Wave-induced Hydraulic Forces on Submerged Aquatic Plants in Shallow Lakes

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INTRODUCTION

The distribution of aquatic macrophytes in shallow lakes is related in various ways to the physical characteristics of the lakes and their bottom sediments (Chambers, 1987; Kautsky, 1987; Vestergaard and Sand-Jensen, 2000). The ability of the wind to induce waves and currents in a lake depends on the fetch (i.e. the continuous length of open water) in a particular direction and therefore is influenced by the size, shape and orientation relative to wind direction of the lake. Fetch and wind speed, in combination with the depth profile, determine the potential for the development of waves. It is likely that the physical (hydraulic) forces arising from waves and currents and the varying responses of plants to such forces represent important determinants of plant establishment and survival in shallow lakes. Schutten and Davy (2000) have examined and modelled the hydraulic forces exerted on submerged plants by laminar currents. The hydraulic effects of wave action on submerged plants in shallow lakes have been largely ignored previously, although the effects of waves on emergent shoreline plants and their interactions with bank erosion have been studied by Coops et al. (1996) and Coops and van der Velde (1996).

In contrast, the relationships between organisms and the much more energetic waves of the shallow coastal zone have been studied extensively (Denny et al., 1985, 1998; Gaylord et al., 1994; Blanchette, 1997; Koehl, 1998; Denny and Gaylord, 2002). However, waves generated in deep offshore waters that eventually overtop in shallower water and break on the coast, creating a surf-zone with reversing undercurrents, are fundamentally different from the waves in shallow lakes. Nevertheless, the forces resulting from breaking waves might be important for explaining, at least partially, the generally observed absence of freshwater aquatic plants in the very shallow water (0–0.2 m depth) near exposed beaches (Scheffer et al., 1992).

Shallow lakes support relatively diverse communities of submerged macrophytes that are rooted in the bottom sediments; potentially they can extend over the entire areas of the lakes (e.g. Kennison et al., 1998). These communities are important for the trophic structure and functioning of shallow-lake ecosystems. Many such lakes have become eutrophic, as a result of excessive nutrient loading, and the associated phytoplankton blooms have eliminated their

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macrophytes. Restoration requires the re-establishment of clear water and normally involves a reduction in nutrient loading and the biomanipulation of fish populations to remove predation on zooplankton, which in turn consume the phytoplankton (Jeppeson and Sammalkorpi, 2002). Clear and turbid water thus become alternative stable states and the re-establishment of macrophyte communities can also help to stabilize the clear-water state, by providing refugia for zooplankton. Consequently, the re-introduction and management of submerged macrophytes have become crucial in developing strategies for the restoration of degraded shallow-lake ecosystems (Weisner and Strand, 2002).

An examination of the magnitude and effects of wave-induced hydraulic forces is important both for a fundamental understanding of the limitations on the distribution of submerged aquatic plants and also for lake restoration. Such forces will be likely to contribute to those resulting in uprooting, breakage or other damage, depending on the mechanical properties of the plants and bottom sediments (Schutten and Davy, 2000; Handley and Davy, 2002; Sand-Jensen, 2003). The work described here aimed to: (a) quantify the forces experienced by a range of submerged plants as a result of wave action in shallow water; (b) develop and test mechanistic models for the prediction of these forces from shoot size and architecture; and (c) compare the magnitudes of forces likely to be experienced with those arising from unidirectional currents in shallow waters.

