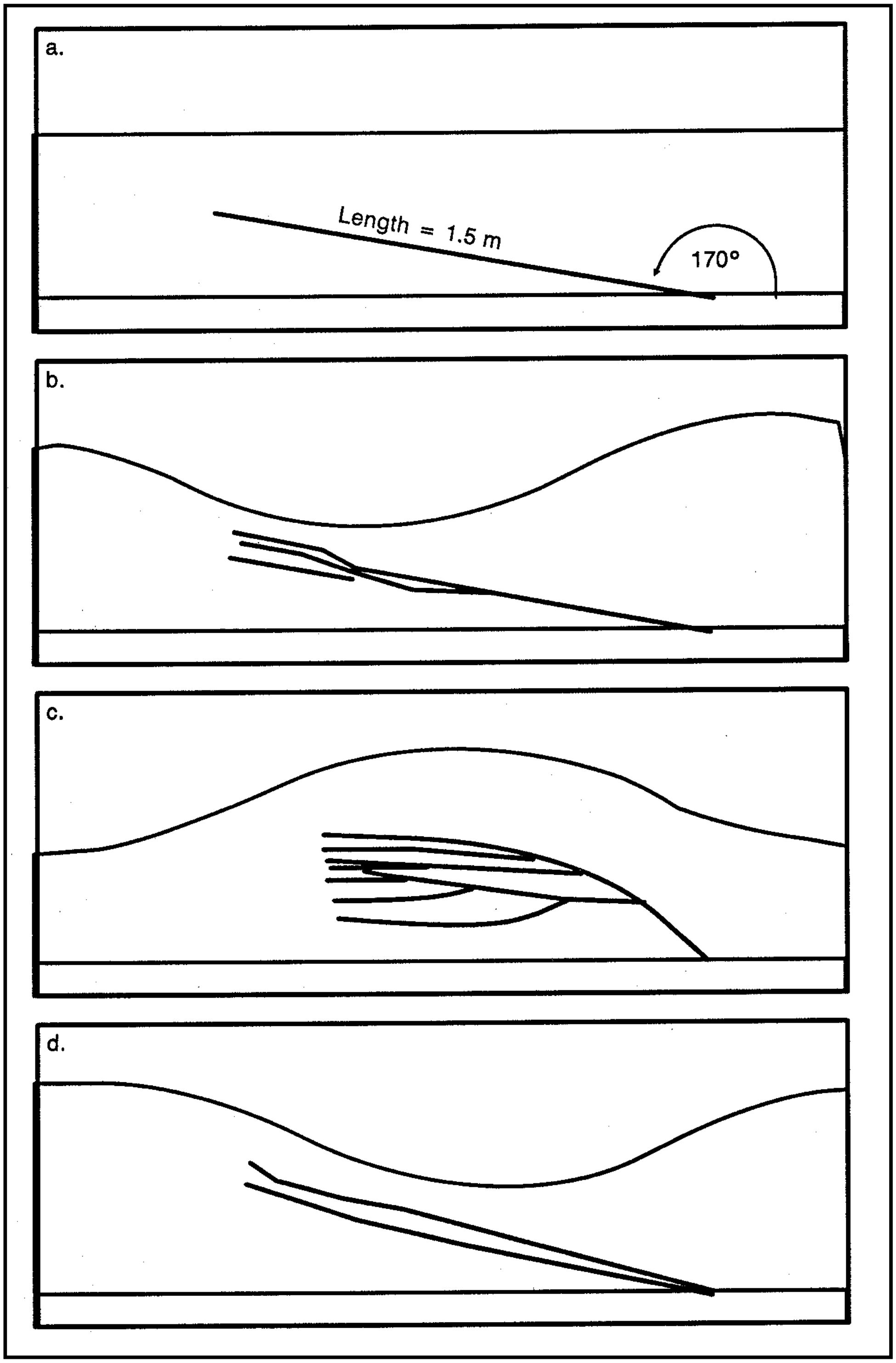

Figure 12. Illustration of generalized movement patterns of 8-week-old Eurasian watermilfoil shoots during passage of a 0.3-m wave under the high current velocity (0.25 m/sec) treatment

