

Trade-off between drag reduction and light interception of macrophytes: comparing five aquatic plants with contrasting morphology

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Summary

1. Macrophytes in running waters experience an often dynamic and harsh environment. To avoid breakage, plants have to reduce the experienced drag force. However, by reducing leaf area, photosynthetic production is less. Aquatic plants therefore have to find a balance between reducing drag and maintaining photosynthetic capacity.
2. In the experiments in this study, we assessed to what extent different morphological strategies (emergent vs. submerged) were able to minimize drag while maximizing leaf area.
3. From our measurements, it is clear that with increasing water velocities, emergent plant species have a drag value three to four times higher than submerged species.
4. To test the versatility of leaves, leaves were removed and their effect on drag and bending was investigated. Almost 60% of the drag is contributed by the leaves, and stems bend less when leaves are removed.
5. Because high submerged leaf area increases not only plant drag but also photosynthetic yield, a trade-off between both parameters was investigated in the function of stream velocity. Emerged species had a more favourable trade-off at low stream velocities. However, with increasing stream velocity, submerged species could reduce their drag more in comparison with blunt objects. Within these submerged species, a clear distinction was seen between those (*Potamogeton natans*) concentrating their leaf area on or just beneath the water surface (*Stuckenia pectinata*) and those with more or less evenly distributed biomass (*Callitriche platycarpa* and *Ranunculus penicillatus*).
6. These results indicate that aquatic plants with an emergent strategy are able to take better advantage of zones with reduced hydraulic forces than submerged plants. Additionally, this plant occurrence will be determined by the relationship between total plant drag and root strength.

Key-words: characteristic area, drag coefficient, flume, hydraulic forces, macrophytes, stream velocity

Introduction

Subjected to a given current velocity, macrophytes experience a drag force 25 times higher than terrestrial plants exposed to a similar wind speed (Denny & Gaylord 2002). Consequently, mechanical stress originating from hydrodynamic drag forces is a main structuring factor in aquatic vegetation communities (Biggs 1996; Spink & Rogers 1996).

Hence, aquatic plants have both below- and above-ground adaptations to enable establishment and persistence in dynamic and harsh environment (Usherwood, Ennos & Ball 1997).

Below-ground root anchorage strength must balance above-ground drag forces. On the one hand, anchorage increases with root size and substrate type (Schutten, Dainty & Davy 2005) increasing sediment stability by compaction (Thorne 1990; Castellanos, Figueroa & Davy 1994; Angers & Caron 1998). On the other hand, root biomass is often

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negatively related to nutrient stream concentration, and at high pelagic nutrient availability, demands can be satisfied by foliar uptake (Maitai & Newton 1982). Uprooting is therefore more commonly seen than plant failure by stem breakage (Riis & Biggs 2003; Bouma *et al.* 2005).

In addition to high anchorage strength, macrophytes also have morphological characteristics to reduce drag. Many sessile organisms have non-rigid parts enabling them to reduce the experienced drag by bending of their surface area (Koehl 1984; Sand-Jensen 2003; Bouma *et al.* 2005). This bending is dependent on the length and thickness of the shoot (Manz & Westhoff 1988), with longer shoots generally being more flexible and thicker shoots being less flexible. This bending is species specific (Sand-Jensen 2003) and along with flow speed determines leaf position within the water column (Green 2005).

Above-ground adaptations to minimize drag may interact with important aspects of plant functioning. For example, increasing leaf area is beneficial for plant photosynthesis, but at the same time increases the experienced drag. We expect that this relationship between photosynthetic surface area and drag depends on morphological strategies. Rooted aquatic plant species dominating river systems can be divided into three general morphological strategies: (i) emergent species with an upright stem protruding the water column, (ii) submerged species with floating leaves and (iii) fully submerged species.

Emergent species with stiff stems experience large drag forces compared with flexible species (Bouma *et al.* 2005). With respect to the latter, floating leaved vegetation experiences higher drag forces than fully submerged species. Light interception and photosynthesis, however, is more efficient in emergent and floating leaved species, potentially providing them with a competitive advantage that offsets their disadvantage in having to cope with higher drag forces. Additionally, some emergent species are able to engineer their environment (Asaeda, Rajapakse & Kanoh 2010) enabling them to grow in comparable velocity conditions as submerged species. *e.g.* *Sparganium erectum* can change its life-form from submerged to emergent (Britton & Brown 1913; Kankaala *et al.* 2000; Riis, Sand-Jensen & Vestergaard 2000). A thorough understanding of cost-effectiveness between leaf area and drag on photosynthetic capacity is needed for in-depth understanding of morphological vegetation strategies. With this knowledge, the dominant morphological plant strategy of a river could be predicted and more accurately coupled with hydraulic river drag.

The objective of our experimental study was twofold: (i) to assess to what extent leaf area contributes to drag experienced by species with contrasting morphological strategies and (ii) to enhance insight into how these morphological strategies affect the cost-effectiveness involved in minimizing drag surface while maximizing photosynthetic light-intercepting surface. Hence, we compared drag and light-intercepting surface as a function of current velocity for emergent species, species with floating leaves and fully submerged species. We hypothesize that leaves of macrophytes will generate relatively more

drag than stems (a) and that emergent growth forms are more efficient in reducing drag (b).

