

Biomechanics of aquatic plants and its role in flow-vegetation interactions

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ABSTRACT: The reconfiguration of aquatic plants in water flow to reduce drag forces strongly depends on their ability to withstand bending and tension forces and as a consequence on their biomechanical properties. We studied the relation between biomechanical traits and flow conditions with tension, bending and cyclic loading/unloading tests on the stems of four river plant species inhabiting a spectrum from low to high flow velocities: *Glyceria fluitans*, *Ranunculus penicillatus*, *Myriophyllum alterniflorum* and *Fontinalis antipyretica*. The length, diameter, cross-sectional area and second moment of area of the stems were determined with an image analysis software from captured photos of stems and stem cross-sections. Uniaxial tension tests were performed by measuring the force-displacement curve during extension and calculating breaking force, breaking stress, breaking strain, work of fracture and 'tension' Young's modulus. From uniaxial three-point bending tests flexural rigidity and 'bending' Young's modulus were calculated. Under high water velocities plants have flexible stems with a low 'bending' Young's modulus and flexural rigidity and a high 'tension' Young's modulus, breaking force and breaking stress. In habitats with less fierce flow plants possess less flexible stems with lower breaking stresses and breaking forces. The most rigid stems are found for plant species in slow-flow habitats. These characteristics have further implications for the reconfiguration of leaves and stems to alter drag forces, mass-transfer at the leaf surface and turbulence dynamics around plant stems, individual plants and plant patches. This study allows determining critical flow conditions under which invasive, exotic species can be eradicated or rare, protected species can be preserved.

Keywords: *Biomechanics, Macrophyte, Hydraulic resistance, Plant reconfiguration, Drag force, Bending, Tension, Cyclic loading/unloading, Young's modulus, Flexural rigidity, Breaking force*

1 INTRODUCTION

Water plants in many riverine ecosystems occur in a wide range of habitats. To a large part, freshwater macrophyte distribution in streams is governed by the physical environmental conditions, especially flow velocities and associated drag forces acting on the plants. To persist and grow under certain flow conditions stream macrophyte species have developed specific morphological and biomechanical adaptations. Under high flow velocities aquatic plants show shape reconfiguration, i.e. they become more compressed and adopt a streamlined shape, thereby reducing their drag coefficient (Sand-Jensen 2003, O'Hare et al. 2007). A strong reconfiguration under high flow velocities reduces the drag forces acting on an organism, e.g. a plant species (Vogel 1994), and hence its hydraulic resistance. Floodings due to an increase

in hydraulic resistance by massively growing freshwater plants are of major economical concern.

The ability of a plant shoot to reconfigure largely depends on its biomechanical traits, especially its bending and tensile properties. Although a large amount of research on this has been done so far with a focus on terrestrial plants (Niklas 1992, Schulgasser & Witztum 1997, Niklas et al. 2006), studies on aquatic plants are rare and focused on marine plant species, especially seagrasses (Patterson et al. 2001, Davies 2007, Fonseca et al. 2007) and macro-algae (Boller and Carrington 2007, Harder et al. 2006, Mach et al. 2007).

Marine seagrasses and macro-algae have evolutionarily adapted to resist high, oscillating wave forces (Boller & Carrington 2007, Patterson et al. 2001). Their stems (or stipes for ma-

cro-algae) have a high breaking strength and high flexibility. Comparable adaptations to wave forces have been found for freshwater plants in lakes (Brewer & Parker 1990, Schutten et al. 2005, Etnier & Villani 2007)

However, in rivers, water flow is unidirectional and in order not to be washed away downstream and to keep their position, forces exerted by water flow on plants have to be balanced by the bending, tension and dampening biomechanical characteristics of the plant. If the biomechanical properties of river plant species are known, their persistence and growth under specific flow conditions can be predicted. This is important for the preservation of rare native species or for the destruction of invasive species. In this study we investigated the relation between the biomechanical properties of four freshwater macrophyte species (*Ranunculus penicillatus*, *Myriophyllum alterniflorum*, *Glyceria fluitans* and *Fontinalis antipyretica*) from Northeastern Scotland and their occurrence in river habitats that are varying in their flow characteristics, ranging from high to low water velocities. The biomechanics of plant stems were investigated with tension and bending tests and analysed with respect to the species-specific habitat conditions in order to understand their adaptations to water flow.