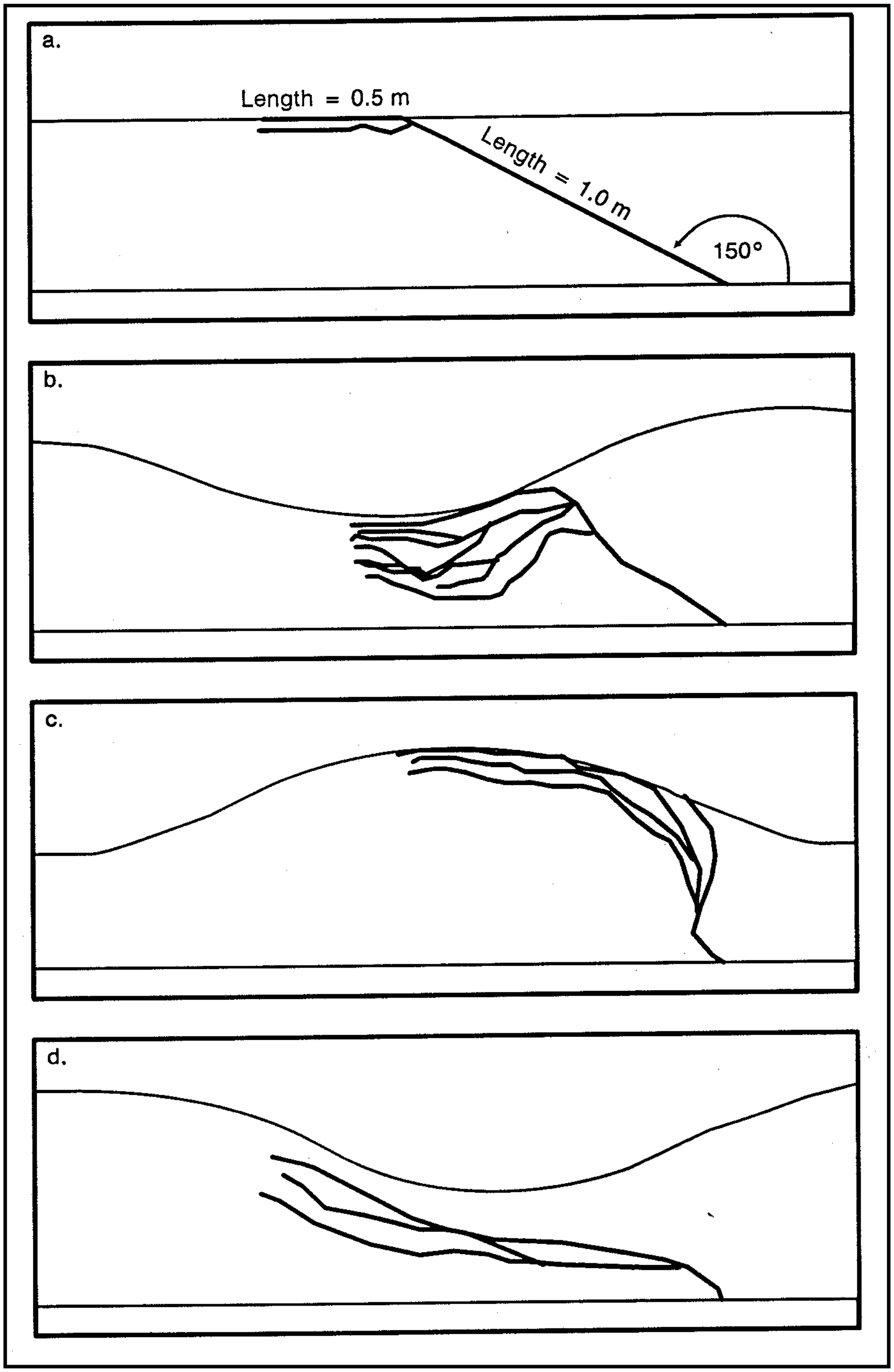

Figure 13. Illustration of generalized movement patterns of 8-week-old Eurasian watermilfoil shoots during passage of a 0.3-m wave under the intermediate current velocity (0.10 m/sec) treatment