Materials and methods

PLANT SPECIES

Five morphologically differing macrophyte species were selected as representatives of (i) emergent species (*S. erectum* L.), (ii) species with submerged but superficial positioned leaves (*Stuckenia pectinata* L.) or floating leaves (*Potamogeton natans* L.) and (iii) fully submerged species with leaves along the entire length of the stem (*Callitriche platycarpa* Kütz and *Ranunculus penicillatus* (Dumort.) Bab.). The grouping was based on how the physical structures of the plant (*i.e.* the leaves) are distributed throughout the water column, as this is of main importance for determining both drag and light interception. Because of the plasticity of macrophyte morphology (Puijalon & Borette 2004), it is possible that a single species can change between morphologies and thus shift between groups. Macrophyte groupings in this research are therefore a reflection of morphologic behaviour rather than species name based. *S. erectum* was included in the experiments because it is an emergent macrophyte that can grow within the river channel (Asaeda, Rajapakse & Kanoh 2010) being exposed towards the same velocities as the submerged species. All plants used in the experiments were collected from lowland rivers (Desselse Nete and Wamp) in the Nete catchment, a tributary to the Scheldt River in Belgium.

The length of the different plants varied between 0.5 and 1 m reflecting their natural difference in stature. Rather than searching for individuals with the same stature, individuals were collected that had the same growing period as proxy for their age. For the submerged species, this meant that all plants reached the water surface. *S. erectum* was the tallest species with a length of *c.* 1 m, always extending from the water column. All plants were exposed to similar stream velocities.

FLUME MEASUREMENTS OF DRAG FORCES (AS PROXY FOR THE COST) AND PHOTOSYNTHETIC SURFACE AREA (AS PROXY FOR THE BENEFITS)

All measurements were taken in a racetrack-shaped flume channel at the Netherlands Institute of Ecology – Centre for Estuarine and Marine ecology (NIOO-CEME) in Yerseke, where plants can be exposed to a range of reproducible current velocities. These velocities, determined from a calibration curve of the flume, were averages for the entire water column. This is in accordance with the statement that for entire macrophytes, velocity should be integrated over the height of the stand (Green 2005; Statzner *et al.* 2006).

The flume channel is 17.55 m long and 0.6 m wide and contains up to 10 m³ of water. Water flow is generated with a conveyor belt. At the start of the experimental section, the water passes through PVC tubes with a diameter of 0.02 m, in order to collimate the flow. For a more detailed flume description, see Bouma *et al.* (2005). In all experiments, water depth was maintained at 0.3 m for the different current velocities.

Drag was measured as the force (parameter *F* in eqn 1) at the bottom of the stem. Therefore, aquatic vegetation was mounted on a force transducer that was sunken into the bottom of the flume to reduce interference with the plant stems. This transducer consisted of a stiff solid platform, carried by two steel cantilever beams, with four temperature-corrected strain gauges mounted in pairs on opposite

sides of each of the two steel cantilevers (for details see Bouma *et al.* 2005). Calibration was made according to Stewart (2004). Voltage output of this transducer was linear with forces up to 10 N. During the experiments, voltage readings were collected on a data logger. On top of this transducer, a small metal strip allows mounting four or five shoots, depending on the size of the species. Plants were mounted on this strip using a tar-like substance fixing the basal part of the shoot but still allowing natural bending behaviour. In case of *S. erectum*, we could only mount 1 shoot to the force transducer. To obtain plant drag, the drag generated by the small metal strip was subtracted. Drag measurements were taken for a range of current velocities from 0.01 to 0.37 m s⁻¹. Measurements at velocities close to zero (< 0.08 m s⁻¹) have to be interpreted with care because drag is close to zero and interference with opposing forces, owing to mounting of the plant, can occur resulting in negative values. To compare morphological strategies, drag was expressed as a function of the plant surface area. Therefore, plant individuals were spread out on a grid pattern with known area and photographed. Importing these pictures into ARCVIEW (version 3.2 a; ESRI; USA) enabled us to digitally process the individuals.

To determine the effect of bending by the flow on the plant surface area, the angle of deflection and the relative photosynthetic surface area were measured. The angle of deflection with the horizontal was determined from pictures taken through the transparent side of the flume (Bouma *et al.* 2005). Because stems bent in an arc, the angle with the horizontal was arbitrarily measured at the lowest 5 cm of the stem because bending was constant at this part. The relative photosynthetic surface area at different stream velocities was determined from pictures taken above the water surface (*c.* 30 cm above the flume). This relative photosynthetic surface area is the same as the parallel-to-flow area as defined by Statzner *et al.* (2006). A reference grid pattern with known surface area was drawn on the bottom of the flume to digitally determine the relative photosynthetic surface area using ARCVIEW. We have chosen to use the term 'relative photosynthetic surface area' to make a possible link with the photosynthesis of plants. As mentioned by Nikora (2010), this projected surface area is an underestimation of the real area exposed towards light because of leaf flapping exposing earlier shadowed surfaces. Because light attenuates with water depth (Beer–Lambert), the position of the leaves within the water column was measured through the transparent side of the flume. An overview of the measurement errors on the key parameters (drag, velocity, surface area measurements and depth) of this study is shown in Table 1.