**THEORY**

Surface waves give rise, underwater, to an orbital movement of water with exponentially decreasing amplitude with depth. These water movements and, therefore, the resulting forces can be resolved at each point into vertical and horizontal components. The main concern is with the vertical upward forces which act on the plant, producing an uprooting tendency. The horizontal ‘pressure’ component acting on the plant is unlikely to be a major factor in uprooting. The vertical component of the water-motion will produce a frictional drag on the shoot surface analogous to the forces resulting from laminar flow (Schutten and Davy, 2000). Gaylord et al. (1994) have also shown that the drag coefficients calculated from samples of marine algae in an oscillatory flow were near to those measured on the same species in steady flow. Denny (1988) has produced a set of practical equations describing the two components of the orbital water movement in the water column when a wave passes. The equations differ for deep and shallow water because, for example, in shallow water friction with the bottom sediment plays a significant part. Water is defined as deep when the water depth is greater than half the wavelength \( d > L/2; \) Denny, 1988). The water depth in the experimental wave-flume used, which represents northwest-European shallow lakes, is slightly less than half the wavelength (water depth = 0.7 m, wave length = 1.5 m), which implies that these conditions are near the borderline of validity for the deep water equations. However, shallow water has also been defined as a situation in which the water depth is less than 1/20 of the wavelength (Denny, 1988), which is certainly not true for the flume used, nor realistic in the open water zone of shallow lakes. Consequently, the simpler formulae for the deep-water approximations for linear wave theory were used (Denny, 1988) and these provided a good fit to the data. As explained above, the main concern is with the vertical, pulling component of the wave, resulting from the frictional drag created by the water current. Denny (1988) gives the following equation for the vertical component of the orbital velocity for deep-water waves:

\[
\mathbf{w} = \left( \frac{\pi H}{T} \right) e^{kz} \sin(kx - \omega t)
\]

where \( w = \) orbital velocity \((m\ s^{-1}), H = \) wave height \((m), T = \) wave period \((s), k = \) wave number \((2\pi/L; m^{-1}), L = \) wave length \((m), z = \) depth of observation \((negative\ in\ the\ column; m)\) and \( \omega = \) radian wave frequency \((2\pi/T; s^{-1}), x = \) the point or place of observation of the wave \((m)\) in the horizontal direction and \( t = \) time of observation \((s)\). This indicates that the vertical component of the orbital velocity decreases exponentially with depth, \( e^{kz}\), and that it has a periodic component \((\sin(kx - \omega t))\); this periodic component has a (periodic) maximum at values of \( x = \) 0-25L and 0-75L, i.e. when the elevation of the water surface is zero, between crest and trough. This is unlike the corresponding formula for the horizontal component of the velocity, which indicates that it is in phase with the surface wave, i.e. it peaks at the maximum of the surface elevation.

**Forces produced by waves**

At every depth where shoot material is present, a water current will pass over the surface of the shoot. The resistance or drag on this shoot is theoretically dependent on the ratio of the frontal area over the plan-form area, the size of the shoot, its flexibility or streamlining, and the vertical component of the orbital current velocity. As the concern is with the forces which tend to uproot or break plants growing on the bottom of shallow lakes, only the vertical component of the orbital velocity is considered. The drag of the horizontal currents should not contribute significantly to the vertical pulling forces; it is considered that the horizontal component of the orbital currents tends to bend the shoot, and the residual current moving along its leaves creates a small additional drag which is being neglected in the treatment. Model calculations (Westphal, 1996) predict that the vertical component of the orbital velocity in shallow lakes with wave-heights up to 0.4 m will be up to 0.4 m s\(^{-1}\), as a maximum. At these relatively low current velocities for relatively flexible and streamlined plants, surface friction is expected to be the dominant process as compared with pressure drag (for a full discussion of this subject, see Schutten and Davy, 2000). The following equation (see Schutten and Davy, 2000) is used to describe the basic relationship between force, current velocity, shoot size and shape:

\[
F = A' S v^{1.5}
\]
where \( F \) is the force (N or kg m s\(^{-2}\)), \( v \) is velocity (m s\(^{-1}\)), \( S \) is an appropriate measure of the shoot size and shape (related to either the plan-form shoot area or the dry mass) and \( A' \) is a species-specific factor incorporating the roughness and other surface characteristics and intrinsic properties. The units of \( S \) and \( A' \) will depend upon whether we are using plan-form area or dry mass.