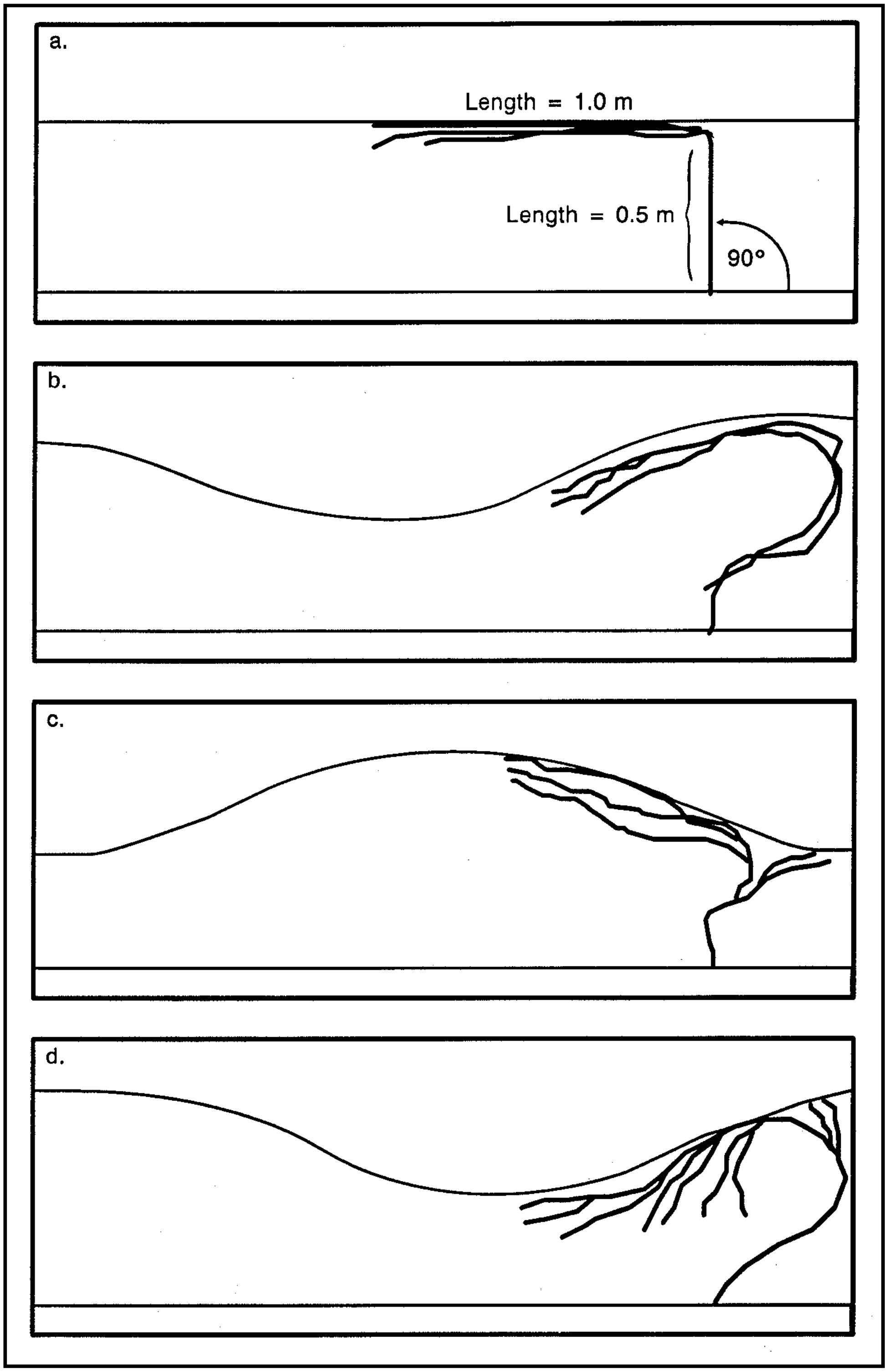

Figure 14. Illustration of generalized movement patterns of 8-week-old Eurasian watermilfoil shoots during passage of a 0.3-m wave under treatments with no ambient current

this also lead to considerable entanglement of shoot material floating on the water surface. During wave passage, orbital currents on the backside of the wave reoriented shoot material at the water surface and changed the angle of orientation of the main shoot axis to approximately 115 deg. Because the majority of the shoot mass was either floating or near the water surface and consequently exposed to the main wave orbit, considerable entanglement occurred during wave passage. It appears that this entanglement led to the increased loss of shoot mass from these treatments.

Species and age effects

The observations described above were made for 8-week-old milfoil plants under the different ambient current velocity treatments. In comparison to the observations described above for 8-week-old milfoil plants, 8-week-old vallisneria plants exhibited the same general movement patterns. However, due to the smooth texture of vallisneria leaves and to the lack of branches on individual leaves, vallisneria plants did not exhibit the same tendency to become entangled as did milfoil shoots. Consequently, very little damage occurred from breakage due to entanglement except, perhaps, to flowers. Vallisneria flower pedicels, which become coiled after seed fertilization to effect the resubmergence of the seed pod, did show a tendency for entanglement and subsequent breakage, especially under the intermediate current velocity treatments.

Regarding the effects of plant age on wave exposure and damage, the major difference was the reduced amount of entanglement in 4-week-old plants. For 4-week-old milfoil plants, which had less mass near the water surface under intermediate and no-current treatments, shoots became entangled to a lesser degree than in 8-week-old plants. Also, 4-week-old milfoil plants had fewer flower spikes, which were observed to be more brittle than vegetative shoot sections and which significantly contributed to 8-week-old fragment collections (Figure 8). For vallisneria, 4-week-old plants had significantly less mass than 8-week-old plants, and due to reductions in leaf length, leaf tips were held below the water surface during treatments with positive ambient currents. Consequently, 4-week-old plants had fewer leaf tips exposed to waves than 8-week-old plants. Further, 4-week-old vallisneria plants did not have any flower pedicels from which to generate fragments.