A BRIEF THEORETICAL BACKGROUND & DATA ANALYSIS

Flexible structures enable aquatic vegetations to reduce the experienced drag by reducing the surface area that is exposed to flow by bending (Koehl 1984; Sand-Jensen 2003; Bouma *et al.* 2005). Such

Table 1. An overview of the measurement errors on the collected parameters

Parameter	Unit	Measurement errors
Drag	N	< 0.0002 N
Velocities (flume related)	m s ⁻¹	< 25% (Jonsson <i>et al.</i> 2006)
Depth	cm	< 1 cm
Relative photosynthetic surface area	m ²	< 10%
Plant surface area	m ²	< 10%

reconfiguration by bending of the plants results in complicated mathematics (Alben, Shelley & Zhang 2002), which are often resolved by using a simplified method explained below. In unidirectional flow conditions, the drag (F) of an object (N, equal to kg m s⁻²) is proportional to a power of velocity

$$F = 0.5 C_d \rho A U^\beta \quad (1)$$

with β being 2 for rigid objects but $\beta < 2$ for flexible objects that reconfigure by bending, ρ the mass density of water (kg m⁻³), A the characteristic area (m²), U the fluid velocity (m s⁻¹) and C_d the drag coefficient. This equation is also often used in a slightly different formulation where β is replaced by E with $E = \beta - 2$. When the E value is below zero ($\beta < 2$), a reconfiguration is realized which produces a drag that is less than expected for a bluff body [according to the relation drag \propto (velocity)²]. Care, however, must be taken because this simplification is only applicable when drag is dependent on velocity (E -values higher than -2).

An important parameter in eqn 1 is the characteristic area of an object. For blunt objects that experience mainly profile or form drag, the characteristic area should equal the projected area. For streamlined objects that mainly experience skin or friction drag, the wetted area is more suitable (Vogel 1994). For a given surface area oriented parallel to the flow, skin drag is often negligible compared with profile drag. In our comparative analysis of plant strategies, the drag was expressed as a force per unit plant surface area (N m⁻²), because the way plants expose this surface area to the flow is an inherent part of their strategies (Bouma *et al.* 2005).

Results

INFLUENCE OF LEAVES ON THE TOTAL DRAG

Drag and relative photosynthetic surface area were measured on aquatic vegetation plants with different leaf morphologies when exposed to a range of current velocities. Not surprisingly, absolute drag forces imposed on the various aquatic vegetations increased with current velocity (Fig. 1a) and were significantly different between the investigated species. A *post hoc* Tukey's test showed that the absolute drag forces for *S. erectum*, up to 1.2 N, was significantly higher than for all other species ($P < 0.05$). Drag was three to four times higher than for the submerged species (*R. penicillatus* and *C. platycarpa*) and superficial or floating leaved species (*P. natans* and *S. pectinata*; Fig. 1a). To compare growth strategies, drag was also expressed per unit of plant surface area. The drag experienced by the relatively flexible floating and submerged species was comparable when expressed per unit of plant surface area (Fig. 1b). The stiffer emergent species *S. erectum* had a higher increase in relative drag with velocity than all other species (up to 28 N m⁻² vs. 7–10 N m⁻² for the other species).

To assess to what extent leaves contribute to the absolute drag experienced by aquatic species with contrasting morphological strategies, drag was determined before and after leaf removal. Removal of the leaves showed that for floating leaved and submerged species, the ratio of drag with leaves (N) to drag without leaves (N) was higher than 1 (Fig. 2). Along the different velocities, on average 60% ($\pm 6\%$) of the absolute drag was contributed by the leaves. The emergent