The force expressed in eqn (2) will vary along the length of the shoot, with depth below the water surface, and according to the shape of the shoot. Two different distributions of the plant over depth are investigated: (1) equal distribution as a cylinder and (2) a greater proportion of the shoot near the surface, as an inverted cone or triangle. The maximum vertical orbital velocity, \( w \), varies exponentially with depth according to eqn (1). \( S(z) \) will be, in general, a function of the depth, \( z \), and it is written as \( S(z) \), meaning the surface parameter at depth \( z \), per unit length (m); thus the magnitude of \( S(z) \) at the point \( z \) will be \( S(z) \). The maximum total force on the plant is given by the sum of all the elements of force, i.e. the integral in the following equation:

\[
F = z_{1} \int^{z_{2}} A' (w)^{1.5} S(z) \, dz
\]

where \( z_{1} - z_{2} = l \) (the length of the plant). Hence

\[
F = A' z_{2} l^{2} (\pi HT)^{1.5} \exp(-1.5kz)S(z) \, dz
\]  

This integral can be evaluated mathematically for both of the shoot size descriptors and mass distribution descriptors as (a) a rectangle (even depth distribution, surface area), (b) a triangle (surface area concentrated near the top of the shoot), (c) a cylinder (even depth distribution, shoot mass) and (d) an inverted cone (shoot mass concentrated near the point). This will result in the following equations:

**Rectangle**

\[
F = A' \left( \frac{\pi HT}{T} \right)^{1.5} \frac{a}{6} [\exp(-6(d - l)) - \exp(-6d)] \tag{4a}
\]

**Triangle**

\[
F = A' \left( \frac{\pi HT}{T} \right)^{1.5} \frac{a}{6} [\exp(-6(d - l)) - \exp(-6d)] \tag{4b}
\]

\[
Cylinder
\]

\[
F = A' \left( \frac{\pi HT}{T} \right)^{1.5} \frac{s_{m} 1}{1} \frac{l}{\rho} \frac{1}{6} [\exp(-6(d - l)) - \exp(-6d)] \tag{4c}
\]

**Cone**

\[
F = A' \left( \frac{\pi HT}{T} \right)^{1.5} \frac{s_{m} 1}{1} \frac{l}{\rho} \frac{1}{2H} \left[ (l^{2} - \frac{2}{6} + \frac{1}{18}) \exp(-6(d - l)) \right] - \frac{1}{18} \exp(-6d) \tag{4d}
\]

where \( a \) is diameter of the shoot (or surface area/shoot length, if diameter unknown), \( d \) is water depth, \( l \) is shoot length, \( s_{m} \) is shoot dry mass and \( \rho \) is shoot density. For a wavelength of about 1.5 m, \( k \) is approximately equal to 4 (see eqn 1) and so 1.5k is taken as equal to 6.

The "predictor" of the total force, i.e. the integral in eqn (3) without the factor \( A' \), has been calculated for the specimen plants used in the flume experiments for two ways of assessing \( S \), the plan-form area and the dry mass, and for two plant shapes, cylindrical and inverted cone. The details of this calculation are not given here; they are available from the authors.

**MATERIALS AND METHODS**

All the measurements were performed in a wave-flume (5 m long, 0.6 m wide and 1 m deep) constructed at the University of East Anglia (Fig. 1). The wave generator
could produce approximately running waves with a sinusoidal profile at a fixed wave period of 1 s and with a wavelength of approx. 1.5 m. The wave height was variable, ranging from 0.05 to 0.20 m with a water depth of 0.7 m. Reflection of the waves against the end of the flume and thus the build-up of a standing wave was nearly completely damped using a wave absorbing slope dressed with coarse cobbles (5–10 cm in diameter). The heights of the waves and the forces on the individual shoots were directly measured with tension transducers (Washington Transducer Type D; Palmer-Washington BioScience, Sheerness, Kent, UK) interfaced to a Macintosh Quadra 700 computer via A/D converters (MacLab/4; ADInstruments Pty Ltd, Australia). The plant specimen was clamped for these measurements near the top of the shoot, and weighted at the bottom with a 50-g weight to assure vertical positioning of the shoot. Each individual shoot was placed so that the base of the shoot, with the weight attached, was 5 cm from the flume bottom. Hydraulic resistance of the clamp and weight were subtracted from the recorded forces to obtain forces generated specifically by the plant specimen. The wave characteristics (wave height, period and length) were measured with a partly submerged 40-cm long aluminium cylinder, with 20 cm below the static water surface. A change in water level resulted in a change to the length of the cylinder, with 20 cm below the static water surface. A change in wave level resulted in a change to the length of cylinder submerged and thus a change in force on the tension transducer. The relationships between submerged depth of the aluminium cylinder, force and voltage produced by the transducers was calibrated at the start and end of each experiment.