Wave Height Effects on Tensile Loading

Estimates of tensile loading on 8-week-old milfoil shoots under the hydrological conditions used in Treatments 10, 11, and 12 are shown in Figure 15. Under these current velocity and wave period conditions (T10-T12, Table 2), wave heights of 0.1 m generated a peak tensile load in the range of 25-50 g (Figure 15a). At wave heights of 0.2 m, peak tensile loads ranging from 75 to 100 g were recorded (Figure 15b). Exposure to wave heights of 0.3 m generated peak tensile loads predominately between 100 and 150 g (Figure 15c).

Obviously, increases in wave height resulted in greater tensile loading generated on the basal portion of the milfoil shoot. Also illustrated in Figure 15 is the fact that the peak load was only generated for a small portion of time during wave passage. In Figure 15, the plant's movement pattern in response to exposures to repeating 5-sec waves (i.e., wave period) is apparent. Peak loading occurred for a short duration and indicates that portion of time during wave passage that the plant shoot was fully extended in the direction of the passing wave (Figure 13d). The reductions in loading between loading peaks indicated in Figure 15 are the result of the plant being recoiled by the counterclockwise current in the wave troughs between wave crests (Figure 13b).

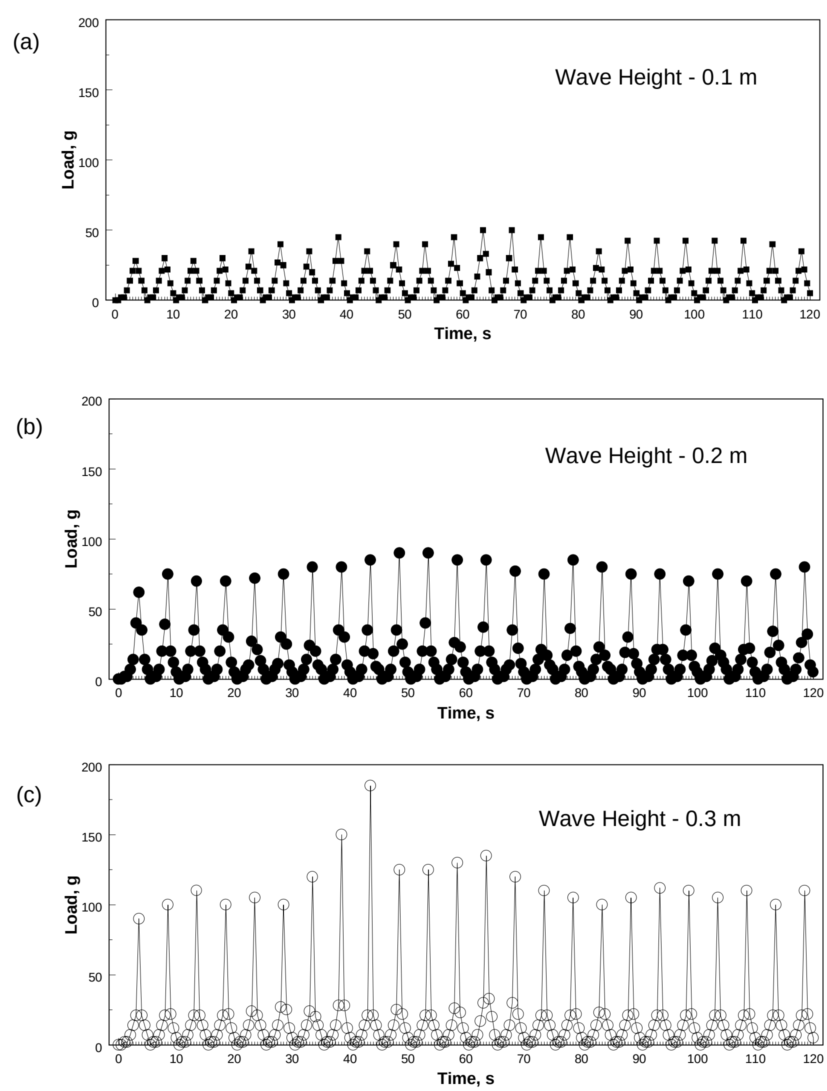

Figure 15. Tensile loading measured on an 8-week-old Eurasian watermilfoil shoot during exposure to a repeating series (W_p = 3 sec) of waves with heights of (a) 0.1 m, (b) 0.2 m, and (c) 0.3m. (Ambient current velocity = 0.10 m/sec). Tensile load measured at base of the sheet)

