



Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments

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Abstract

The mechanical adaptations of the stems of four species of *Ranunculus* to their respective environments were studied by combining tensile, bending and flow-tunnel tests, with anatomical observation.

Stems of the two terrestrial species, *R. acris* and *R. repens*, had high values for rigidity, *EI*, because they were stiffened by large quantities of peripherally placed lignified material. This trend is less evident in *R. repens*, which had a lower rigidity, though it withstood a higher breaking strain than *R. acris*. This may adapt *R. repens* to its creeping habit and help it withstand trampling.

The aquatic *R. peltatus* and *R. fluitans*, which live in still and fast-flowing water, respectively, are both more flexible and have higher breaking strains, of 0.1–0.15, than terrestrial plants, which may allow them to withstand sudden tugs due to flow. *R. peltatus* maintains the central lumen, places structural elements away from the centre, and has a higher rigidity than *R. fluitans*, which may allow it to avoid self-shading, and support itself when the water level falls.

The stem of *R. fluitans* shows adaptations for withstanding drag from fast-flowing water. The stem has a low rigidity which allows it to minimize inertial drag forces by aligning itself parallel to the direction of the local flow. However, the rigidity (and the second moment of area, *I*) does not appear to be minimized. This may allow the plant to avoid drag due to flag-like fluttering. A weak region of the stem near the base may act as a 'mechanical fuse' which protects the root system by allowing seasonal growth to be lost.

Key words: *Ranunculus*, mechanics, flow, anatomy.

Introduction

The mechanical design of stems in terrestrial plants (Haberlandt, 1914; Gordon, 1978; Vincent and Jeronimidis, 1991; Ennos, 1993; Speck, 1993; Spatz and Speck, 1994), aquatic vascular plants (Haberlandt, 1914; Fritsch and Salisbury, 1938), and the stipes of marine algae (Koehl and Wainwright, 1977; Vincent and Gravell, 1986), has been the subject of much research. Most authors have emphasized the importance, in land plants, of placing structural material such as collenchyma, vascular bundles and sclerenchyma, away from the neutral axis and towards the perimeter. This will increase the bending rigidity and strength of aerial stems, helping them stand up and support leaves and flowers. In contrast, it has been noted that, in marine algae and aquatic vascular plants which are supported by buoyancy, the structural material is placed nearer the centre, where it may better withstand tensile forces imposed by waves or currents. However, the plants discussed by these authors come from a wide range of often distantly related groups so it is difficult to tell whether these differences are truly adaptive.

In this study, therefore, the anatomy and mechanical characteristics of the stems of each of four species within the single genus *Ranunculus* have been investigated, making it possible to determine whether these plants show adaptive differences which are related to differences in their natural environments. This intra-generic study should be able to distinguish between incidental differences due to phylogeny, and differences due to selection for mechanically adaptive forms.

Species within the genus *Ranunculus* certainly show extensive morphological adaptations for life in very different habitats. The meadow buttercup, *Ranunculus acris* L., has upright stems allowing it to compete

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effectively in moderately productive meadows (Grime *et al.*, 1990), whereas the creeping buttercup, *R. repens* L., is typical of disturbed and damp sites and survives trampling well (Clapham *et al.*, 1987), but rarely has self-supporting stems growing to the heights typical of *R. acris*. The water crowfoots grow under and on the surface of water in flow regimes ranging from stagnant to torrential. *R. peltatus* Schrank grows in still or slowly flowing streams, and has leaves which reach and may extend from the water surface. In contrast, *R. fluitans* Lam. grows typically in fast-flowing rivers prone to spate and is subject to regular washing out (Jeffries and Mills, 1990).

This study also investigates the way the mechanical properties of the stems of *R. fluitans* vary along their lengths, and relates these to measurements of drag made using a flow tunnel. Results of these tests may have some bearing on potential control methods for *R. fluitans*, and for its close relative, the economically important *R. penicillatus* var. *calcareus* (RW Butcher) CDK Cook, which frequently causes flooding (Westlake and Dawson, 1988; Dawson, 1989) by increasing the resistance of river channels.

Materials and methods

Samples of *Ranunculus acris* and *R. repens* were collected from disturbed sites around Hulme, Manchester. *R. peltatus* was collected from the River Ashop in the Peak District and *R. fluitans* was collected, with permission, from the River Bollin at Styal Country Park. All samples, particularly the aquatic species, were kept immersed in water until testing.

