

Reconfiguration as a Prerequisite for Survival in Highly Unstable Flow-Dominated Habitats

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ABSTRACT

Unstable and mechanically demanding habitats like wind-exposed open fields or the wave-swept intertidal require rapid adaptive processes to ensure survival. The mechanism of passive reconfiguration was analyzed in two plant models exposed to irregular flow of water or air, two species of the brown seaweed *Durvillaea* and the giant reed *Arundo donax*. Irrespective of the surrounding media and the subsequent Reynolds numbers ($Re \sim 10^5$ – 10^7), reconfiguration seems to be the key strategy for streamlining to avoid overcritical drag-induced loads. This passive mechanism is also discussed in the context of the requirement of a maximized surface area for light interception, so that morphological adaptations to rapid reconfiguration represent at least a bifactorial optimization. Both tested plant models exhibited the same principles in streamlining. At a specific threshold value, the

proportionality between drag forces and flow velocity can be reduced from the second power close to an almost linear relation. This empirically derived relation could be characterized by a figure of merit or Vogel number (B). A value close to $B = -1$, resulting in a linear increase of drag force with velocity, was found at higher velocities for both the seaweeds and the giant reed, as well as for a variety of plants described in the literature. It is therefore concluded that the ability to reduce velocity-dependent drag force to a linear relation is a potentially important adaptation for plants to survive in unstable flow-dominated habitats.

Key words: Reconfiguration; Streamlining; Vogel number; Flow exposure; Linear velocity dependency; Biomechanics; Drag force

INTRODUCTION

Plants can adapt to outer mechanical conditions by various mechanisms, for example, by growth reactions or by rapid adaptive reactions such as reconfiguration (Ennos 1999). Growth reactions as an

adaptation or response to physical loads are widespread among many plant groups, typically taking place on a time scale of hours, days or even years (Sinnot 1952; Wainwright and others 1976; Telewski and Jaffe 1986). For plants growing in habitats dominated by high flow velocities of the surrounding medium, adaptive mechanisms involving growth reactions are often too slow. Although this type of reaction is frequently found, for example, in wind-bent trees (Ennos 1995;

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Telewski 1995; Mattheck 1996; Mattheck and Breloer 1996; Brüchert and Gardiner 2000), rapid adjustments are often necessary to reduce loads in response to short-time events like gusts or large waves (Vogel 1984; Vogel 1989).

Habitats like the wave-swept intertidal or wind-exposed fields can be characterized as unstable and mechanically very demanding, although this may only be true in times of extreme loading (Gaylord and others 2001). The frequency of occurrence of these events can change on a small spatial scale (Helmuth and Denny 2003) and may be difficult to estimate for individuals (Denny and Gaines 1990; Gardiner 1995). Active rapid adaptive processes to flow conditions are common in animals. In the absence of a rapid regulatory sensory and nervous feedback system, plants have to rely on passive means to cope swiftly with various flow regimes. Additionally, to allow rapid adjustments to the shape of an organism, the various structural units of a plant body have to be flexible enough (Vogel 1984). The overall morphology of a plant subsequently needs to be adapted in such a way that survival at flow-dominated habitats is ensured.

One of the main functions of the lamina is the interception of light (Niklas 1992a; Niklas 1997). Under benign conditions it is therefore advantageous to have a maximized photosynthetically active area. Conversely, under potentially damaging and irregular flow conditions, it is of paramount importance to reduce drag and thus the danger of flow-induced overcritical loads. As plants usually attempt to maximize their photosynthetically active area (Niklas 1992a), a high degree of adaptation to extreme loading events can potentially pose a competitive disadvantage. If, for example, the size of the lamina of intertidal seaweeds is reduced, it is only an appropriate adaptation at sites with frequent severe and possibly fatal wave action (Hay 1994). The individual morphology therefore represents the result of a multifactorial adaptive process (Niklas 1999).

The main form of mechanical loading in flow-dominated habitats is commonly caused by drag (Gaylord 2000), which can effectively be reduced by streamlining. Etnier and Vogel (2000) found that daffodil flowers change shape and orientation in response to wind velocities above a threshold value of 5 m/s which led to a reduction of drag by approximately 30%. For quantitatively analyzing the mechanics of a flexible biological structure, approaches originally derived in the engineering sciences for rigid bodies are used. However, a variety of amendments have been proposed (Vogel 1988; Niklas 1992b; Wood 1995).