2 MATERIALS AND METHODS

2.1 Experimental preparation

The tension and bending properties of the stems of the four species *G. fluitans*, *R. penicillatus*, *M. alterniflorum* and *F. antipyretica* (Fig. 1), collected from 9 March to 27 April 2009 in streams around Aberdeen (Scotland), were studied using a Hounsfield S-series bench top testing machine Model H10K-S UTM with a 100 N load cell. Contrary to homogeneous materials, composite (i.e. inhomogeneous) materials such as plant tissues (Niklas 1992) may show different results for the Young's modulus determined from tension and bending tests, since tissue structure and properties differ when measured along and across the plant stem. Hence we refer to the Young's moduli derived from tension and bending tests as 'tension' (E_t) and 'bending' (E_b) Young's modulus, respectively.

Due to slippage of the stem between the clamps, only 'tension' Young's modulus, but not breaking stress, breaking force, breaking strain and work of fracture could be measured during the tension tests of *G. fluitans*. The bending tests were not conducted for *F. antipyretica*, since the

resolution and accuracy of the used 100 N load cell were too low to measure the small forces during the bending of the highly flexible *F. antipyretica* stems.

For each plant stem three stem sections from the bottom, middle and top of the stem were cut. For tension and bending tests stem diameter to length ratios of 1:10 and 1:15 were used to minimise the effect of shear stress when measuring 'tension' and 'bending' Young's modulus. The stem section length for tension and bending tests was standardised to 25 mm and 45 mm for *F. antipyretica*, *M. alterniflorum* and *R. penicillatus*

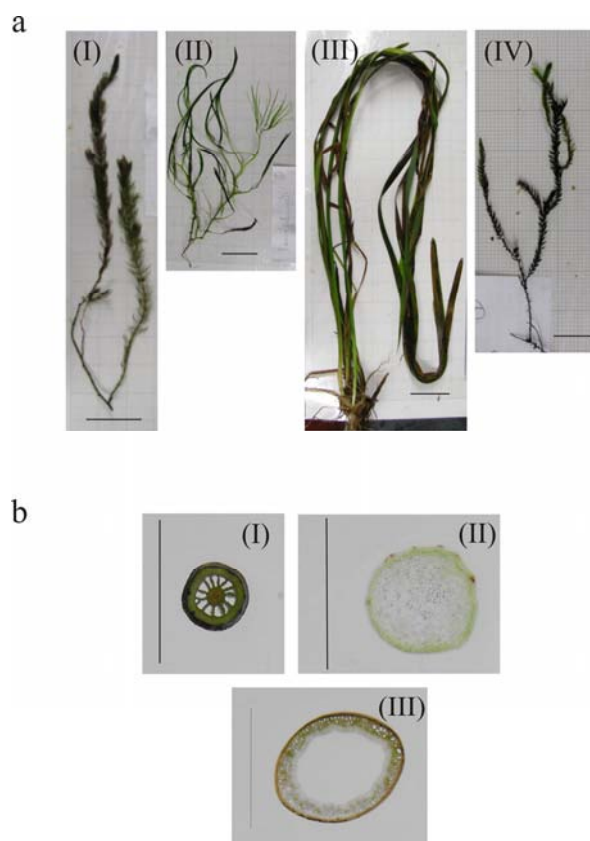


Fig. 1. Morphology of shoots (a) and stem cross-sections (b) of *M. alterniflorum* (I), *R. penicillatus* (II), *G. fluitans* (III) and *F. antipyretica* (IV). The bars in a and b have a length of 2 cm and 4 mm, respectively. *F. antipyretica* stems were very small in diameter (mm) so that no cross-sectional areas could be measured.

and 50 mm and 70 mm for *G. fluitans*, respectively. A length of 10mm was provided on the end of each stem part for fixation to the testing device. Cross-sections of *M. alterniflorum*, *R. penicillatus* and *G. fluitans* with a thickness thinner than 1 mm were cut with a razor-blade and pictures of cross-sections were taken with a photo camera (Fuji FinePix S1000fd, Fujifilm, Tokyo, Japan) on a light table (Illuma System, Bencher Inc., Chicago, U.S.A.). *F. antipyretica* stems were too thin to dissect and hence pictures of the whole stem to measure the diameter were taken. Cross-sectional area and diameter mea-

measurements were taken with the software Makrophyt (developed by the University of Konstanz, Konstanz, Germany). Two cross-sectional areas from each end of a plant stem section were measured. At each end of the thin *F. antipyretica* stem sections two diameters were measured. Subsequently, the cross-sectional areas were calculated as $A = \pi d^2/4$ where A = cross-sectional area and d = diameter. From the four measured values of the cross sectional area the mean cross sectional area for each plant stem section was calculated. For uniaxial tension tests the ends of the stem parts were glued into 10 mm long brass tubes with cyanoacrylate glue to protect the plant tissue against mechanical deformation when clamped into the testing device.