Mechanical tests were carried out on the basal 25 mm to 100 mm of the stems, using an Instron universal testing machine (model 4301) with a computer interface capable of simultaneously measuring applied force, F , and deflection, δ .

Tensile tests

Basal lengths of the stem were cut off the plant and their diameters measured using dial callipers. They were then clamped individually into the jaws of the Instron at their bases and at the first node, leaving a free length of 20–135 mm, and were then stretched at a rate of 10 mm min^{-1} until they broke. Fifteen different stems were tested in this way for each species. The computer produced a graph of applied force versus deflection which was used to calculate several different properties, both of the structure and of the material. The tensile strength, F_{\max} , is simply the maximum load the sample could withstand before breaking. The breaking stress and the breaking strain at yield could also be calculated. Stress, σ_{\max} , is given by the formula

$$\sigma_{\max} = 4F_{\max}/\pi D^2 \quad (1)$$

where D is the diameter of the stem. Breaking strain, ϵ_{\max} , is given by the expression

$$\epsilon_{\max} = \delta_{\max}/L \quad (2)$$

where δ_{\max} is the extension at which the stem broke and L is the original length of the sample.

The Young's modulus (in tensile tests, E_t) of each stem section was calculated by taking the initial, computer fitted

gradient $dF/d\delta$ from the force against displacement graph. It was calculated from the formula

$$E_t = 4LdF/\pi D^2 d\delta \quad (3)$$

Values of F_{\max} and δ_{\max} were considered reasonable only if the break in the sample occurred away from the clamping. The strength and form of samples from terrestrial species meant that, to prevent them from slipping from the clamps, clamping would have to be so firm that it severely damaged the structure. This meant that the only parameter which could be calculated for the terrestrial buttercups was the Young's modulus, E_t .

Three-point bending tests

Stem sections taken from the base of each stem were placed on metal supports, which were spaced a distance of at least 15 times the diameter apart, so that sample lengths were 75 mm and 25 mm for terrestrial and aquatic species, respectively (Fig. 1). An aluminium probe of end radius 5 mm was attached to the crosshead and lowered to the midpoint of the span until it just touched the sample. The probe was lowered at a rate of 10 mm min^{-1} thus bending the sample. The computer produced a graph of applied force versus deflection. Since bending such a structure involves stretching the bottom half and compressing the top half, this graph can be used to calculate several other properties of structure and material. The flexural strain at yield, ϵ_{flex} , is given by the expression

$$\epsilon_{\text{flex}} = 6\delta_{\max}D/S^2 \quad (4)$$

where S is the span. A computer-fitted slope, $dF/d\delta$, for the initial gradient of the force-extension graph was used to calculate the bending rigidity, $E_b I$, which is given by the equation

$$E_b I = S^3(dF/d\delta)/48 \quad (5)$$

(Gordon, 1978).

Since the second moment of area, I , for a circle is $\pi D^4/64$ and Rigidity = $E_b I$, a value for the Young's modulus derived

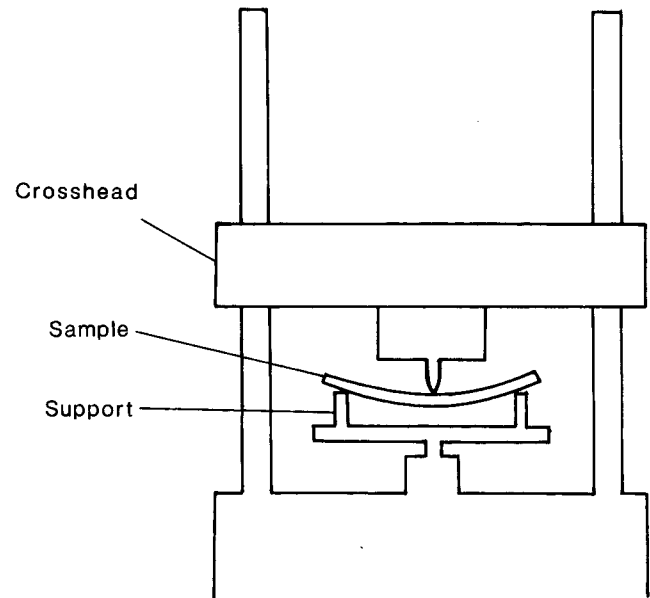


Fig. 1. Set-up for bending tests.

from bending tests, E_b , can be calculated using the following formula.

$$E_b = 4 S^3 (dF/d\delta) / 3\pi D^4 \quad (6)$$

Values of strain at yield were considered reasonable only for the terrestrial buttercups as the aquatic species were flexible enough to allow significant slippage, and be pushed completely inside the span without deforming plastically. Fifteen stems were tested for each species.