In each experiment, force and water level data were captured at a rate of 40 measurements s⁻¹ for 30 s, after an initial period of 15 s for stabilization of the waves. The data were stored on the computer for subsequent data analysis. The maximum wave height and the maximum hydraulic force were extracted at three sampling times from each run (approx. 10, 15 and 20 s after the start of the measurements) and the averages taken for subsequent analysis.

Measurements with plastic replicas of plants

Plastic replicas of Elodea sp. with regular whorls of five leaves (Aquascapers; Metaframe Corporation, Maywood, NJ, USA) 0.09 m long and with a plan-form area of 12 ± 1 m² × 10⁻⁴ were used as a physical model to examine the validity of the linear wave theory in the experimental flume. Records of water level and the magnitude of the vertical component of the hydraulic forces were tested for fit with linear wave theory as sinusoidal functions of time. Theory predicts that wave height and pulling force should be 1/4 period out of phase (see eqn 1) and this was assessed by visual comparison. Measurements were made at depths ranging from 5–40 cm for each of seven wave heights: 5, 6, 9, 10, 13, 17 and 20 cm to test the prediction of an exponential decline in pulling force with water depth. Data from all of these combinations were used to test the predictive power of the model by regressing (predicted orbital velocity raised to the power 1.5; it measures with real plants

Individual specimens of Ceratophyllum demersum L., Chara intermedia A. Braun, Elodea canadensis Michaux, Myriophyllum spicatum L., Potamogeton natans L. and Potamogeton obtusifolius Mert. & Koch were placed in the flume and subjected to waves of 20 cm height to examine the hydrodynamic characteristics of each species and to evaluate both shoot size and shoot-size distribution descriptors. The number of replicate shoots varied between 14 and 27, depending on species. After each plant shoot was removed from the flume, measurements were made of a number of shoot size and architectural characteristics: length, maximum width, plan-form surface area and dry mass after drying for 72 h at 70 °C. Plan-form surface area was measured as the projected area of a portable area meter (Li-3000; Li-Cor, Nebraska, USA). The peak measured force was regressed on predicted force, derived from the model as the product of maximum orbital velocity raised to the power 1.5 and either dry mass or plan-form area. The slope of such a regression is the species-specific factor $A'$, which describes the hydraulic resistance per shoot-size unit and velocity raised to the power 1.5; it should be influenced by shoot shape and flexibility.

RESULTS

Assessment of the wave model

Figure 2 shows representative simultaneous records of water level and hydraulic pull on a plastic replica of Elodea over an interval of 2 s. Changes in water level with time are described well by the fitted sinusoidal function, despite small systematic deviations arising from slightly sharp peaks to the waves that are probably a consequence of the
geometry of the flume. Changes in pulling force with time are similarly well fitted by the sinusoidal vertical orbital velocity function derived from the linear wave theory for deep water, as described under ‘Theory’ above. Again the peaks are slightly sharper than predicted, because of the wave form. It is striking that the pulling force lags almost exactly 0.25T behind water height, such that the maximum force on the shoot is at mean water level, as predicted by the wave theory.

The measured hydraulic pulling forces on artificial Elodea probes at depths from 5 to 40 cm and with wave heights ranging from 5 to 20 cm are shown in Fig. 3. At all wave heights, the measured force declined with the depth of the artificial Elodea probe. Negative exponential regressions (measured force = ae^{bd}) provided significant fits to all of these declining curves (Table 1), with values of r^2 ranging from 0.61 to 0.91. Our artificial plant should obey eqn (4a); for this small probe a simple exponential is a good approximation to this equation and these data clearly demonstrate the predicted exponential decline in force with depth (e^kz in eqn 1). The maximum pulling force increased linearly with wave height, as predicted by theory (eqn 1). At a probe depth of 5 cm, where measured forces were maximal, the linear regression of hydraulic force on wave height was highly significant but with an intercept not significantly different from zero (y = 0.00191 + 0.00918 x; P < 0.01; r^2 = 0.92).