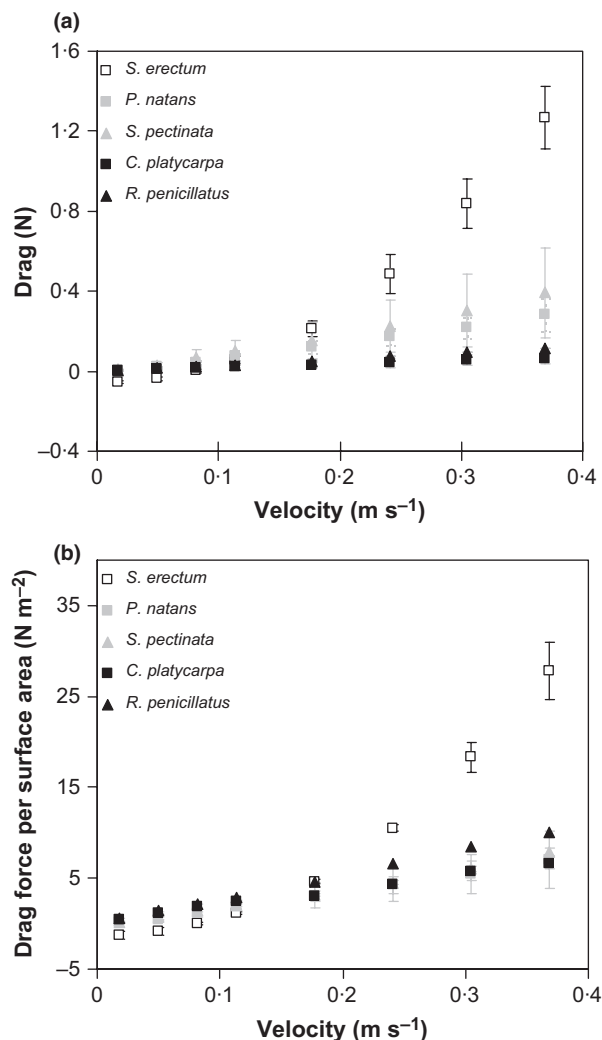


Fig. 1. Absolute (a) and relative drag (b) of various macrophyte groups (white = emergent, grey = superficial or floating leaved, black = submerged) in function of increasing velocity. Standard deviations (number of replicates for each species: $n = 2$) are shown, but not all visible, within the graph. This increase in drag with current velocity was significant (two-way ANOVA, $P < 0.001$, $F = 7.5$, d.f. = 7), and significant differences between species were observed ($P < 0.001$, $F = 7.8$, d.f. = 4).

species *S. erectum* had the same absolute drag (N) with or without leaves (not shown). The latter can be explained by the fact that most leaves of this emergent species are outside the water column. Calculating the ratio of the relative drag per plant surface area in the presence of leaves (N m^{-2}) to the relative drag per surface area without leaves (N m^{-2}) typically resulted in values slightly below 1 (Fig. 2), meaning that per unit of surface area, stems generate more drag than leaves. Floating leaved species had the tendency to have higher absolute and relative drag ratios than submerged species.

BENDING

Bending increased in the following order: *S. erectum* (emergent) < *P. natans* (superficial or floating leaved) = *R. peni-*

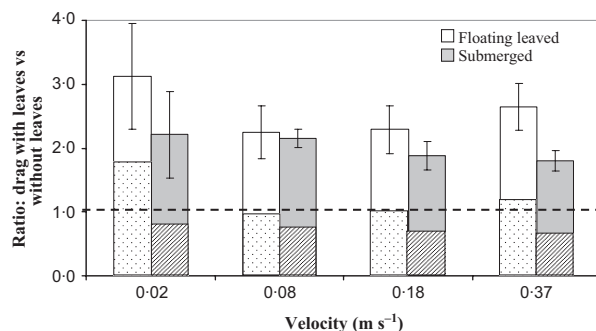


Fig. 2. The average ratio of absolute drag with leaves (N) to absolute drag without leaves (N) for both floating leaved (white) and submerged species (grey). The average ratio of relative drag (N m^{-2}) with leaves to relative drag without leaves (N m^{-2}) for both floating leaved (dotted) and submerged species (striped). Error bars show the standard error ($n = 4$) for both groups (floating leaved vs. submerged).

cillatus (submerged) < *S. pectinata* (superficial or floating leaved) = *C. platycarpa* (submerged) (Fig. 3a) (two-way ANOVA $P < 0.001$, $F = 59$, d.f. = 4). No significant differences were detected (Scheffé *post hoc* test) between *P. natans* and *R. penicillatus* on the one hand and *C. platycarpa* and *S. pectinata* on the other hand ($P > 0.95$). Our results indicate that emergent species fall in a different group than the floating and submerged species with respect to bending. The bending effect of the different species was significantly influenced by current velocity ($P < 0.001$, $F = 13$, d.f. = 7),

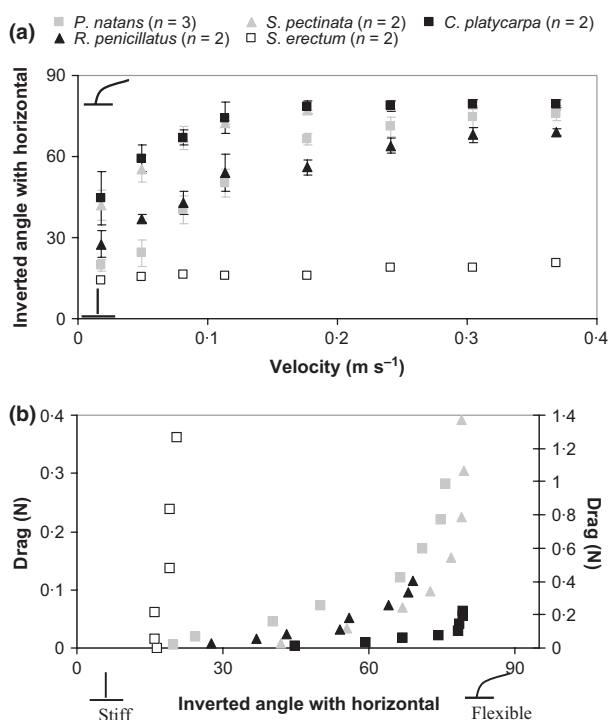


Fig. 3. Bending of the different macrophyte species in function of stream velocity (a) and the resulting absolute drag (b) experienced by these macrophytes. In graph b, standard errors on both axes are shown. Note that the right axis (*Sparganium erectum*) in graph b is at a different scale. Legend of both figures is shown above.

with increasing velocity stimulating bending angles up to a maximal level (Fig. 3a). For *C. platycarpa* and *S. pectinata*, the fitted parameters for the relationship between current velocities (U) and bending (α) were identical (Table 2). With removal of the leaves, the angles with the horizontal plane increased slightly (two-way ANOVA, $P = 0.05$, $F = 4$, d.f. = 1) resulting in stems remaining longer in an upright position with increasing velocity. This decreased bending response with velocity was observed for all submerged species.