Paired tests

To determine more precisely how the Young's moduli of each species derived from tensile and bending tests differ, and to remove scatter due to within species variation, 15 sets of paired tensile and bending tests were also carried out on stems of all species except *R. peltatus*. First, tensile tests were performed, but only to a maximum of 10% of the average breaking strain for the aquatic species, or until the samples slipped in the case of the terrestrial samples. Bending tests were then done on the same samples, while avoiding the regions damaged by the clamping. It was impossible to use *R. peltatus* in paired tests, as both tensile and bending tests damaged the samples, even at small displacements.

Variation along the stem of *R. fluitans*

Seven tensile and three bending tests were performed on *R. fluitans* down its entire length. While bending tests could be performed on each of the 15 or 16 internodes from base to tip, alternate internodes had to be missed in the tensile tests in order to give room for clamping (thus providing eight testable internodes per plant).

Flow tunnel tests

Tests were carried out in a water flow tunnel of cross-section 305 mm (12"), 3 m long and with a maximum flow speed of 1.3 m s^{-1} . Complete *R. fluitans* samples were attached at their base to a probe using a small elastic band. The probe was joined to a moveable frame on a frictionless air bed. The frame was free to move on the airbed, a movement which was resisted only by a hacksaw blade with a strain gauge attached. This apparatus could then be used to measure the force due to water flow on the probe, with or without attached weed (Fig. 2). The drag of the weed would then be the difference between the drag on the probe with and without the sample. Two different sets of tests were performed. In the first, the drag of a single piece of weed of length 1480 mm was measured at seven different flow speeds from 0.44 m s^{-1} to 1.3 m s^{-1} . In the second, drag was measured on ten different weeds varying in length from 680 mm to 1620 mm exposed to flow of 1.3 m s^{-1} . In each case, the base of the sample was positioned as close to the bottom of the tank as possible, and in the middle of the stream.

The water speed both of the flow tank, and also of the River Bollin on 1 July, was measured by timing how long it took a piece of buoyant expanded polystyrene to travel 3 m.

Anatomy

Stem sections were cut using wet Wilkinson Sword double edged razor blades. Samples were supported during cutting in a piece of fresh carrot with a prepared groove, and were prevented from drying out during sectioning. Stem sections were stained with phloroglucinol or toluidene blue, to show up lignified material, and were studied using a dissecting microscope. Sections were differentiated into the parenchyma, the

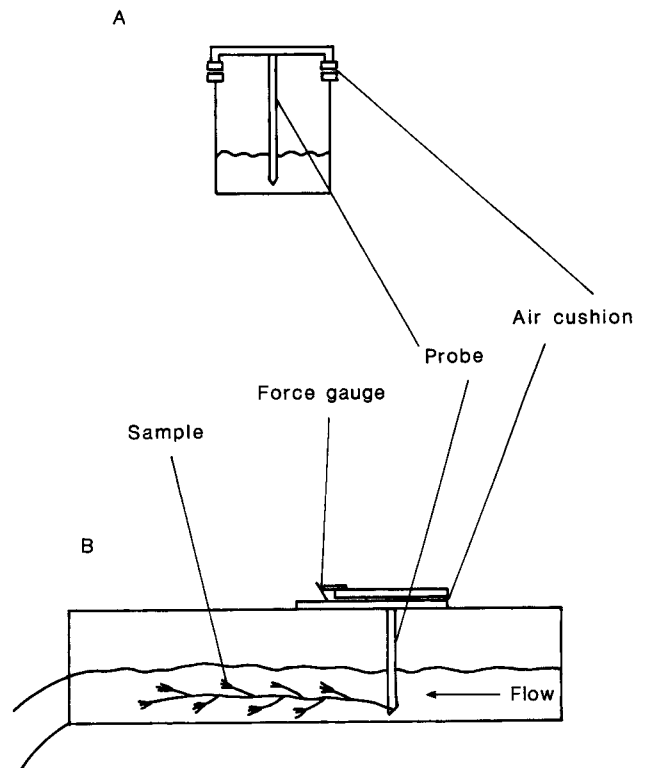


Fig. 2. Set-up for flow tunnel tests shown from the front (A) and side (B).