Measurements made at all combinations of wave height and water depth were used to test their general concordance with model predictions (Fig. 4). A model predictor of force (the product of integrated orbital velocity raised to the power 1.5 and shoot plan-form area) was linearly related to the measured force. The linear regression was highly significant and, as the intercept was not significantly different from zero, passed through the origin (see Fig. 4). The difference in magnitude between predicted and measured values relates to the species-specific constant (A' of eqn 2).

### Table 1. The negative-exponential regressions of the measured force (F) as a function of depth (d) of an artificial Elodea probe of 12 cm^2 plan-form area

<table>
<thead>
<tr>
<th>Wave height (cm)</th>
<th>a (N) ± standard error</th>
<th>b (m^-1) ± standard error</th>
<th>r^2</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>0.052 ± 0.0058</td>
<td>-4.6 ± 0.46</td>
<td>0.85</td>
<td>24</td>
</tr>
<tr>
<td>6</td>
<td>0.073 ± 0.0048</td>
<td>-6.3 ± 0.45</td>
<td>0.89</td>
<td>27</td>
</tr>
<tr>
<td>9</td>
<td>0.117 ± 0.0070</td>
<td>-5.5 ± 0.44</td>
<td>0.91</td>
<td>24</td>
</tr>
<tr>
<td>10</td>
<td>0.096 ± 0.0060</td>
<td>-4.5 ± 0.41</td>
<td>0.88</td>
<td>23</td>
</tr>
<tr>
<td>13</td>
<td>0.090 ± 0.0116</td>
<td>-4.4 ± 0.78</td>
<td>0.61</td>
<td>24</td>
</tr>
<tr>
<td>17</td>
<td>0.164 ± 0.0162</td>
<td>-5.7 ± 0.73</td>
<td>0.79</td>
<td>24</td>
</tr>
<tr>
<td>20</td>
<td>0.219 ± 0.0144</td>
<td>-4.6 ± 0.43</td>
<td>0.87</td>
<td>24</td>
</tr>
</tbody>
</table>

Equation: F = ae^{bd}.
Parameters a and b are given ± standard errors.

**FIG. 3.** The relationships between measured hydraulic pulling force on an artificial Elodea probe (12 cm^2 plan-form area) as a function of depth of the probe in the water column, for a range of wave heights. Fitted curves are negative exponential regressions (see Table 1 for parameters). Wave heights: 5 cm (A); 6 cm (B); 9 cm (C); 10 cm (D); 13 cm (E); 17 cm (F); 20 cm (G).
These very good agreements between the behaviour of the experimental flume system and the predictions made prompted the decision to adhere to the approximations for simple linear wave theory for deep water as the basis for further investigations with real plants.

The theory allowed predictions of the total wave force per individual shoot on the basis of two different models of shoot distribution with length (cylinder and inverted cone) and two different plant size descriptors (plan-form area and dry mass), as represented in eqns (4a)–(4d). Table 2 presents the results of linear regressions of measured forces on predicted forces for six submerged macrophyte species of varying form, using all four combinations of size descriptor and shape, i.e. (1) plan-form area and cylinder, (2) plan-form area and cone, (3) dry mass and cylinder, and (4) dry mass and cone. Initial analysis indicated that shoots longer than the flume depth, which thus had part of their biomass floating on the water surface during the measurements, behaved completely differently from completely submerged shoots. Since it was the quantifying forces on submerged macrophytes which was of interest, only data for completely submerged shoots were included. For theoretical reasons and because no significant intercept had been found in Fig. 4, all regressions were forced through the origin. Table 2 shows that in all cases there was a highly significant linear relationship between predicted and measured forces. In each case, the slope of the regression represents the species-specific coefficient ($A'$) that incorporates surface roughness and other intrinsic properties. Using the coefficient of determination ($r^2$) as an indicator of the strength of the relationships, there was little difference between the cylinder and inverted cone shape models for any species. The efficacy of plan-form area and mass as size descriptors varied between the species: area explained a higher