Mechanical Properties of Field Plants

Collections of plant specimens for seven species were made from Lake Onalaska, WI, during August 1995 to provide measurements of the mechanical properties of UMR field-propagated plants. Breaking forces of the basal (Zone 1) and apical (Zone 3) sections of dominant shoots of these field-collected plants are compared with similar measurements of greenhouse-cultured milfoil plants used in this study in Figure 16. As shown in Figure 16a, Zone 1 breaking forces were higher in six of the seven field-collected plant species, with only *Ceratophyllum demersum* showing breaking forces as low as 4-week and 8-week milfoil cultures used in this study. Zone 3 breaking forces for five of the seven field-collected species were higher than milfoil plants used in this study (Figure 16b). Also, field-collected milfoil specimens had a Zone 3 breaking force of approximately twice that of greenhouse-cultured plants.

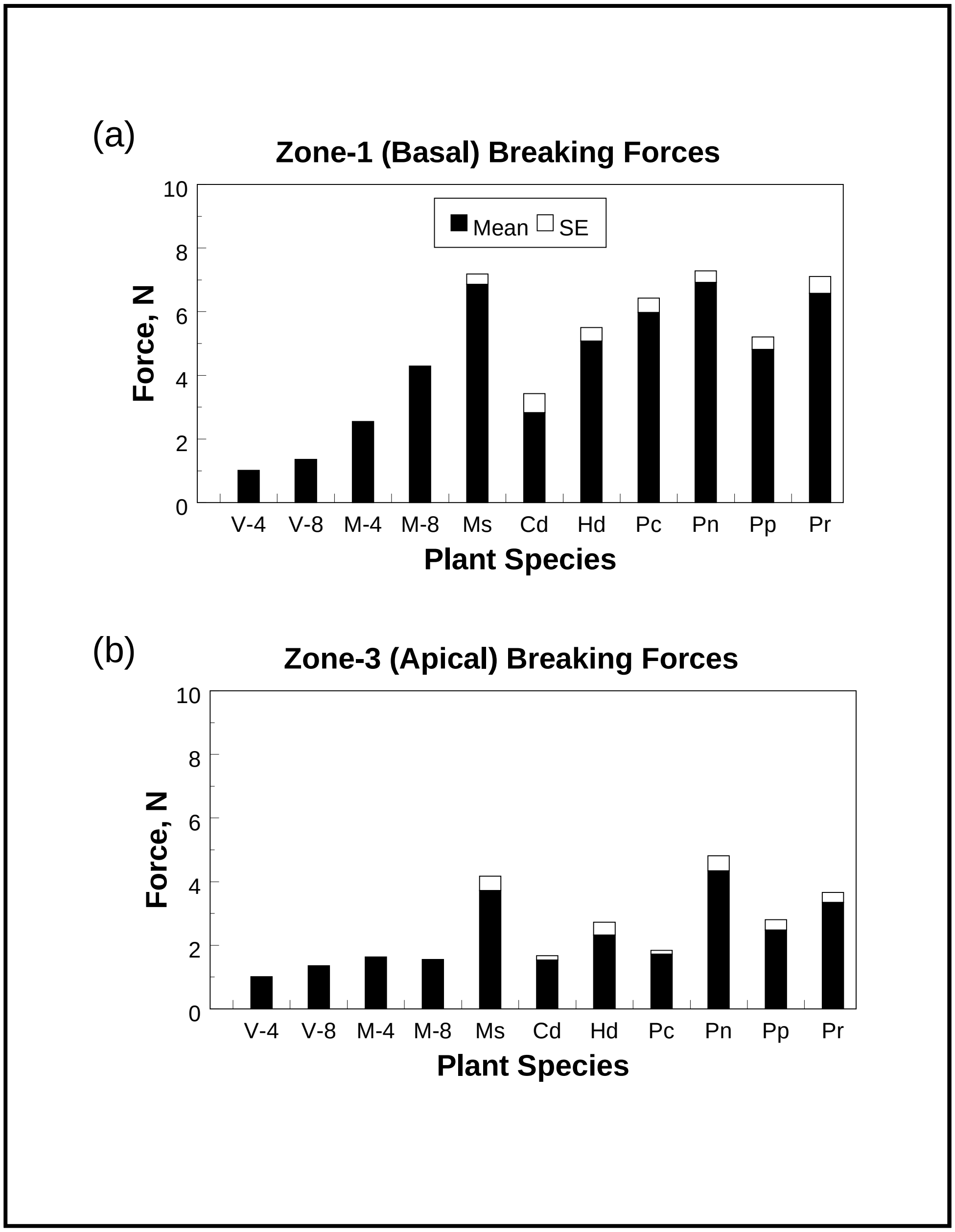

Figure 16. Breaking forces of plant shoots collected from Lake Onalaska, WI, August 1996. (Species are: Ms – Eurasian watermilfoil, Cd – coontail, Hd = water stargrass, Pc – curly-leaf pondweed, Pn – American pondweed). For comparison breaking forces are also shown for both 4- and 8-week-old greenhouse-cultured plants used in this study)