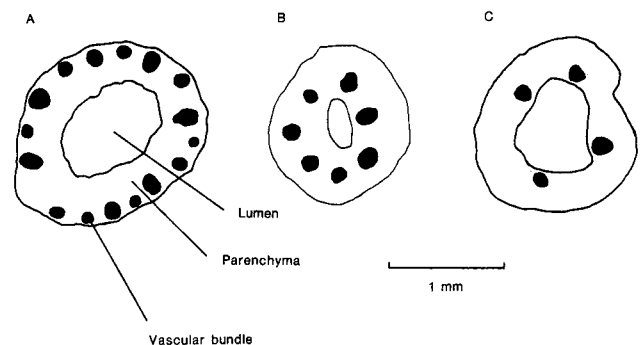


Fig. 3. Anatomy of transverse sections of stems, showing lumen, parenchyma and vascular bundles containing lignified tissue. *R. acris*, the meadow buttercup, shows placement of the structural elements around the perimeter, and a large central lumen. *R. repens* (B) and *R. peltatus* (C) show less extreme maximization of the second moment of area, I .

central lumen, vascular bundles and other lignified regions, and were drawn with the aid of a drawing tube.

Results

Bending and tensile tests

Mechanical properties of the stems of the four species are shown in Table 1. Terrestrial species, particularly *R. acris*, have high values for E_t , rigidity, and E_b , though *R. repens* has significantly lower values than *R. acris*, and can

Table 1. Mean properties (\pm s.d.) of stems calculated from mechanical tests

Differences between species, calculated using ANOVA, are significant at the $P < 0.05$ level in all cases except for E_b/E_t between *R. acris* and *R. repens*. E_t was significantly different from E_b within each species, except for *R. peltatus*. Missing values for *R. acris* and *R. repens* are due to damage on clamping associated with their structures and the high tensile breaking forces. Missing values for *R. peltatus* and *R. fluitans* are due to their flexibilities, which allowed them to deflect between the supports before yield was reached.

	<i>R. acris</i>	<i>R. repens</i>	<i>R. peltatus</i>	<i>R. fluitans</i>
Stem diameter (mm)	3.76 ± 0.99	3.84 ± 0.87	2.03 ± 0.266	1.45 ± 0.064
Mechanical property				
Tensile strength (N)			3.29 ± 0.86	2.26 ± 0.61
Maximum tensile stress ($\text{N m}^{-2} \times 10^{-6}$)			0.72 ± 0.20	1.98 ± 0.41
Maximum tensile strain			0.108 ± 0.515	0.152 ± 0.038
E_t ($\text{N m}^{-2} \times 10^{-6}$)	481.3 ± 138.6	76.5 ± 53	11.3 ± 1.97	42.3 ± 8.9
Initial rigidity, $E_b I$ ($\text{N m}^2 \times 10^{-6}$)	$12\,620 \pm 10\,561$	$2\,346 \pm 1\,892$	20.6 ± 12	10.5 ± 5
Bending strain at yield	0.016 ± 0.004	0.069 ± 0.027		
E_b ($\text{N m}^{-2} \times 10^{-6}$)	$1\,231 \pm 284$	165.6 ± 66.8	22.4 ± 15.3	46.8 ± 17.6
Paired tests				
E_b/E_t	2.51 (a) ± 0.612	2.53 (a) ± 0.984		0.768 (b) ± 0.180

withstand a higher bending strain before it yields. The aquatic species have low values for tensile strength, tensile stress, E_t , rigidity and E_b , while withstanding high tensile strains (0.10 for *R. peltatus* and 0.15 for *R. fluitans*, see equation 2 and Table 1) compared with the values for land plants (typically 0.02–0.03, see Vincent and Jeronimidis, 1991).