![FIG. 4. The relationship between predicted hydraulic pull and measured hydraulic pulling forces on an artificial Elodea probe (12 cm² plan-form area) subjected to waves ranging in height from 0.05 to 0.2 m and presented at depths ranging from 0.05 to 0.40 m. The wavelength was approx. 1.5 m. The predicted pull was calculated as the integration of the product of plan-form area and orbital velocity raised to the power 1.5 over the length of the probe. Linear regression: $y = -3.0 \times 10^{-6} + 1.32 \times 10^{-3}x$ ($n = 170, r^2 = 0.83, P < 0.001$).](https://academic.oup.com/aob/article-abstract/93/3/333/147023/fig?image=fullsize&image_format=pdf&image_id=fig.png)

### TABLE 2. Linear regressions of the hydraulic pulling forces predicted from four types of model on the measured forces for six species of submerged macrophyte

<table>
<thead>
<tr>
<th>Species</th>
<th>Calculation method</th>
<th>Slope</th>
<th>$r^2$</th>
<th>$n$</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ceratophyllum demersum</em></td>
<td>Rectangle, area</td>
<td>215 ± 21</td>
<td>0.82</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Triangle, area</td>
<td>145 ± 15</td>
<td>0.81</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Cylinder, dry mass</td>
<td>1460 ± 92</td>
<td>0.92</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>Cone, dry mass</td>
<td>818 ± 59</td>
<td>0.90</td>
<td>23</td>
</tr>
<tr>
<td><em>Chara intermedia</em></td>
<td>Rectangle, area</td>
<td>1130 ± 172</td>
<td>0.77</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Triangle, area</td>
<td>903 ± 138</td>
<td>0.76</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Cylinder, dry mass</td>
<td>1040 ± 207</td>
<td>0.65</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>Cone, dry mass</td>
<td>729 ± 149</td>
<td>0.64</td>
<td>14</td>
</tr>
<tr>
<td><em>Elodea canadensis</em></td>
<td>Rectangle, area</td>
<td>359 ± 25</td>
<td>0.89</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Triangle, area</td>
<td>253 ± 18</td>
<td>0.89</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Cylinder, dry mass</td>
<td>3690 ± 163</td>
<td>0.95</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Cone, dry mass</td>
<td>2180 ± 96</td>
<td>0.95</td>
<td>27</td>
</tr>
<tr>
<td><em>Myriophyllum spicatum</em></td>
<td>Rectangle, area</td>
<td>119 ± 13</td>
<td>0.79</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>Triangle, area</td>
<td>80 ± 1.87</td>
<td>0.78</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>Cylinder, dry mass</td>
<td>4160 ± 213</td>
<td>0.94</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>Cone, dry mass</td>
<td>2370 ± 118</td>
<td>0.95</td>
<td>24</td>
</tr>
<tr>
<td><em>Potamogeton natans</em></td>
<td>Rectangle, area</td>
<td>826 ± 10.4</td>
<td>0.82</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>Triangle, area</td>
<td>569 ± 7.2</td>
<td>0.82</td>
<td>15</td>
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<tr>
<td></td>
<td>Cylinder, dry mass</td>
<td>103 ± 16</td>
<td>0.74</td>
<td>15</td>
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<tr>
<td></td>
<td>Cone, dry mass</td>
<td>56 ± 2.9</td>
<td>0.72</td>
<td>15</td>
</tr>
<tr>
<td><em>Potamogeton obtusifolius</em></td>
<td>Rectangle, area</td>
<td>250 ± 16</td>
<td>0.91</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Triangle, area</td>
<td>191 ± 12</td>
<td>0.92</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Cylinder, dry mass</td>
<td>284 ± 25</td>
<td>0.84</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>Cone, dry mass</td>
<td>182 ± 17</td>
<td>0.83</td>
<td>25</td>
</tr>
</tbody>
</table>

Models involved factorial combinations of two shoot shapes (cylinder and inverted cone) and two size descriptors [plan-form area (m²) and dry mass (kg)].