The increased bending of plants allows the total drag on them (i.e. that which needs to be resisted by root anchorage, as opposed to the drag per surface area) to remain approximately constant with increasing flow velocity (see Fig. 1a cf. Fig. 1b for *C. platycarpa* and *R. penicillatus*). However, if maximal bending is approached, drag increased quickly with increasing velocities for both submerged and floating leaved species (Fig. 3b) at higher current velocities. At low horizontal angles, drag was slightly higher for the floating leaved species than for the submerged species. This difference is reflected in the calculated E -values, respectively, around -0.8 and -1.1 for the floating leaved and totally submerged species (Table 2). For the emergent species (*S. erectum*), drag increased more with current velocity owing to the bluff body behaviour of the stem. Relative drag in all submerged species was between 7 and 10 N m^{-2} at low horizontal angles. *S. erectum* experienced relative drag values up to 25 N m^{-2} (Fig. 1b).

COST-EFFECTIVENESS

In the floating leaved species *P. natans*, increasing current velocity caused a sharp decline (Table 1) ($R^2 = 0.93$, $P < 0.001$, $F = 77$) of the relative photosynthetic surface area from c. 200 to 100 cm^2 (Fig. 4a), whereas *S. pectinata* only experienced a small reduction in its relative photosynthetic surface area at the highest current velocity (Fig. 4a). For *C. platycarpa* and *R. penicillatus*, this flattening down and overlapping of the leaves against the stem, resulting in a decline of the relative photosynthetic surface area, were less pronounced (30% and 15%, respectively). Relative photosynthetic surface area did not decline for the non-flexible emergent species *S. erectum*. This re-alignment of plant stems

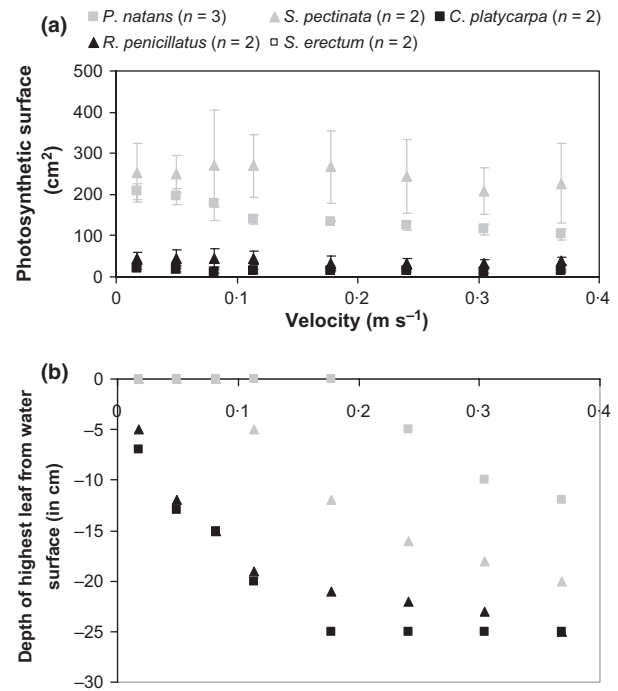


Fig. 4. The amount of available photosynthetic light-intercepting surface in function of stream velocity for all submerged and floating leaved species (a) and bending angles with the horizontal (b) for all tested species. Standard errors ($n = 2$) are shown.

with increased velocity is defined as reconfiguration (Sand-Jensen & Pedersen 2008).

Not only relative photosynthetic surface area diminishes but also the light flux reaching the leaves reduces (Beer–Lambert law) because of increased submergence with increased velocity. When the distance of the submerged leaves towards the water surface was plotted, a faster decline was seen for *C. platycarpa* and *R. penicillatus* (Fig. 4b).

If the ratio of relative photosynthetic surface area to drag was plotted against current velocity, the three different growth strategies (emergent vs. superficial or floating leaves vs. totally submerged) were easily distinguished (Fig. 5). For all submerged and floating leaved species, the ratios were significantly related with velocity (two-way ANOVA, $P < 0.005$, $F = 15$) and species (two-way ANOVA, $P = 0.002$, $F = 5.6$).