Anatomy

Figures 3 and 4 show typical cross-sections of the stems for each species, displaying the structurally important components. There are some notable differences. *R. acris* (Fig. 3A) has a large central lumen and structural elements placed around the perimeter. *R. repens* and *R. peltatus* (Fig. 3B, C) show less displacement to the perimeter and have relatively smaller lumens. Figure 4 displays the changes of structure down the stem of *R. fluitans* where even the small lumen present in central sections is lost at the base, which is solid.

Flow tank tests

Figure 5A shows that, at a flow rate of 1.3 m s^{-1} there is an approximately linear relationship between the length of a *R. fluitans* stem and the drag. The linear relationship

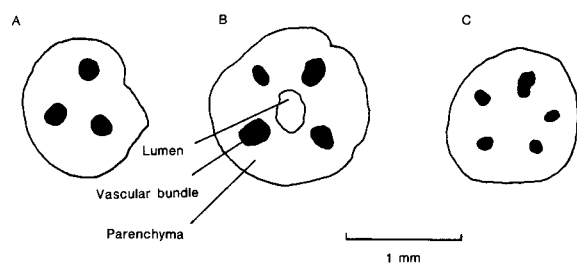


Fig. 4. Anatomy of transverse sections down the length of *R. fluitans*. The base (A) and tip (C) has no lumen, whereas the central section (B) maintains it.

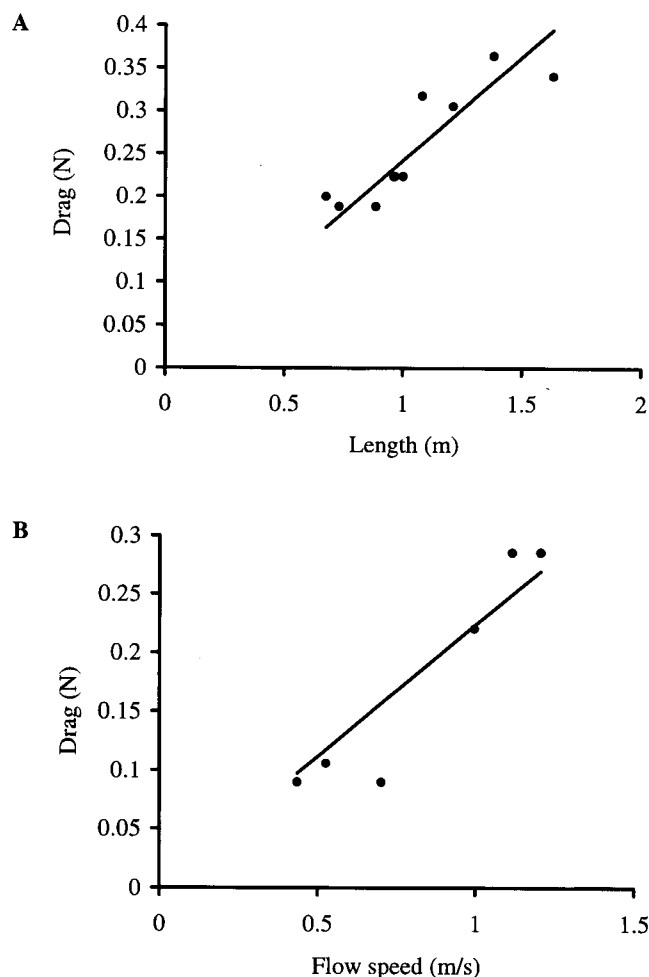


Fig. 5. The relationship for *R. fluitans* between drag and length (A) at a flow speed of 1.3 m s^{-1} , and drag and flow speed (B) using a specimen of length 1.48 m, determined from flow tunnel tests.

cannot be rejected statistically as the line of best fit for logged data has a slope of 0.843, which is not significantly different from 1.

Similarly, Fig. 5B shows that the relationship between drag and flow speed also appears to be linear. The line of best fit for logged data has a slope of 1.24, which is not significantly different from 1, but is significantly ($P < 0.05$) different from 2 (which would imply a squared relationship).