2.2 Tension tests

The ends of each stem section were placed into friction grips, which trap the stem between a rough textured sprung cylinder and a piece of sand paper, and stretched at a displacement rate of 10 mm min^{-1} until the breakage of the stem. The Hounsfield (now: Tinius Olsen, Salfords, UK) computer software recorded a force - displacement curve to determine the breaking force.

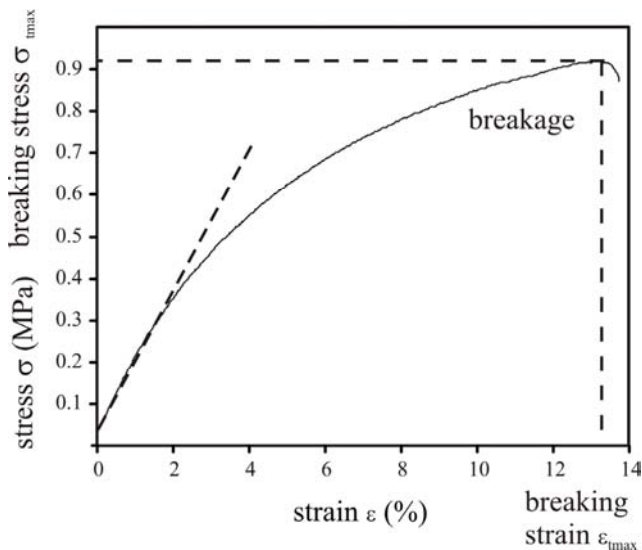


Fig. 2. Stress-strain curve and calculated biomechanical parameters from a tension test performed on a *R. penicillatus* stem piece. The slope of the initial linear part of the curve is used to calculate the 'tension' Young's modulus.

Subsequently the force-displacement curve was transformed into a stress-strain curve (Fig. 2) with $\epsilon = \delta/L$, $\sigma = F/A$, ϵ = strain (m m^{-1}), δ = displacement (m), L = length of the stem piece (m), σ = stress (N m^{-2}), F = force (N) and A = cross-sectional area (m^2). From this curve the 'tension' Young's modulus E_t was determined as the slope of the initial linear part. Breaking strength σ_{tmax} was obtained as the maximum nominal stress, breaking strain ϵ_{tmax} as the maximum nominal strain and the area under the stress-strain curve

until breakage (work of fracture per volume ($[W/V]_{\text{break}}$) in J m^{-2}) were also calculated.

2.3 Bending tests

A metal bar was lowered from above on a stem part that was located centrally on two support bars at a displacement rate of 10 mm min^{-1} . The vertical deflection Δ in mm and the corresponding force F in N were recorded (Fig. 3). The flexural rigidity $EI = (s^3F)/(48\Delta)$ was calculated from the slope of the force-deflection curve, using s as the horizontal span of stem.

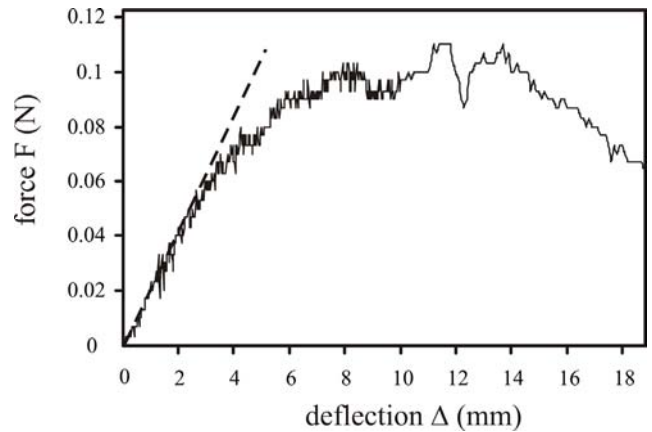


Fig. 3. Force-displacement curve from a bending test performed on a *R. penicillatus* stem piece. The slope of the initial linear part of the curve is used to calculate the 'bending' Young's modulus.