DRAG FORCE AND VOGEL NUMBER

In engineering, the drag force is commonly determined by (Niklas 1992b):

$$F_d = \frac{1}{2} \rho A_c C_d u^2 \quad 1.1$$

where F_d : drag force, ρ : density, A_c : characteristic area, C_d : drag coefficient, and u : fluid's velocity relative to an object. The relative importance of these components depends on the size of an organism and the density of the surrounding medium. The flow regime can be characterized by the Reynolds number (Denny 1988; Denny 1990). Although the different densities of water and air entail different Reynolds numbers for plants of comparable size subjected to flows of comparable velocities, both aquatic and terrestrial plants are mainly threatened by pressure drag. In this study, the approximate Reynolds numbers ranged from 10^5 to 10^7 .

It is a well-known observation that organisms that are exposed to flow-induced drag often reduce the effective velocity-dependent load by streamlining (Telewski and Jaffe 1986; Ennos and others 2000; Koehl and others 2003). With animals for example, in dolphins, and penguins, streamlining is often a permanent feature of their body shape (Culik and others 1994a; Culik and others 1994b; Nachtigall 2002). In contrast, streamlining in plants is frequently non-permanent but achieved through the passive process of reconfiguring plant parts, as a response of flexible structural elements to the dynamical loading by the fluid (Vogel 1984). Studies on plants with diverse morphologies and surrounding media such as trees (Telewski and Jaffe 1986; Wood 1995), aquatic buttercups (Usherwood and others 1997), and a variety of other freshwater plants (Schutten and Davy 2000; Schutten and others 2004), or seaweeds (Carrington 1990; Koehl 2000) have shown that this phenomenon is widespread.

With flexible organisms, the plant's overall shape and its behavior in flow are not constant (Koehl 2000). Assuming a constant drag coefficient and a constant relevant area yields an expected increase of drag with the velocity squared (Denny 1988). Due to reconfiguration events, the shape of a body changes, therefore its drag coefficient also changes with increasing velocity (Gaylord and others 1994; Wood 1995).

Comparisons of behavior in flow between different conspecific individuals or different species are subsequently often restricted to certain flow condi-

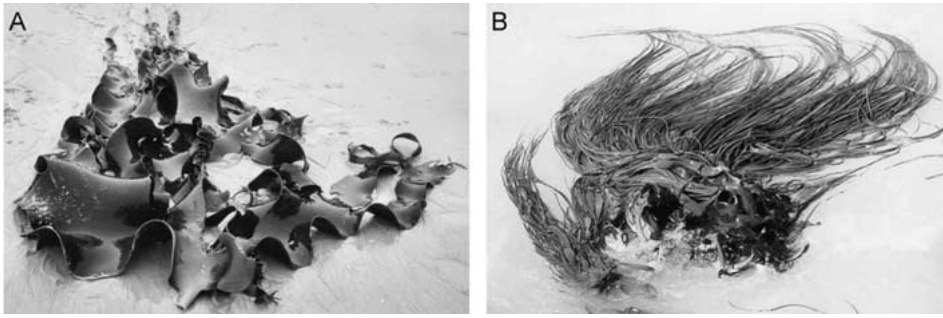


Figure 1. Two morphotypes of the brown seaweed *Durvillaea antarctica*. At wave-sheltered sites, the lamina is broad and cape-like with large undulations (**A**), whereas at more wave-exposed sites, the lamina is subdivided into many thin strips (**B**). Photographs were taken near Dunedin, New Zealand. Those shown are approximately 5-7 m long.

tions and velocities (Gaylord and Denny 1997; Koehl 2000). There are several suggestions for accommodating to the variations of the overall body shape typically found in flexible biological bodies in different flow regimes (Wainwright and others 1976; Vogel 1996; Koehl and others 2003): (1) Because the shape is not constant, a more general shape factor that varies with flow velocity can replace the constant drag coefficient (C_D) (Hoerner 1965; Gaylord and Denny 1997). (2) Another possibility is to regard the relevant area (A_c) as varying with velocity (Speck 2003). (3) The most realistic, but also considerably more complex description would be to regard both parameters as variable. (4) A fourth very useful and significant method to consider this phenomenon was introduced by Vogel (1984; 1989). It describes the process of reconfiguration, which leads to a lower increase of drag than could be expected by considering both relevant area and drag coefficient as constant. The relation deviating from the second power between drag and velocity is accounted for by the introduction of a figure of merit as an addend in the power function, retaining the mechanistic scaling of $F_D \sim u^2$ (Gaylord and others 1994; Stevens and others 2002). For clarity and simplicity, Gaylord and others (1994) have introduced the term ‘Vogel number’, which is used henceforth (however, rather than the whole exponent, only the addend B is considered as the relevant figure):

$$F_d = \frac{1}{2} \rho A_c C_d u^{2+B} \quad 1.2$$

where B is the Vogel number. The more negative the Vogel number, the smaller is the increase in drag forces with increasing velocity. It is therefore a means of quantifying the beneficial effect of reconfiguration.