Observation of the specimen at a range of flow speeds also indicated that there was little drag-reducing reconfiguration at speeds up to 1.3 m s^{-1} . Assuming a linear relationship (due to the evidence described above), going through the origin, between drag and both length and flow speed, the following expressions are obtained.

$$\text{Drag} = 0.242 \times \text{length} \quad (\text{at flow speed of } 1.3 \text{ m s}^{-1})$$

$$\text{Drag} = 0.224 \times \text{flow speed} \quad (\text{with length of } 1.48 \text{ m})$$

where Drag is in Newtons (N), length is in m and flow speed is in m s^{-1} . Combined, these give the approximate expression

$$\text{Drag} = 0.17 \times \text{length} \times \text{flow speed}.$$

Safety factors

The flow speed for the River Bollin, on 1 July, was $1.0\text{--}1.5 \text{ m s}^{-1}$ near the stands of *R. fluitans*. The maximum flow speed for the experiments was 1.3 m s^{-1} , and so is reasonably close to a natural value. The mean length of the plants tested was 1.05 m and the mean breaking strength was 1.89 N. Given this, the expressions above can be used to estimate that the maximum length to which a plant can grow without breaking, at normal flow speeds and without extra strengthening, is 7.8 m, giving a safety factor of 7.4. Similarly, the maximum flow speed a plant of average length could survive is 8.4 m s^{-1} , giving a safety factor of 6.5.

Mechanical properties along the stems of *R. fluitans*

Figures 6A and B show, respectively, the resistance to bending, and tensile strengths of internodes, according to position along the stem (1 being the value for the tip). The resistance to bending of middle sections (mean = 0.083 N , s.d. = 0.026) of the stem was significantly higher than for internodes at both tip (mean = 0.046 N , s.d. = 0.005) and base (mean = 0.039 N , s.d. = 0.024). For these bending tests, the maximum resistance to bending (i.e. the maximum resultant force on the probe in Newtons) of the sample across a constant (25 mm) span was more accurate and useful than rigidity. This is because loads were low, so computer-generated estimates of E_b were occasionally extremely inappropriate, and the samples

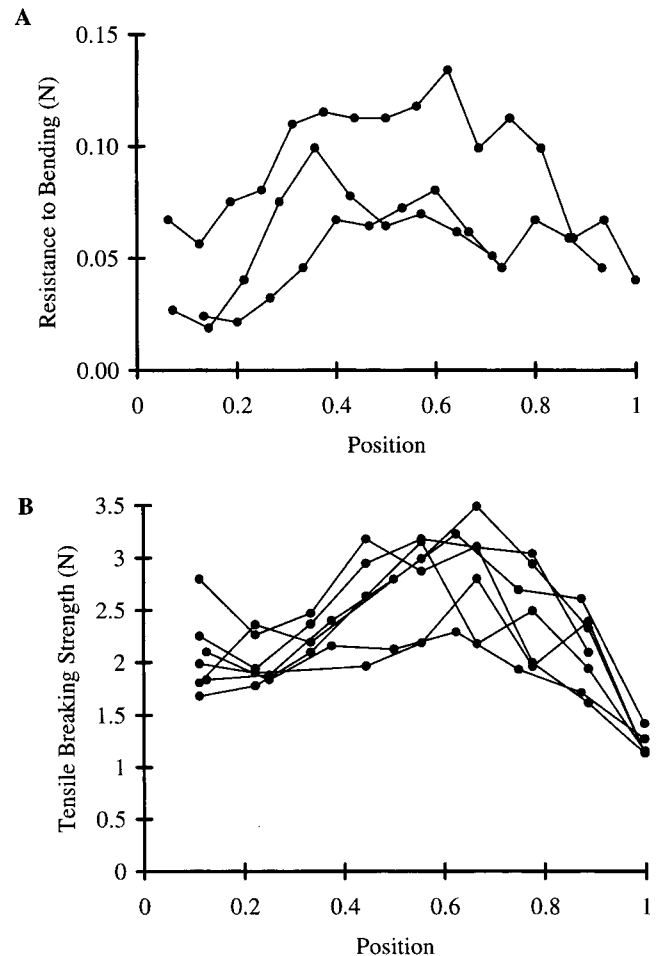


Fig. 6. Mechanical properties along stems of *R. fluitans* (position 1 being the tip) determined from 3 bending and 7 tensile tests. Resistance to bending (A) and tensile strength (B) is significantly lower at the base than the middle of the stem.

always deflected enough to go between the supports before the yield point was reached.