All regression models and slopes are highly significant ($P < 0.001$).
proportion of the variance in *Chara intermedia*, *Potamogeton natans* and *P. obtusifolius*, and mass was the better predictor in *Ceratophyllum demersum*, *Elodea canadensis* and *Myriophyllum spicatum*; in general they performed similarly well. As there was no consistently best combination, a representative series of relationships between measured and predicted hydraulic forces on individual plants (based on mass and inverted cone) is shown for all species in Fig. 5. The linear relationships between observed and predicted forces were generally sustained over the wide range of forces generated by the different shoot sizes and architectures of the six species; for instance, the forces on *Myriophyllum spicatum* were on average three-fold higher than those on *Elodea canadensis* or *Ceratophyllum demersum* and ten-fold higher than those on *Potamogeton obtusifolius*.

**DISCUSSION**

Wave-forces on aquatic macrophytes in shallow lakes may be complex and change rapidly in both direction and magnitude. The forces are the result of water currents passing along leaves, and thus will change rapidly during the passage of a wave. Wind-induced waves in lakes also change frequently with time. However, a pragmatic framework has been established that provides the basis for

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**Fig. 5.** The relationship between observed and predicted hydraulic forces, using the inverted cone model to describe shoot vertical distribution and mass as shoot-size descriptor, for *Ceratophyllum demersum* (A), *Chara intermedia* (B), *Elodea canadensis* (C), *Myriophyllum spicatum* (D), *Potamogeton natans* (E) and *Potamogeton obtusifolius* (F).
TABLE 3. Architectural characteristics of each species (leaf width, leaf shape, shoot shape and shoot flexibility) in relation to the calculated species-specific hydraulic roughness factor \((A')\) for both inverted cone and cylinder models

<table>
<thead>
<tr>
<th>Species</th>
<th>Leaf width (mm)</th>
<th>Leaf shape</th>
<th>Shoot flexibility</th>
<th>(A') for cone wave model</th>
<th>(A') for cylinder wave model</th>
<th>(A') for uni-directional flow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Potamogeton obtusifolius</td>
<td>4</td>
<td>Flat</td>
<td>Flexible</td>
<td>182</td>
<td>284</td>
<td>797/491</td>
</tr>
<tr>
<td>Potamogeton natans</td>
<td>50</td>
<td>Flat</td>
<td>Flexible</td>
<td>56</td>
<td>103</td>
<td></td>
</tr>
<tr>
<td>Myriophyllum spicatum</td>
<td>2</td>
<td>Flat</td>
<td>Rigid</td>
<td>2374</td>
<td>4160</td>
<td>2560/969</td>
</tr>
<tr>
<td>Elodea canadensis</td>
<td>3</td>
<td>Flat</td>
<td>Rigid</td>
<td>2184</td>
<td>3686</td>
<td>1260/1360</td>
</tr>
<tr>
<td>Chara sp.</td>
<td>1</td>
<td>Round</td>
<td>Rigid</td>
<td>729</td>
<td>1036</td>
<td>154</td>
</tr>
<tr>
<td>Ceratophyllum demersum</td>
<td>2</td>
<td>Round</td>
<td>Rigid</td>
<td>818</td>
<td>1462</td>
<td>1220/1020</td>
</tr>
</tbody>
</table>

Equivalent values for unidirectional flow (from Schutten and Davy, 2000) are also shown.
All values are based on dry mass as size-descriptor for ease of comparison. Only significant values \((P < 0.05)\) are shown.