The aim of this study was to quantify the reduction in drag forces by reconfiguration in two plant

models, intertidal brown seaweeds and a wind-exposed giant reed. This paper focuses on three main aspects: 1) the Vogel number as a quantitative measure of how plants can minimize the increase in drag force with increasing velocity, 2) a threshold value of velocity where the Vogel number changes and thus the proportionality of drag forces to velocity, 3) the differential adaptations to flow regimes of morphotypes. Based on drag tests on the two plant models, reconfiguration is addressed as a key factor for successfully occupying ecological niches in unstable flow-dominated habitats.

MATERIALS AND METHODS

Model 1: Wave-Exposed Seaweed

The southern bullkelp [*Durvillaea antarctica* (Chamisso) Hariot and *D. willana* Lindauer] belongs to the Phaeophyceae and is probably the largest intertidal seaweed (Stevens and others 2002). Its distribution is restricted to the temperate rocky shores of the southern hemisphere (Hay 1994). The morphological setup is very simple with a holdfast, stipe, and lamina. The lamina of *Durvillaea* is approximately 4–7 m long and often subdivided into thin strips depending on the wave exposure of a particular site (Figure 1). It is thus possible to assess local wave exposure at least qualitatively (Hay 1994).

A total of eight individuals of *Durvillaea antarctica* and two individuals of *D. willana* were haphazardly collected from Brighton Beach, New Zealand (46°S, 170°E), during low tide. They were cut just above the holdfast and transported to a nearby laboratory in Dunedin, New Zealand, and tested within 24 hrs of collection.

Drag forces were measured in a flume at the Human Performance Centre, Dunedin, New Zealand (Figure 2), similar to the experimental setup described by Stevens and others (2002). Prior to



Figure 2. Experimental setup of the drag tests on *Durvillaea* in a flume (Human Performance Centre, Dunedin, NZ). The specimen of *D. antarctica* shown had an approximate length of 7 m and was reduced in ‘bulkiness’ as part of the lamina had been lost due to wave action and only a few but very long strips of the lamina remained.

tests, a specimen’s stipe was fastened with a hose clamp, which was fixed to a swivel by four pieces of low-strain yachting rope 4 mm in diameter. A swivel was connected to another piece of low-strain rope, which was redirected via a pulley and attached to a force transducer (RDP Group, Model 41–250 lb) outside the water. The pulley was screwed to a wing spar, which had only a small influence on the flow behavior of the flume and was therefore considered negligible. The dimensions of the flume were $B \times W \times D = 10 \times 2.5 \times 1.4$ m. The tests were conducted at velocities of 0.5, 1.0, 2.0, and 2.8 m/s, the latter being the maximum possible velocity of the flume. Each test run was recorded for at least two minutes at a frequency of 10 Hz.

The focus of this part of the study was on *D. antarctica*. The sample of this species was further grouped by morphotypes. In each group, four individuals were pooled as ‘wave-exposed’ or ‘wave-sheltered/intermediate’, based on a qualitative assessment of the overall morphology. Two individuals of *D. willana* were tested as a comparison of a sympatric congeneric species with a narrower range of suitable habitats with respect to wave exposure.

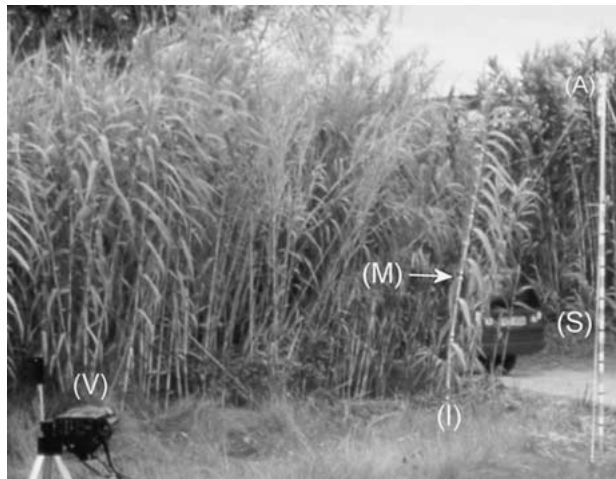


Figure 3. Individualized plant of the giant reed (*Arundo donax*) from a natural stand in southern France. The experimental setup allowed the synchronized recording of wind velocities and wind-induced changes in shape. The plants shown are approximately 3–4 m tall. (A) hot-wire anemometer; (I) individualized tested plant (height: 3.3 m); (M) marker on individualized plant; (S) scale; (V) videocamera.