4 Discussion

Factors Affecting Direct Damage

Direct damage to greenhouse cultured vallisneria and Eurasian watermilfoil plants in this study was shown to be influenced by interactions between the hydrological treatment conditions, the test plant species, and plant age. These interactions appear in part to be related to the amount of plant biomass and to how that biomass is oriented in the water column during exposure to passing waves.

Under high current velocity treatments, damage to Eurasian watermilfoil and vallisneria appeared to be more dependent on the length of the exposure than on waves. Under these treatments, the 0.25-m/sec ambient current lowered the position of the shoot material in the water column and, thereby, prevented exposure to the full energy of the waves (Figure 12). Consequently, for both species, 8-week-old plants were not damaged significantly more than were 4-week-old plants under the high-current velocity treatment series (T1-T3 and T4-T6) (Figures 7a and 8a).

Under treatment series with either intermediate current velocity (0.10 m/sec) or no current, 8-week-old plants generally received more damage than did 4-week-old plants (Figures 7b-7c and 8b-c). Observations made during these treatment runs suggest that damage was related to the amount of shoot material floating on the water surface prior to initiation of wave exposures. Because 8-week-old plants were longer and had more shoot length and biomass exposed on the water surface than did 4-week-old plants (Figure 3), higher numbers of fragments and biomass losses occurred from 8-week-old plants. Similarly, for between treatment comparisons of fragment losses from the same species and age group, higher losses of fragments and biomass resulted from treatments with no current than from treatments with the intermediate current. These observations suggest that damage from waves may be inversely related to current velocity under conditions where waves and ambient currents are unidirectional.

Results obtained from this study suggest that shoot material entanglement may have contributed to the level of plant damage. Tensile load measurements (Figure 15) recorded at the base of 8-week-old milfoil shoots exposed to waves of different heights under intermediate current velocities increased with wave height. Maximum peak loadings of 150 g (1.5 N) were measured for the 0.3-m wave height exposures and were less than the measured breaking forces for the basal sections (i.e., Zone 1) of both 4-week- and 8-week-old milfoil plants (Figure 4). Since tensile loads should have decreased distally along the shoots, tensile loadings significantly less than this value probably occurred toward the shoot apices and probably did not exceed breaking forces of the upper-shoot sections. However, visual observations during test runs suggest that shoot entanglement may have made plants more susceptible to breakage. During test runs, shoot entanglement probably caused increased loading on some shoot sections while weakening other sections by crimping them at locations of excessive bending. Similar explanations were suggested by Koehl and Wainwright (1977) for observed breakage of giant kelp stipes. These same researchers noted that the tensile load capacity of kelp tissues was often lessened by herbivory.

The fact that entanglement was a major factor determining the amount of direct damage from wave exposures would help explain why Eurasian watermilfoil plants, which have numerous leaf whorls and branches projecting along their shoots, experienced greater damage than did vallisneria plants, whose shoot mass is composed of individual, smooth, ribbon-like leaves. According to Haslam (1978), these and other morphological features of submersed aquatic plant species can be used to explain their riverine distribution patterns. An extension of the findings of this study would suggest that plant species with numerous branches and leaves projecting off the main shoot axis will probably be more susceptible to direct damage from waves than are species with shoot structures that resist entanglement. If this relationship is true, then plants such as *Potamogeton nodosus* and *P. richardsonii* should also be susceptible to direct wave damage due to their branched shoot morphology, even though field-collected plants showed higher breaking force requirements (Figure 16) than did test plants used in this study. However, it must be kept in mind that plant growth forms are usually adaptive to ambient conditions. Plants that successfully grow under high energy conditions similar to test conditions used herein will probably have morphologies more adaptive to resist direct damage than did the greenhouse-cultured plants used in this study.

Ecological Consequences of Direct Damage

The long-term consequences of repeated daily exposure of submersed aquatic plants to navigation-generated waves has previously been documented in several case studies. In European canals, Murphy and Eaton (1983) related the distribution and species richness of submersed aquatic plant communities to a critical frequency of recreational boat traffic. It was noted that direct damage from waves played a significant role in causing differences in plant communities between high traffic and low traffic areas. Similarly, Schloesser and Manny (1982 and 1989) showed that shipping channels in the Detroit and St. Clair Rivers had less diversity of submersed macrophytes than non-shipping channels. Overall abundance of aquatic species was less in shipping channels, and shorter, more narrow-leaved species were more common. These differences were attributed to waves and current reversals resulting from ship passage.