The second moment of area was calculated as $I_c = \pi r^4/4 = \pi d^4/64$ for a circular cross-section (*F. antipyretica*, *M. alterniflorum* and *R. penicillatus*, r = stem radius = $d/2$, d = stem diameter) and as $I_e = (a^3b - a_1^3b_1)\pi/4$ for a hollow elliptic cross-section (*G. fluitans*, a = conjugate radius, b = transverse radius, a_1 = inner conjugate radius, b_1 = inner transverse radius). From the flexural rigidity EI and the second moment of area I the 'bending' Young's modulus E_b was calculated as $E_b = EI/I_c = ((s^3F)/(48\Delta))/(\pi d^4/64) = (4s^3F)/(3\Delta\pi d^4)$ for a circular cross-section and as $E_b = EI/I_e = ((s^3F)/(48\Delta))/((a^3b - a_1^3b_1)\pi/4) = (s^3F)/(12\Delta\pi (a^3b - a_1^3b_1))$ for hollow elliptic cross-sections.

2.4 Statistical analyses

A one-way analysis of variance (ANOVA) was performed with SAS 9.1 to analyse differences in biomechanical parameters between the species.

3 RESULTS

3.1 Tension tests

The stress-strain curves of all species have a characteristic shape (Fig. 2), with an initial linear part, which is used for the calculation of the ‘tension’ Young’s modulus and then a gradually flattening slope until breakage occurs at maximum breaking stress (Fig. 2). *G. fluitans* as the strongest species has a significantly higher ‘tension’ Young’s modulus than the other three species. Breaking stress, breaking strain, breaking force and work of fracture could only be measured for *F. antipyretica*, *M. alterniflorum* and *R. penicillatus*, since *G. fluitans* slipped inside the clamps or the brass tubes at high forces. ‘Tension’ Young’s modulus, breaking stress and work of fracture were significantly different between the species (Table 1).

All three parameters were highest for *F. antipyretica*, medium for *M. alterniflorum* and lowest for *R. penicillatus*, at least partially as a consequence of the small stem diameter of *F. antipyretica* stems (Table 1). The breaking force was significantly larger for *R. penicillatus* than for both *F. antipyretica* and *M. alterniflorum* (Table 2). The highest breaking strain, i.e. the highest extension before breakage, was found for *M. al-*

terniflorum, being significantly higher than for *R. penicillatus* (Table 2).

3.2 Bending tests

Since no bending tests to calculate the flexural rigidity and the ‘bending’ Young’s modulus of *F. antipyretica* could be performed due to the sensitivity of the used load cell which was too low, we can assume that *F. antipyretica* had the highest flexibility of all four studied species. For the other three species the ‘bending’ Young’s modulus and the flexural rigidity were calculated from the slope of the initial part of the force-displacement curve (Fig. 3). However, no breakage occurred, since the flexible stems at the end of the experiment slipped from the bars of the experimental setup.

The ‘bending’ Young’s modulus of *R. penicillatus* was significantly lower than that of *M. alterniflorum* and *G. fluitans*. *G. fluitans* is the stiffest species, having a significantly higher flexural rigidity than *M. alterniflorum* and *R. penicillatus* due to its higher second moment of area. *G. fluitans* has the highest second moment of area of all four species as a consequence of the large stem diameter (Table 1). This compensates for its hollow stem which would lead to a reduced second moment of area when compared to a solid stem with a similar diameter.

Table 1: Mean \pm S.D. of the morphological and biomechanical characteristics of the studied species *R. penicillatus*, *M. alterniflorum*, *G. fluitans* and *F. antipyretica* (n=30) and velocity ranges for the river sections where the respective plant species were sampled. Please note that we report here values for flexural rigidity (EI) obtained from bending tests which provided direct measurements of EI. # For the hollow elliptically shaped *G. fluitans* stems the transverse diameter, calculated as two times the transverse radius b (see Materials and Methods section, Bending tests) is given here. ## Since no bending tests were performed for *F. antipyretica* the second moment of area calculations are based on diameters measured in stems for tension tests