Model 2: Wind-Exposed Giant Reed

The giant reed (*Arundo donax* L.) grows in dense stands from the Mediterranean region to China and Japan (Walters and others 2004). It is a large rhizomatous perennial that belongs to the grass family of Poaceae. The aerial shoot of the tested plant was 3.3 m high with a diameter of 1.7 ± 0.1 cm, arising from an extensive and persistent underground rhizomatous system. The hollow stems are divided into nodes and internodes that decrease in length from the middle part of the plant to both base and apex (mean length of internodes: 14 ± 5 cm). The alternate flat leaves were up to 62 cm long and up to 5.1 cm wide at the base. They were regularly spaced in two opposite ranks orientated in the same plane. The field measurements were carried out in the natural habitat of *A. donax* in the Camargue, southern France (Figure 3). The neighboring plants were cut and removed to allow measurements on a single giant reed. The experimental setup of an individualized *A. donax* can be justified as relevant to plants at the edge of a stand, where plants frequently behave as individuals.

The individualized wind-exposed plant was videotaped from the side by a video camera (Sharp, Model VL-C750S), which was arranged in such a way that the camcorder and plant were in line with the main wind direction. The wind velocity was measured with a hot-wire anemometer (Tri-Sense

Model No 37000-00, Cole-Palmer), which recorded wind velocity only for the main wind direction, 3.4 m above ground. The display of the anemometer was videorecorded by a second camera (Sony, Model CCD-V800E). The recordings of the plant in bending and the corresponding wind velocities were merged with a video splitter (Panasonic, Digital AV Mixer WJ-MX 20).

Selected video frames were transferred from the external video device onto the hard disk of a computer with a frame grabber and the software Oculus (Computer Products, Inc.). The projected surface areas of the stem and leaves of the tested specimen were measured in individual images electronically with the software SECTION. This program was used to calculate the areas of specified regions of each image once the magnification of each image was specified. Points on the stem of the plant at five levels above ground were marked with high contrast tape. The SECTION program was also used to measure the linear distance of the defined-object points with respect to ground level in each image. An estimate of the drag forces was calculated according to eq. (1.1) taking into account that the total projected surface area was a function of wind velocity and could be characterized by a decreasing second-order polynomial (Speck 2003), assuming that $C_D = 1.0$ (Niklas 1994; Vogel 1996).

Figure of Merit/Vogel Number

The process of reconfiguration was quantitatively assessed by the Vogel number. Considering the factor $1/2 \rho A C_d$ of equation (1.2) as constant gives the following proportionality:

$$F_d \sim u^{2+B}. \quad 2.1$$

The Vogel number, B , is defined as the slope of a double-logarithmic plot of the velocity-specific drag as a function of velocity (Koehl 2000):

$$B = \frac{\log\left(\frac{E_d}{u^2}\right)}{\log(u)}. \quad 2.2$$

The greater the absolute value of the negative slope, the better the reconfiguration process is considered to be.

RESULTS

With the brown seaweed *Durvillaea antarctica* and *D. willana*, the efficiency of reconfiguration processes was characterized by the Vogel number. All tested individuals exhibited an increase in drag with increasing velocity less than could be expected from

eq. (1.1). For the tested range of velocities, no threshold could be identified at which the relation between drag force and velocity changed significantly. Vogel numbers ranged from $B = -0.25$ (smallest measured reconfiguration) to $B = -1.21$ (maximal detected reconfiguration), with a mean of $B = -0.86$ for *D. antarctica* and $B = -0.52$ for *D. willana*, which cannot grow at severely wave-exposed sites. Grouped by morphotypes, the Vogel number of *D. antarctica* was more negative for wave-exposed individuals (compare Figure 1B) at $B = -1.00$ than for the wave-sheltered ones (compare Figure 1A) at $B = -0.73$ (Figure 4).

In comparison, two Vogel numbers could be determined for *A. donax* depending on the ranges of wind velocity. For small wind velocities up to 1 m/s, a Vogel number of $B = -0.12$ was found, mirroring that the drag force is in good approximation proportional to the square of the wind velocity (Fig. 4B). Beyond a threshold value of 1.5 m/s, however, the Vogel number was more negative ($B = -0.71$), mirroring very pronounced streamlining and a nearly linear proportionality between drag and velocity.