In this study, a given treatment series of exposures to the three wave heights resulted in a total exposure time of 75 min. Bhomik, Demissie, and Guo (1982) determined that daily secondary wave exposures generated by navigation traffic can reach this duration at certain locations in the UMR. Therefore, these results provide a satisfactory first approximation of the potential amount of daily direct damage to submersed aquatic plants in the UMR by navigation-generated secondary waves. In the UMR system, these direct effects will mainly be restricted to plant communities bordering the main river channel. Direct damage from navigation-generated waves will probably not be a widespread occurrence in most backwater sites since they are protected by islands and/or distance from secondary waves generated in the main channel.

In shallow water locations, high wave forces may penetrate to the bottom and heavily damage, or possibly completely uproot, submersed aquatic plants. This and related factors (e.g., upslope sediment characteristics) have been shown (Brewer and Parker 1990; Keddy 1982, 1985; and Wilson and Keddy 1985) to determine the upslope distributions of submersed macrophytes in sites with high wave exposure and may help explain the paucity of submersed plants in the shallow water areas along the main channel borders of the UMR system. Findings from this study suggest that in deeper water sites within the UMR system main channel border, direct damage from waves will be affected by the amount of plant biomass near the surface of the water. For this reason, species with a growth tendency toward canopy formation (e.g., Eurasian watermilfoil) will be more susceptible to damage, and damage should vary seasonally with peak biomass attainment. These findings further suggest that damage from secondary waves will be more extensive in sites with low ambient currents.

For vallisneria, measured biomass losses in this study were very low and illustrate the suitability of this species to occupy high energy areas. It would appear that factors other than fragmentation (e.g., high light attenuation, sediment instability) are responsible for the inability of this species to colonize the main channel border. Results of this study do indicate that vallisneria flowers may be susceptible to direct wave damage. Since little is known about vallisneria seedling ecology in the UMR system (Kimber, Korschgen, van der Valk 1995), the long-term consequences of this type of direct damage are currently not understood.

Other questions concerning the long-term consequences of navigation effects remain unanswered by the results of this study. For example, indirect impacts of shoot breakage may be much more significant than the mere removal of biomass, which in this study never exceeded 30 percent of exposed biomass. In the high turbidity environment of the UMR system, seemingly insignificant losses of shoot material from canopy-forming species such as Eurasian watermilfoil may, in fact, be indirectly detrimental if the plant is prevented from positioning photosynthetic tissues in a favorable light climate at the surface. Likewise, the tendency of higher ambient current velocities to lower the water column positioning of the plants may similarly have negative impacts stemming from reducing light availability. These factors, in addition to direct losses in biomass, may be responsible for the lack of plant establishment at intermediate depths (i.e., depths not influenced by “drawdown” from passing vessels) along the main channel border area.

Finally, though most submersed macrophyte beds in the UMR system are currently located in backwater areas that are not subject to navigation-generated waves, significant damage in backwater areas may be caused by recreational boat traffic, which is capable of generating secondary waves similar to those tested in this study (Bhomik and Soong 1992). If direct damage in these areas is indeed occurring, their impacts may be especially pronounced during this time of aquatic macrophyte recovery from declines that occurred at the beginning of this decade. Currently during this recovery period, Eurasian watermilfoil is colonizing shallow water areas previously occupied by vallisneria (Rogers 1994). The ability of boat waves to produce additional fragments from these milfoil colonies throughout the growing season may increase Eurasian watermilfoil's expansion rate.

Limitations of Present Study

Because the number of treatment conditions and plant species utilized in this study were limited, the results reported herein are not intended to provide comprehensive information on levels of direct damage that will result from increasing navigation traffic in the UMR system. Instead, the primary objective of this study was to provide a first approximation of the amount of direct damage that waves and currents characteristic of those generated by navigation traffic in the UMR system will cause to the submersed aquatic plant communities bordering the main channel border.

Chief among the limitations of this study was the exclusive use of unidirectional waves and currents, a limitation imposed by the test flume capabilities. Based on our observations, it appears that significant damage occurred under conditions which caused shoot entanglement. Therefore, the study was limited by the exclusion of other treatments (e.g., wave direction at an angle to ambient current, current reversals) representative of navigation-generated hydraulic disturbances that likely would cause extensive shoot entanglement. The present study was further limited by the incorporation of a uniform water depth in all treatments. In this study, maximum wave energy in even the highest wave height treatments did not penetrate to the sediment surface. Had water depth been sufficiently shallow to allow penetration of maximum wave forces to the sediment, it is likely that higher levels of damage, perhaps including uprooting, would have occurred. Under these conditions, susceptibility to uprooting would also depend on (1) the stability of the sediments, and (2) to how firmly the plants were anchored in the sediment. Because sediment characteristics would affect both of these factors, utilization of a single sediment type is a further limitation of this study.