predicting the maximal magnitude of forces experienced by plants, because such forces are likely to be an important determinant of shoot survival in a particular situation. The experimental measurements indicate that the use of the linear wave deep-water theory (Denny, 1988) provides a realistic and relatively simple approach to the complexity of water-wave physics. As expected, the pull on the plants maximizes as the water level is in-between trough and crest; this confirms that the vertical orbital velocity is the main component of the pull measured in the wave-flume, as intended, since the horizontal velocity is in phase with the water level. Here the concentration is on the vertical components of the forces experienced, because they are most likely to lead to uprooting or stem breakage in a shallow-lake environment, where macrophytes may colonize the entire area of lake floor. However, the horizontal components may also have ecological significance in some situations. It is clear that mathematical integration with depth of the velocity measurements resulting from the linear wave theory provides a predictor of force that is linearly related to the actual force, measured at various depths and at several wave-heights (cf. Fig. 3). It should be pointed out that this simple approach would only work for completely submerged plants in relatively shallow water and with plant lengths shorter that the wave length. Likewise it would only be appropriate for the relatively low-energy wave environment of shallow lakes, where each passing wave creates its own individual vertical pull. This contrasts with the more violent, bi-directional flows of the nearshore coastal environment (Denny, 1988; Koehl, 1998; Denny and Gaylord, 2002).

Schutten and Davy (2000) developed a formula to predict the hydraulic force resulting from water passing along a leaf as a function of velocity raised to the power 1.5, at low velocity in a unidirectional flow. Application of this formula in the wave environment also proved to be effective. The relationships between measured pulling force and the product of mass and velocity raised to the power 1.5 (Fig. 5) were remarkably linear for Elodea canadensis, Myriophyllum spicatum and Potamogeton obtusifolius, even when regressions were forced through the origin. In the cases of Ceratophyllum demersum and Chara intermedia, there was evidence of a more systematic scatter of residuals that could represent a non-linear response associated with greater streamlining and mutual protection at the highest velocities and masses (Sand-Jensen, 2003). This could also be true for Potamogeton natans but any non-linearity is heavily dependent on a single experimental observation. The slopes of these regression lines (Fig. 5) are theoretically equivalent to the species-specific hydraulic roughness values of Schutten and Davy (2000) in unidirectional flow. The values from the wave environment, using both the cylinder and cone plant shapes, are of similar orders of magnitude to the previous ones derived for linear flow (Table 3). There was no systematic difference between the inverted cone and cylinder models of plant shape, suggesting that species are to varying degrees intermediate between the two ideals. Likewise, there was no systematic difference between the use of mass or plan-form area as a descriptor of plant size. This is in agreement with earlier observations (Schutten and Davy, 2000) which demonstrated a similar linear relationship between these two variables for a range of aquatic macrophyte species. It is not possible to generalize about the consequences of shoot architecture and leaf size from studies of only these six species. However, the two relatively flexible Potamogeton species had a much lower resistance per unit shoot than the other four, rather more rigid species examined (Table 3), as would be expected (Vogel, 1984; Sand-Jensen, 2003); this also agreed with results under conditions of unidirectional flow (Schutten and Davy, 2000). Further investigation would be needed to interpret the detailed ecological significance of these findings for different species.

The potential ecological significance of wave action for submerged macrophytes in shallow lakes is considerable. The shear stresses generated may result in resuspension of sediment, resulting in turbidity and higher concentrations of nutrients that would favour phytoplankton dominance at the expense of macrophytes, especially in eutrophic lakes (Hamilton et al., 1997). On the other hand, moderate exposure to wave action may remove epiphyton that would otherwise be detrimental to the macrophytes (Strand and Weisner, 1996). Our prime interest was in the more direct
effects of the maximum pulling forces experienced. The maximum hydraulic pulling forces on plant shoots, generated by relatively small waves (0.2 m) acting on shoots of up to about 5 g dry mass in a 0.7-m water column were approx. 0.2 N. However, the plants may grow substantially bigger, and larger waves are possible at this depth; deeper water, locally or within the fetch, would allow even larger waves to develop. All of these conditions would lead to greater forces on the plants. The response of a plant shoot to such forces may involve absorption of the energy by the shoot, breakage of the shoot or uprooting. Depending on the species, these outcomes will be important determinants of shoot survival in a particular situation and thus of community structure.

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LITERATURE CITED