Figure 5 shows the relationship between measured wind velocity and calculated drag forces of an individualized giant reed. If *A. donax* was subjected to increasing wind velocities it responded with reconfiguration, especially of its stem and leaves. The video recording showed that reduction of the total projected surface area with increasing wind speed resulted in streamlining. Even at relatively small wind velocities, the leaves of the plant and the uppermost part of the stem changed orientation leeward. Especially at high wind velocity, the leaves were entirely streamlined. In addition, the stem bent curvilinearly with an acropetally increasing curvature (Figure 6). Up to 1 m/s, the linear distance with respect to ground level of the marker point at a relative height of 0.76 of the stem was reduced by 9%, whereas a reduction of 48% of the linear distance of this marker point was found for the maximum wind velocity measured (10 m/s). Therefore, under high wind loads, reconfiguration of the overall plant's shape resulted in streamlining.

DISCUSSION

Streamlining is a potentially important adaptation for withstanding high flow-induced loads. With intertidal seaweed, large flow-induced forces may occur within stands, highlighting the mechanical importance of streamlining as a general mechanism. For terrestrial plants, this is more frequently true for

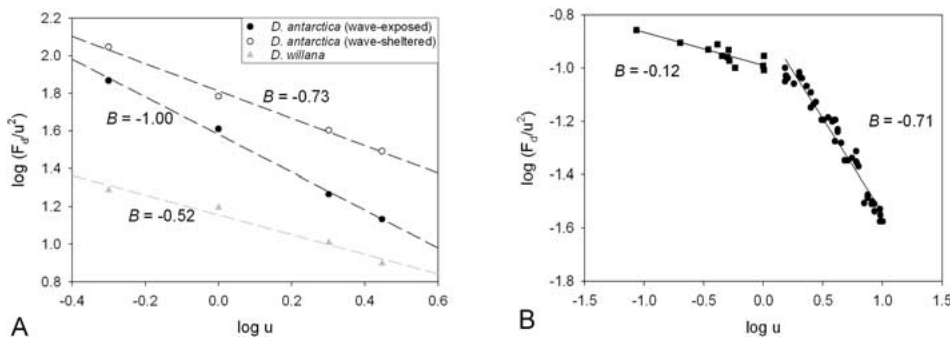


Figure 4. The way drag forces are minimized as velocity increases can be described by the Vogel number, B , determined by the slope of a regression line of the velocity-specific drag plotted against the velocity. **(A)** Drag tests on the southern bullkelp yielded small values for *Durvillaea willana* and larger values for *D. antarctica*. Grouped by morphotypes, wave-exposed individuals of *D. antarctica* had a more negative value of B . The relation between drag force and velocity is on average linear for the wave-exposed morphotype. **(B)** *A. donax*: The Vogel number for wind velocities between 0 and 1 m/s amounts to $B = -0.12$. For small velocities the drag force increased approximately with the velocity squared. Beyond a threshold velocity of about 1.5 m/s, however, the Vogel number was constant at $B = -0.71$, mirroring a nearly linear proportionality of drag and wind velocity.

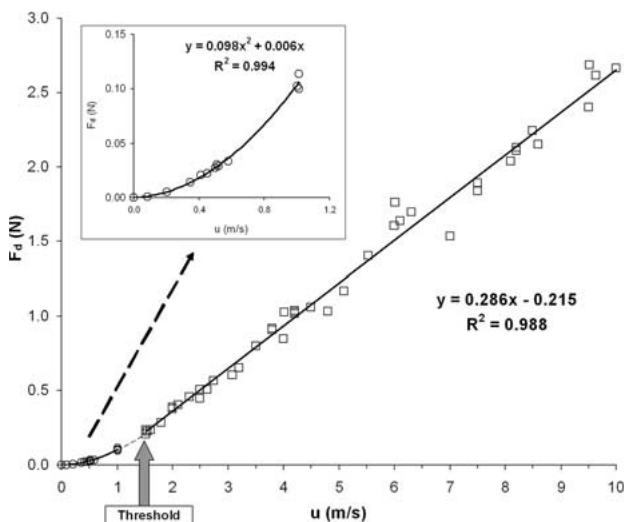


Figure 5. Wind speed plotted against drag force of an individualized giant reed. The drag force is calculated taking into account that the projected surface area is a function of wind speed. Subjected to small wind velocities up to 1.0 m/s, the drag on *A. donax* was in good approximation proportional to the square of the ambient wind speed (see insert). However, beyond a threshold value of 1.5 m/s, a nearly linear proportionality resulted (adapted from Speck, 2003).