Table 2. Relationship between current velocity (U) and bending (α), the relationship of current velocity with available leaf area (L) and the ratio of photosynthetic surface area to absolute drag in function (T) of the stream velocity for various macrophyte species

Species	Bending capacity				Leaf area vs. velocity			Ratio		
	$\alpha = xU^\beta$				$L = z\ln(U) + c$			$T = qU^\gamma$		
	x	β	R^2	E -value	z	c	R^2	q	γ	R^2
<i>Sparganium erectum</i>	68.9	-0.03	0.80		No decline			3	-3.38	0.90
<i>Potamogeton natans</i>	8.7	-0.60	0.90	-0.76 ± 0.02	-84	72	0.93	83	-1.52	0.99
<i>Stuckenia pectinata</i>	5.5	-0.55	0.97	-0.78 ± 0.16	Linear		0.42	160	-1.30	0.99
<i>Callitriche platycarpa</i>	5.6	-0.53	0.96	-1.09 ± 0.24	-4	12	0.57	74	-1.03	0.98
<i>Ranunculus penicillatus</i>	15.5	-0.38	0.93	$-1.06 \pm \text{NA}$	Linear		0.53	110	-1.06	0.97

E is a value indicating how a flexible structure is different from a bluff body. Notes: q , γ , z , c , x and β are fitted parameters.

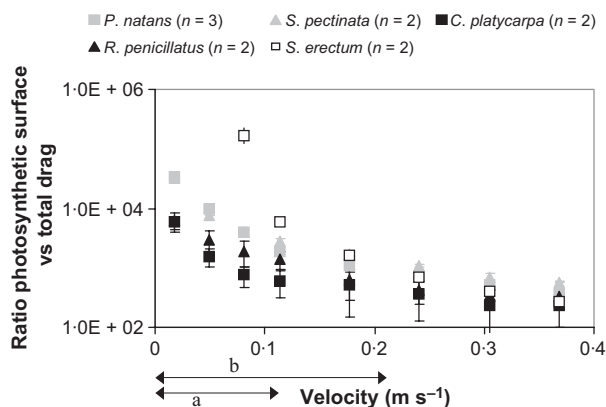


Fig. 5. The relationship between photosynthetic surface area and absolute drag ($\text{cm}^2 \text{N}^{-1}$) in function of the stream velocity (m s^{-1}) for plants with leaves. Error bars are shown. The arrows below the x-axis indicate the typical velocity range they occur in for emergent (a) and broad-leaved macrophytes (b) according to Newson *et al.* (1998), Kemp, Harper & Crosa (1999) and Clifford *et al.* (2006).

S. erectum was not added in the ANOVA owing to negative values at the lowest velocity. These small negative values for *S. erectum* are negligible artefacts that occur because it is impossible to mount stems perfectly straight upward on the drag sensor. A minor deviation from perfectly vertical will cause the weight of the plant to impose a small force on the drag sensor. A *post hoc* Scheffe test indicated that *P. natans* and *S. pectinata* significantly ($P = 0.1$) differed from *C. platycarpa*/*R. penicillatus* and vice versa. This ratio between photosynthetic surface area and drag decreased with a power γ ($T = qU^\gamma$) over current velocity (Table 2). This power γ ranged between -3.4 and -1.0 , with the lowest value for the emergent species *S. erectum*.

Discussion

Aquatic vegetation is characterized by a range of flexibilities from very rigid species to flexible species (Kouwen & Unny 1973). Owing to this bending capacity, drag is increasingly reduced from what it would be for a rigid object (of the same initial frontal surface area) with increasing velocity (Sand-Jensen 2003; O'Hare *et al.* 2007). However, with increased bending towards the river bottom, photosynthetic surface area decreases. Also, the increased submergence will reduce the amount of light received by the leaves owing to attenuation. Aquatic plants have to find an optimal balance between reducing drag and maintaining enough photosynthetic surface area. From our results, we must reject the hypothesis that leaves generate more relative drag (N m^{-2}). Instead, they seem to facilitate the bending capacity of stems. At low velocities and water depths, emergent growth forms have lower relative drag values partly supporting our initial hypothesis (b).

INFLUENCE OF PLANT MORPHOLOGY

Our results clearly indicate that contrasting morphological strategies result in different photosynthetic area vs. drag

ratios. Beneath stream velocities of 0.2 m s^{-1} , emergent species, like *S. erectum*, have a competitive advantage in intercepting more light per unit of drag experienced. The natural niche of emergent species is below stream velocities of 0.1 m s^{-1} (Newson *et al.* 1998; Kemp, Harper & Crosa 1999; Clifford *et al.* 2006) matching with our observation that *S. erectum* has the highest photosynthetic area vs. drag ratios beneath 0.1 m s^{-1} . However, our results indicate that emergent species also have a more beneficial ratio between 0.1 and 0.2 m s^{-1} . An explanation for this discrepancy is that with increased velocity, anchorage strength of the roots is exceeded with root failure as a consequence. Anchorage strength of submerged species with a dense network of roots varies between 0.25 and 12 N (Madsen *et al.* 2001; Schutten, Dainty & Davy 2005). Because shoot drag of emergent species increases sharply with velocity (Fig. 2a), we hypothesize that shoot drag generated around 0.2 m s^{-1} is higher (0.5 N) than anchorage strength (0.25 N) at these velocities. Therefore, emergent species will have increased risk of root failure with increasing velocity.