parameter	unit	Mean \pm S.D.			
		<i>G. fluitans</i>	<i>F. antipyretica</i>	<i>R. penicillatus</i>	<i>M. alterniflorum</i>
Mean diameter	mm	4.03 \pm 0.54 [#]	0.44 \pm 0.053	2.39 \pm 0.39	1.59 \pm 0.19
Mean area	mm ²	6.79 \pm 2.09	0.15 \pm 0.037	4.19 \pm 1.5	1.78 \pm 0.58
‘Tension’ Young’s modulus	MN m ⁻²	80.84 \pm 27.5	379.1 \pm 146.16	14.8 \pm 5.7	19.3 \pm 16.21
Breaking stress	kN m ⁻²	-	19338.8 \pm 5858.58	972.9 \pm 276.63	1820.2 \pm 612.61
Breaking strain	%	-	14.46 \pm 3.73	12.86 \pm 3.75	15.87 \pm 4.47
Breaking force	N	-	2.94 \pm 0.94	3.82 \pm 1.15	3.11 \pm 0.94
Work of fracture	kJ m ⁻³	-	1814.64 \pm 814.51	87.36 \pm 38.27	194 \pm 62.38
‘Bending’ Young’s modulus	MN m ⁻²	89.82 \pm 33.07	-	12.53 \pm 7.12	89.43 \pm 37.63
Second moment of area	mm ⁴	8.39 \pm 4.07	0.0017 \pm 0.00084 ^{##}	1.8 \pm 0.96	0.3 \pm 0.13
Flexural rigidity	N mm ²	678.14 \pm 276.94	-	21.57 \pm 14.26	25.22 \pm 10.68
Velocity	m s ⁻¹	0.28 – 0.47	0.59 – 0.64	0.85 – 1.14	0.73 – 0.91

Table 2: Comparison of the morphological and biomechanical stem characteristics that are described in Table 1 between the four studied species *R. penicillatus*, *M. alterniflorum*, *G. fluitans* and *F. antipyretica* with an one-way ANOVA. Values that are significantly different between the species are indicated by A, B, C and D. Please note that we report here values for flexural rigidity (EI) obtained from bending tests which provided direct measurements of EI. # For the hollow elliptically shaped *G. fluitans* stems the transverse diameter, calculated as two times the transverse radius *b* (see Materials and Methods section, Bending tests) is given here. ### Since no bending tests were performed for *F. antipyretica* the second moment of area calculations are based on diameters measured in stems for tension tests.

parameter	df	F	p	Duncan test result			
				<i>G. fluitans</i>	<i>F. antipyretica</i>	<i>R. penicillatus</i>	<i>M. alterniflorum</i>
Mean diameter	3	952.12	<0.0001	A [#]	D	B	C
Mean area	3	753.18	<0.0001	A	D	B	C
'Tension' Young's modulus	3	317.62	<0.0001	B	A	D	C
Breaking stress	2	1164.54	<0.0001	-	A	C	B
Breaking strain	2	3.36	0.05	-	AB	B	A
Breaking force	2	4.81	0.0163	-	B	A	B
Work of fracture	2	425.37	<0.0001	-	A	C	B
'Bending' Young's modulus	2	155.37	<0.0001	A	-	B	A
Second moment of area	3	785.65	<0.0001	A	D ^{###}	B	C
Flexural rigidity	2	256.71	<0.0001	A	-	B	B

4 DISCUSSION

In this study the biomechanical properties of *G. fluitans*, *M. alterniflorum* and *R. penicillatus* were analysed in detail for the first time. For *F. antipyretica* some preliminary data on tension and bending characteristics already exist (Biehle et al. 1998).

In general our tension and bending experiments on *F. antipyretica* resulted in values comparable to those achieved by Biehle et al. (1998). Biehle et al. (1998) found significant differences in 'tension' Young's modulus between specimens from two river sites differing in flow velocities with values of $488 \pm 160 \text{ MN m}^{-2}$ at slow flow (0.04 m s^{-1}) and $633 \pm 171 \text{ MN m}^{-2}$ at high flow (0.66 m s^{-1}). Interestingly our value for the 'tension' Young's modulus of $379.1 \pm 146.16 \text{ MN m}^{-2}$ (Table 1) is closer to that of plants sampled at the slow flow site although measured flow velocity in our study was appr. 0.61 m s^{-1} at the site, where *F. antipyretica* was sampled. Since the study of Biehle et al. (1998) was conducted in a different geographical region, in Southern Germany, this observed discrepancy in the 'tension' Young's modulus might be due to differences in environmental and climatic conditions. However, we have to take into account that the 'tension' Young's modulus in our study has a high standard deviation, so that it might hence be not statistically different from the 'tension' Young's modulus value for the high flow habitat of the study of Biehle et al. (1998).