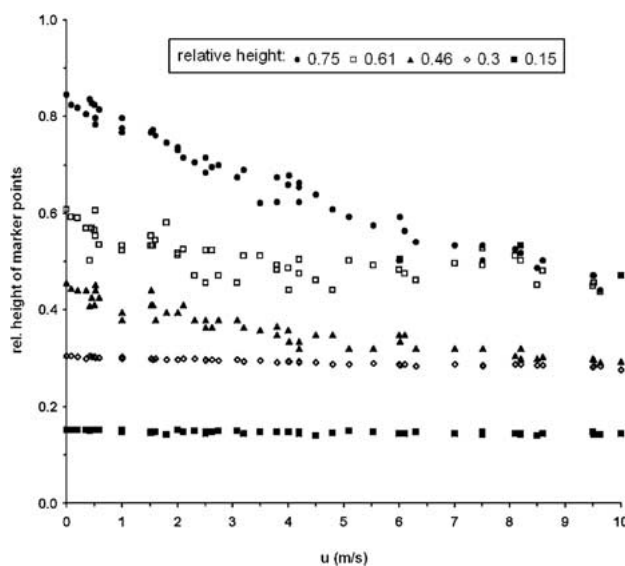


Figure 6. Wind velocities plotted against the relative height of five marker points on the stem of the plant with respect to ground level. 0 indicates the base of the plant and 1 the apical tip.

modelled stand of *D. antarctica* (Stevens and others 2004).

The lamina of *Durvillaea* floats at the surface under calm conditions, maximally spreading its photosynthetic active area. Currents and waves can cause the lamina to fold, resulting in self-shading. The degree of folding is thereby dependent on the morphotype because the wave-exposed morphology will reconfigure more easily into a three-dimensional body than the cape-like lamina of more sheltered individuals (Figure 1). For terrestrial

individual plants and plants at the edge of stands. Within dense stands, streamlining of individuals probably plays a minor role, as neighboring plants may interact and thus form a drag-reducing aerodynamic unit with higher wind velocities. This effect is also well known for compound leaves of trees (Vogel 1989), and has been studied analogly in a

plants, individual plants or plants at the edge have the advantage of increased light availability. In contrast, plants within stands are sheltered from wind but also partly from light by neighboring plants. The rapid process of passive reversible reconfiguration is therefore important for plants frequently subjected to flow to avoid excessive mechanical loads but also to reestablish maximum light interception once the loading subsides.

For both tested plant models, *D. antarctica* and *A. donax*, the mean of B ranged between -0.7 and -1 for high water and wind velocities, respectively, yielding an almost linear increase of drag with velocity. The Vogel numbers found in this study were similar to those reported from other work on flexible seaweeds (Gaylord and others 1994; Koehl 2000) and terrestrial plants (Vogel 1989) (Table 1). This may indicate that there is a general trend to decrease drag dynamically but passively with increasing flow velocities.

With *D. antarctica*, the least negative value of B was found for an individual plant that had a morphology reduced in 'bulkiness'—the thallus was very long but consisted of only a few thin strips of lamina (Figure 2). The previously well-adapted morphology had been disturbed by wave-induced damages. Therefore, the shape of the blade could not be further optimized with increasing flow velocity, as it already resembled a rope. Similarly, the shape of the watermoss *Fontinalis pyretica*, which may avoid overcritical loads by 'escaping' into the boundary layer, can apparently not be further optimized by fast reconfiguration processes, resulting in drag forces increasing linearly with length, but to the square of the velocity (Biehle and others 1998). The most negative Vogel number was found for an individual plant with a wave-exposed morphology and a lamina subdivided into many strips and no apparent damage. This type of morphology seems to be optimized for rapid passive reconfiguration under very unsteady flow conditions. The most effective reconfiguration process and subsequent reduction in drag will probably be achieved only for a limited range of aspect ratios.

Unfortunately, a more detailed analysis of the results reported from other studies is often prevented by a lack of data, for example, the behavior at different ranges of flow velocities, morphotypes, relevant Reynolds number, and so on. As could be seen by the morphotypical differences in *D. antarctica*, the fine-tuning of this adaptive process of reconfiguration is highly dependent on the ambient physical conditions. It is suggested, however, that plants frequently exposed to severe flow regimes will adapt to a Vogel number of approximately

$B = -1$ for high flow velocities, regardless of the respective surrounding medium.