Because of the non-rigid state of all submerged species, bending occurs at lower current velocities, mitigating the increase in drag with velocity. This enables these species to persist under higher velocity conditions than emergent species (Brewer & Parker 1990; Schutten & Davy 2000). For *S. pectinata* and *P. natans*, most of the biomass was situated in the faster flowing upper 10 cm of the water column, explaining the higher absolute drag values. This higher drag is especially seen at lower angles (high velocities). This could be caused by differences in macrophyte movements (flapping of leaves) owing to leaf shapes. This leaf shape, e.g. thickness and degree of branching, is shown to influence the resistance of a plant (Manz & Westhoff 1988). Wide leaves (like *P. natans*) have higher flapping amplitudes than small, flat leaves (like *R. penicillatus*) and will therefore generate more drag (Koehl & Alberte 1988; macroalgae). On the other hand, bending differences, with concomitant reduction in drag, will be the result of differences in biomass distribution within the stems. By investing in structural components like lignin and cellulose, plants regulate their stiffness: with increased lignin concentrations, stems have increased stiffness (Kaufman *et al.* 1999). From Schoelynck *et al.*'s study (2010), it can be seen that aquatic vegetation has variable cellulose (between 104 and 387 mg g^{-1} dry mass) and lignin concentrations (between 3 and 192 mg g^{-1} dry mass). Plant composition will therefore also impact the bending capacity and drag of macrophytes. This non-rigidity of stems also increases the streamlining with velocity resulting in a reduced effective size of the plant and thus reduced drag (Sand-Jensen 2003).

This reconfiguration by bending, expressed in *E*-values, was somewhat lower than found by O'Hare *et al.* (2007) (between -1.43 and -1.62) but comparable with reconfiguration values of the kelp *Nereocystis luetkeana* (-1.07) (Koehl & Alberte 1988) and *Hygrophila corymbosa* (-1.09) (Sand-Jensen 2003). For *Ranunculus fluitans* Lam. and *Ranunculus pseudofluitans*, two related species of *R. penicillatus*, comparable low drag values were shown (Usherwood, Ennos & Ball

1997; O'Hare *et al.* 2007) and both are considered well adapted towards fast flow (Haslam 1978).

INFLUENCE OF LEAVES ON DRAG

The emergent species *S. erectum* had the highest drag values, even per surface area, when exposed to high stream velocities. Watson (1987) stated that this species could maintain a high resistance against flow at relatively high water levels. However, at low stream velocities, this species has similar drag values as submerged species but no reduction in light owing to attenuation by the water (Fig. 6). As stated earlier, this species is able to grow first submerged (Britton & Brown 1913), allowing it to colonize deeper areas, and then become emergent. This species could therefore pose a real flooding hazard when stream velocities in the river centre are low allowing it to colonize not only the margins but also the middle parts of a river (Haslam 1978). Within the submerged species, some plants concentrate their leaves at the water surface and others distribute them more or less evenly along the water column. The latter species will receive less light owing to attenuation with water depth (52% remaining) (Fig. 6). Because their leaves are distributed more evenly along the stem, reconfiguration will result in less self-shading as seen in our study (less reduction in relative photosynthetic surface area). Recent research has shown that light limitation is a main factor in determining the occurrence of species and species communities (Sand-Jensen, Binzer & Middelboe 2007), which is in line with our experiments that there exists a cost-effectiveness between light capture (by means of light-intercepting photosynthetic surface) and drag. However, with increasing stream velocities, plants with an evenly distributed biomass along the

water column will experience lower drag values because of their positioning of less biomass in high-velocity regions near the surface. With increased velocities, these species will reconfigure faster making them less competitive at average stream velocities. From 0.2 m s^{-1} , their relative photosynthetic surface area remains constant, because of positioning of the leaves, giving them a more beneficial trade-off with drag. During plant bending and thus flattening, six regimes with increasing velocities can be identified (Green 2005 and references therein). We state that for species like *R. penicillatus*, regime 5 (stems become prone or densely compacted, with surface leaves submerged) will be reached faster but will be maintained longer before reaching regime 6 (at the highest powers, damage and loss occur to the whole or to parts of plants). Thus, in general, completely submerged life-forms, like *R. penicillatus*, have the best strategy at high stream velocities owing to their lower drag values and flattening. From Fig. 6, we must conclude that water depth is an important parameter making the trade-off between drag and photosynthetic area more complex. However, in small and shallow rivers, we believe that drag will be the determining factor in plant occurrence. In turbid or deeper waters, light will become the more dominant parameter determining occurrence.