For the genus *Ranunculus* Usherwood et al. (1997) compared several terrestrial, amphibious and aquatic species and found a strongly de-

creased 'tension' Young's modulus and flexural rigidity in the aquatic species *Ranunculus fluitans*. Values for breaking stress, breaking strain, 'tension' Young's modulus, 'bending' Young's modulus, second moment of area and flexural rigidity of the related species *R. fluitans* were very similar to those for *R. penicillatus* in our study.

An interesting aspect offers the comparison of the Young's modulus calculated on the basis of tension ('tension' Young's modulus) and bending tests ('bending' Young's modulus). For *G. fluitans* and *R. penicillatus* both Young's moduli were similar, so that we can regard the tissues of these species as consisting of reasonably homogeneous materials. The stems of *G. fluitans* are hollow, whereas *R. penicillatus* stems are solid, i.e. completely filled with cellular material (Fig. 1). In contrast to this, the 'bending' Young's modulus of *M. alterniflorum* is more than four times higher than its 'tension' Young's modulus, suggesting inhomogeneity in plant tissue structure. A possible explanation is the 'wheel'-like cross-sectional structure of *M. alterniflorum* stems (Fig. 1), where large air-filled spaces occur between elongated tissue structures that are extending distally until the stem surface. This structure might strengthen the stem more against bending than against tension forces. The cross-sectional structure of macrophyte stems with regard to the Young's modulus should be studied in more detail and by employing analyses comparing 'bending' and 'tension' Young's modulus of a range of macrophyte species.

The found biomechanical traits enable the plant species to grow and survive in the flow environments, which they inhabit. The four species inhabit a gradient from low to high flow veloci-

ties: Whereas *G. fluitans* lives in slow-flowing streams (Preston & Croft 2001), *F. antipyretica* preferentially grows in fast-flowing mountain streams (Haslam 2006). *M. alterniflorum* and *R. penicillatus* can be found in flow velocities ranging between the habitats of these two species. The adaptations to their typical habitats are reflected in their biomechanical characteristics to resist flow forces.

G. fluitans as an aquatic grass that can grow also emerged has a high 'tension' Young's modulus and is very rigid, since it has a high flexural rigidity. The latter is caused by the high 'bending' Young's modulus and a high second moment of area of the *G. fluitans* stems, which are hollow, but have a large diameter. Hence *G. fluitans* is adapted to survive and grow in slowly flowing burns, where the development of emerged, upright growing terrestrial shoots for reproduction is possible. At high flow velocities tension forces become dominant in determining plant biomechanical and morphological properties. *F. antipyretica* is the most flexible of the four species, since its flexural rigidity and 'bending' Young's modulus could not be calculated as the sensitivity of the load cell was too low. It has the highest 'tension' Young's modulus as well as a higher breaking stress and work of fracture than *M. alterniflorum* and *R. penicillatus*. This enables *F. antipyretica* to survive even in swiftly flowing mountain streams (Haslam 2006). Although *M. alterniflorum* and *R. penicillatus* show the lowest values of 'tension' Young's modulus, breaking stress and work of fracture, the flexural rigidity and the second moment of area of both species ranges between the values for *G. fluitans* and *F. antipyretica*. The intermediate flexural rigidity together with the weak traits to resist forces (Table 1 and 2) allows *M. alterniflorum* and *R. penicillatus* to grow in the middle reaches of rivers with moderate flow velocities, where they are often found in coexistence (Haslam 2006).

The above considerations support the concept of tensile and bending plants introduced by Nikora (2010). Plant with a high flexural rigidity (bending plants, e.g. *G. fluitans*) experience mainly pressure drag since they are growing more upright in the water column. In contrast, plants with a low flexural rigidity (tensile plants, e.g. *F. antipyretica*) are mainly subject to viscous drag forces as they follow the flow. From an evolutionary perspective the biomechanical properties of freshwater macrophytes are constantly changing through evolutionary processes and selection pressures. A plant species under exposure to enhanced flow forces will evolve within its specific developmental constraints

from a bending to a tensile plant. It will become increasingly flexible thereby avoiding bending forces and it will become resistant to breakage and deformation by tensile forces.

The results of our study will be of use to predict under which flow conditions specific plant species will survive and grow. Hence precise measures can be taken to eradicate invasive species or to protect endangered native species. As floodings due to increased hydraulic resistance by a massive growth of river macrophytes can cause major economical damage, our results will be widely applicable to model plant population growth and to estimate hydraulic resistance in order to take specific and precise decisions in the management of streams and rivers.

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