Assuming a Vogel number of $B = -1$, the theoretical reduction in drag due to reconfiguration can easily be extrapolated (Figure 7). At a velocity of 5 m/s, the reduction due to reconfiguration is already greater than 50%. At a velocity of 10 m/s, the reduction is even greater than 75%. In comparison, for *A. donax*, a reduction of 54% for $u = 5$ m/s and 73% for $u = 10$ m/s (Figure 5) was found experimentally. Reconfiguration is therefore an effective general process of passive and dynamic adaptation on a small temporal scale to variable ambient conditions. More studies on different morphotypes of flow-exposed plants and drag reduction are required to confirm the general pattern suggested in our study.

The data set with respect to the Vogel number is still very patchy. Although quite a range of different growth forms and taxonomic groups are represented in Table 1, often there is a lack of information on some important parameters, for example, overall morphology, flow exposure, and range of typical and extreme velocities in a particular habitat. If the relevance of this reconfiguration process is as important as we suspect, more comparative studies need to be conducted. In particular, the morphology of tested plants should be subdivided qualitatively or quantitatively, if possible, into groups of different exposure (for example, "sheltered" vs. "very exposed"). The change in drag should be described for low velocities as well as for higher velocities so that a threshold velocity can be identified beyond which the Vogel number becomes stable. With this set of parameters, the ecobiomechanical constraints of flow-dominated habitats on plants can be characterized more profoundly.

In conclusion, this study showed the importance of reconfiguration as an adaptive process to minimize transient and irregular mechanical loads. Passive streamlining often results in the relation between drag forces and velocity being close to linear. Moreover, it is suggested that for severely exposed individuals, a Vogel number (above a threshold flow velocity) of approximately $B = -1$ is a possible prerequisite for a successful occupation of mechanically volatile habitats.

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Table 1. Quantitative Assessment of the Efficiency of Reconfiguration Processes of Different Plants and Test systems (adapted from Vogel 1994, Gaylord and others 1994, Voehl and others 2003). *u*: flow velocity; *B*: Vogel number.

Species	Shape	<i>u</i> (m/s)	<i>B</i>
Marine rhodophyta			
<i>Calliarthon tuberculosum</i> ⁷	branches	0.5–3.0	–0.34
<i>Chondracanthus exasperatus</i> ¹³	blade		–0.50
<i>Endocladia muricata</i> ³	bush	0.5–4.0	–0.48
<i>Gigartina exasperata</i> ¹¹	bush; far from substratum	0.1–0.5	–0.25
	bush; near substratum	0.1–0.5	–0.48
<i>Gigartina leptorhynchos</i> ⁷	bush	0.1–4.0	–0.52
		0.1–3.0	–0.55
<i>Gigartina spinosa</i> ⁷	bush	0.5–3.0	–0.10
<i>Iridaea flaccida</i> ^{3,7}	blade	0.5–4.0	–0.76
			–1.01
<i>Laurencia</i> sp. ⁷	branches	0.5–3.0	–0.27
<i>Mastocarpus jardinii</i> ³	branches	0.5–4.0	–0.28
<i>Mastocarpus pappilatus</i> ³	branches	0.5–4.0	–0.38
<i>Microcladia</i> sp. ⁷	feathery branches	0.5–3.0	–0.16
Marine phaeophyta			
<i>Durvillaea antarctica</i> ¹⁹	stipe and blades	0.5–2.8	–0.86
<i>Durvillaea willana</i> ¹⁹	stipe and blades	0.5–2.8	–0.93
<i>Egregia menziesii</i> ⁷	long feathery strap	0.5–3.0	–0.49
<i>Eisenia arborea</i> ⁴	stipe and blades	0.2–0.6	–0.68
<i>Fucus distichus</i> ³	branches	0.5–4.0	–0.50
<i>Hedophyllum sessile</i> ¹	blades	0.5–2.5	–0.32
<i>Nereocystis luetkeana</i> ⁹	long stipes and blades	1.3–2.0	–1.11
		1.3–2.0	–0.73
		0.5–1.5	–1.20
		0.25–0.75	–0.75
<i>Pelvetia fastigiata</i> ²	branches	0.5–4.0	–0.33
<i>Pelvetiopsis limitata</i> ⁶	branches	0.5–3.0	–0.48
<i>Postelsia palmaeformis</i> ⁶	stipe and blades	0.5–3.0	–0.30
<i>Sargassum filipendula</i> ¹⁵	branches	0.2–1.5	–1.06
Freshwater algae			
<i>Audouinella violacea</i> ¹⁵	filamentous	0.2–0.75	–0.92
<i>Batrachospermum boryanum</i> ¹⁵	filamentous	0.2–0.75	–0.33
<i>Batrachospermum moniliforme</i> ¹⁵	filamentous	0.2–0.75	–0.65
<i>Batrachospermum virgatum</i> ¹⁵	filamentous	0.2–0.75	–0.45
<i>Chara intermedia</i> ¹⁴	filamentous	0.2–0.35	~–0.5
<i>Lemanea fucina</i> ¹⁵	filamentous	0.2–0.75	–0.83
<i>Sirodotia suecica</i> ¹⁵	filamentous	0.2–0.75	–1.27
<i>Tuomeya americana</i> ¹⁵	filamentous	0.2–0.75	–0.64
Freshwater embryophytes			
<i>Antipyretica fontinalis</i> ²	stalk and leaves	0.1–0.5	~0
<i>Callitriche</i> sp. ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Ceratophyllum demersum</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Elodea canadensis</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Myriophyllum spicatum</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Najas marina</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Potamogeton natans</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Potamogeton obtusifolius</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Potamogeton pectinatus</i>	stalk and leaves	0.2–0.35	~–0.5
<i>Potamogeton pusillus</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Ranunculus fluitans</i> ¹⁶	stalk and leaves	0.5–1.5	~–1
<i>Utricularia vulgaris</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5
<i>Zannichellia palustris</i> ¹⁴	stalk and leaves	0.2–0.35	~–0.5