An additional major limitation of this study was the use of greenhouse-cultured plants. That plants can morphologically adapt to different hydrological conditions has been documented by Haslam (1978). This study has similarly documented that field-collected milfoil plants were stronger and more resistant to tensile breakage than greenhouse-cultured plants. In this regard, levels of direct damage reported in this study may be different than actual direct damage in the field. Also, the combined effects of inherent field conditions (e.g., epiphytic load, nutrient stress, herbivory, and disease) on plant susceptibility to damage was not evaluated in this study. Finally, the study was designed to investigate acute damage resulting from treatments which represented a “typical” total daily exposure to navigation-generated secondary waves. In this respect, results of this study alone were never intended to be used to predict the effects of navigation-generated hydraulic disturbances on long-term growth processes of submersed aquatic plant communities within the UMR system.

5 Conclusions

This study demonstrates that secondary waves characteristic of those generated by navigation traffic in the UMR system are capable of causing significant direct damage to submersed macrophytes. The results indicate that the level of damage will depend on interactions between the ambient current velocity, wave height, exposure time, plant morphology, and plant size. The conclusions are as follows:

a. Under low ambient currents (<0.25 m/sec), damage significantly increases with wave heights greater than 0.1 m.

b. Under ambient currents of 0.25 m/sec or greater, damage appears to be more related to exposure time than to wave height.

c. Eurasian watermilfoil was damaged more than vallisneria; higher damage to milfoil probably resulted from the tendency of its shoots to become entangled by waves.

d. Canopy-forming plant species with leaves and branches projecting from the shoots (e.g., milfoils and pondweeds) will probably be damaged by waves more than species with individual, ribbon-like leaves arising from basal rosettes (e.g., vallisneria).

e. Susceptibility to direct damage to canopy-forming species will increase during the growing season as more biomass is produced and distributed at the water surface.

f. Plants growing under field conditions in the UMR may be able to withstand higher tensile loadings than greenhouse-cultured plants used in this study and, therefore, be less susceptible to direct damage from secondary waves.

Direct damage from navigation-generated secondary waves may be partially responsible for the paucity of submersed macrophytes at intermediate depths along the main channel border area of the UMR system. At these intermediate depths, plant growth is probably limited by both high light attenuation through the water and repeated exposures to secondary waves generated by navigation traffic. These two factors may be working collectively to restrict the growth of species such as vallisneria and milfoil; the former being morphologically adapted (i.e., ribbon-like leaves) to survive repeated wave exposures but fairly intolerant of low light (i.e., basal meristem), and the latter being morphologically adapted (i.e., canopy forming) to overcome low light but fairly intolerant of wave exposures (i.e., susceptibility to entanglement). Other sources of waves (e.g., wind and recreational boating) similar to those tested in this study may generate similar levels of direct damage to submersed aquatic plants. Whereas direct damage from navigation-generated secondary waves is, in most cases, limited to the main channel border area where submersed plant communities are not common, direct damage from other sources of waves may be more widespread.

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In an effort to evaluate the impacts of waves and currents generated by navigation traffic on direct damage to submersed macrophyte communities in the Upper Mississippi River (UMR) system, a study was conducted in a two-dimensional flume facility at the U.S. Army Engineer Waterways Experiment Station. The submersed species, *Vallisneria americana* Michx. and *Myriophyllum spicatum* L., were exposed to 18 treatment combinations of current velocity (0.00, 0.10, and 0.25 m/sec), wave height (0.1, 0.2, and 0.3 m), and wave period (3 and 5 sec). Both 4-week and 8-week-old greenhouse-cultured plants were exposed to each treatment combination for 25 min. Main response variables were numbers of fragments and total fragment biomass. Results showed that the level of direct damage was affected by interactions between treatment conditions and the species and size of the plants. At current velocities of 0.25 m/sec, damage was more related to exposure time than to wave height, as this current velocity forced the shoots downward in the water column and prevented them from being exposed to maximum wave forces. At lower current velocities, plant damage increased with wave height and plant size, and *M. spicatum* was more heavily damaged than *V. americana*. Visual observations indicated that the increased damage was related to plant entanglement resulting from current reversals in the passing wave series. Though no treatments generated biomass losses greater than

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30 percent of exposed plant biomass, repeated daily exposures to secondary waves from current levels of navigation traffic may be partially responsible for the paucity of submersed macrophytes along the main channel border area of the UMR system.