While plant adaptations as result of resource stress (nutrients, light ...) are well documented (Sack 2004), adaptations against mechanical stress (flow) and their interaction with resource stress are largely unknown (Puijalon 2007). A nice, but sparse, example of this interaction is the tendency to develop shallow roots with increased nutrient concentrations resulting in a reduced anchorage and uprooting of the plant (Mainstone *et al.* 1996). Also plants subjected to frequent

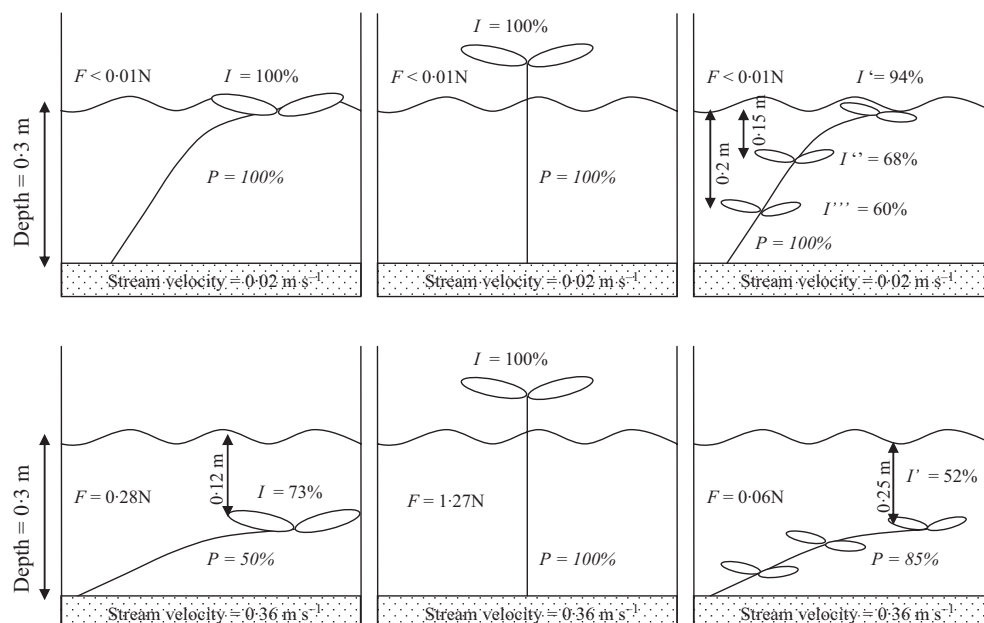


Fig. 6. Visualization of the bending of three different macrophyte morphologies (floating leaved, emergent and submerged with equal biomass distribution) during low and high stream velocities. F represents the measured drag values, and I is the percentage of light compared with the level just above the water surface (calculated according to the Beer–Lambert formula). For the submerged species, light percentages at different depths are shown (indicated with an). P is the relative photosynthetic surface area.

pulse flows will show the undesirable effects of eutrophication at lower nutrient concentrations than rivers not subject to higher velocities (Hilton *et al.* 2006). Resource variables like nutrient availability (Carr & Chambers 1998) and oxygen transport are also important parameters in explaining the occurrence for species. For example, macrophytes with photosynthetic tissue exposed to the atmosphere, like *P. natans*, will transfer oxygen more easily across the boundary layer between air and water (Wilcock *et al.* 1999; Caraco & Cole 2002; Caraco *et al.* 2006) facilitating gas exchange at low stream velocities while generating an additional advantage compared with totally submerged species. Emerged species on the other side will be less dependent on the light conditions in the water column giving them an advantage in turbid waters. Nutrient availability will interact with the light conditions owing to increased epiphyte growth. With increased nutrient levels, epiphyte cover will increase, reducing light availability for macrophytes. However, submerged macrophytes are shade tolerant with saturation points ranging from 10% to 50% compared with full sun light (Spencer & Bowes 1990).

Because leaf morphology is very versatile and strongly dependent on environmental conditions, like stream velocities (Boeger & Poulson 2003), the effect of leaves on absolute drag was estimated. Leaf removal resulted in lower absolute drag values because of a decreased surface area, in accordance with previous research (Koehl 1982). The relative drag per surface area of the remaining stems had a tendency to be slightly higher than the leafed stems. Leaf removal changes the proportion between profile and skin friction drag of the stem. The morphology of leaves thus determines this proportion resulting in different positions in the water column. More work on the contribution of leaf variance, including age differences, towards the total drag of a plant should be carried out in order to estimate the contribution of profile and skin friction drag. Also, the effect of water-level fluctuations should be further investigated. e.g. when water levels increase, overtopping the stems of emerged species, drag would increase drastically and even bending of these inflexible plants would occur. On the other side, a decrease in water level increases the amount of trailing canopies of the flexible species impacting the drag of these individuals.

In conclusion, our research provides evidence that morphological strategies are clearly linked with stream velocities and light capture. With decreased hydraulic forces, plants with an emerged strategy are more beneficial explaining their occurrence in zones with reduced hydraulic forces. In shallow rivers, this decline in hydraulic forces could potentially lead towards an increased dominance of emerged species like *S. erectum*. This increased knowledge of macrophyte occurrence in the function of stream velocity allows river managers to define problem zones with augmented risk of emerged growth forms. However, in natural circumstances, macrophytes are found in patches. Within these patches, shading by neighbouring individuals will reduce light-intercepting surface negatively influencing the optimal balance. On the other hand, less drag is experienced by the individual owing to

reduced water velocity within a macrophyte patch positively influencing this balance. These interactions between drag and photosynthetic area within patches have to be further investigated.

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