(Continued)

Table 1. Continued.

Species	Shape	u (m/s)	B
Terrestrial woody grasses			
<i>Arundo donax</i> ¹⁹	stalk and leaves	0.0–1.0 1.5–10.0	-0.12 -0.71
Trees			
<i>Acer rubrum</i> ¹⁸	leaf cluster	10–20	-0.64
<i>Carya glabra</i> ¹⁸	leaf	10–20	-0.78
<i>Ilex opaca</i> ¹⁷	leaf	8–19	-1.30
<i>Juglans nigra</i> ¹⁸	leaf	10–23	-0.76
<i>Liriodendron tulipifera</i> ¹⁸	leaf	10–24	-0.91
<i>Pinus sylvestris</i> ¹⁷	branch	9–38	-0.72
<i>Pinus taeda</i> ¹⁷	branch	8–19	-1.16
<i>Populus alba</i> ¹⁸	leaf cluster	10–20	-0.60
<i>Quercus alba</i> ¹⁸	leaf cluster	10–20	-0.44
<i>Quercus phellos</i> ¹⁸	leaf cluster	10–20	-1.06
<i>Robinia pseudoacacia</i> ¹⁸	leaf	10–20	-0.52

¹Armstrong 1989, ²Biehle and others 1998, ³Carrington 1990, ⁴Charters and others 1969, ⁵Dudgeon and Johnson 1992, ⁶Friedland and Denny 1995, ⁷Gaylord and others 1994, ⁸Gaylord and Denny 1997, ⁹Johnson and Koehl 1994, ¹⁰Kawamata 2001, ¹¹Koehl 1984, ¹²Koehl and Alberte 1988, ¹³Koehl 2000, ¹⁴Schutzen and Davy 2000, ¹⁵Sheath and Hambrook 1988, ¹⁶Usherwood and others 1997, ¹⁷Vogel 1984, ¹⁸Vogel 1989, ¹⁹present study.

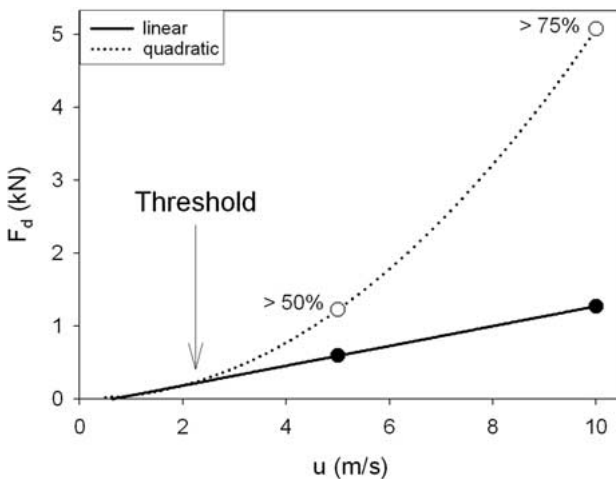


Figure 7. Theoretical model of extent to which drag forces can be minimized by reconfiguration, assuming $B = -1.0$. Beyond a certain threshold velocity, drag is considerably reduced if drag forces increase linearly with velocity rather than to the second power of the velocity. At a velocity of 5 m/s, drag forces can thus be reduced by more than 50%, at a velocity of 10 m/s, the reduction is already more than 75%.

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