The middle sections also had higher tensile strengths than base or tip internodes. Paired analyses show significant differences in tensile strength between base (mean = 2.07 N , s.d. = 0.38), middle (mean = 2.757 N , s.d. = 0.43) and tip (mean = 1.33 N , s.d. = 0.35).

Discussion

Comparisons between aquatic and terrestrial buttercups

The expected trends in both the mechanical properties and the arrangement of structural material within the stem were observed in the four species of *Ranunculus* tested. Terrestrial species were more rigid with respect to bending, which will allow them to support both their own weight and the weight and wind drag of the leaves and flowers. In contrast, the aquatic species, which are supported through buoyancy, are much more flexible with

respect to bending. These differences in rigidity are related both to the different diameters of the stems, and to the arrangement of the structural elements within the stem. Terrestrial species have thicker stems in which the structural elements are placed nearer the perimeter, as would be expected, to maximize rigidity. The term E_b/E_t is the best way of characterizing the mechanical effect of the distribution of the structural elements. Values different from 1 indicate that the value of I is unrealistic (as E_b is derived from rigidity, $E_b I$), and so show that the structural material is not placed evenly throughout the stem. If the value is greater than 1, as with the terrestrial species, I is maximized, and structural material is preferentially placed nearer the perimeter. In *R. fluitans*, the value is less than 1, confirming the observation that the structural material is placed towards the centre, increasing bending flexibility. In addition, of course, unligified tissues such as the epidermis may also play an important role in determining the mechanical characteristics of a stem, and are likely to show some mechanical adaptations related to habitat, but the distribution of these regions, particularly the epidermis, is restricted by their primary roles.

The high breaking strains of the aquatic species (0.10 or 0.15 for *R. peltatus* and *R. fluitans*, respectively) may be related to a lower degree of lignification and to a higher microfibrillar angle in the xylem vessels. This may help the stem cope with sudden tugs in a similar way to seaweeds, which have even larger breaking strains of around 0.38 (Koehl and Wainwright, 1977).

Comparisons between *R. acris* and *R. repens*

The trends described as general in terrestrial species, such as high rigidity and a maximized second moment of area, are better seen in *R. acris*, than in *R. repens*. Figure 3A shows that the structural elements are placed more peripherally in *R. acris*, which may help it to compete in an established meadow environment (where supporting tall structures is advantageous), though there is no significant difference in E_b/E_t .

In contrast, the higher bending strain and lower rigidity of *R. repens* may help it withstand trampling in the disturbed sites where it typically grows. The low rigidity may not be particularly disadvantageous, for the vegetation competing with *R. repens* is generally sparse and low.

Comparisons between *R. peltatus* and *R. fluitans*

R. peltatus has a relatively higher rigidity than *R. fluitans*, and possesses a larger central lumen. This may allow the large leaves which float on, or extend from, the water surface to maintain their positions effectively, and avoid self-shading. The higher rigidity may also be important in allowing *R. peltatus* to survive sub-terrestrially, permitting life on mud when the water level falls. Alternatively, the rigidity of *R. peltatus* stems may simply reflect the

primitive state, and the selective pressure to evolve the flexible stems seen in *R. fluitans*, may not be strong.

The capability to withstand high strains may combine with the low rigidity in *R. fluitans* to allow the stem to deflect away from, and cope with, sudden tugs from temporary, energetic vortices in the turbulent stream.

Drag on *R. fluitans*

The result that drag is approximately proportional to flow speed to the first, rather than second, power, suggests that drag is dominated by viscous rather than inertial forces. This appears reasonable considering that *R. fluitans* is long and thin, and lies parallel to the flow. Viscous surface drag will therefore play a larger role than in upright plants, which present a large profile to the flow.

The linear relationship found between drag and plant length is also of interest as it suggests that drag due to flag-like fluttering, which is considered a significant component of drag in some aerial leaves (Vogel, 1981), is relatively unimportant. Fluttering in flags is caused by local flow separation which, in turn, causes further flow separation, thus, by positive feedback, causing more fluttering and drag. Hoerner (1965) displays results showing that the drag coefficient on a flag is directly proportional to the ratio of its length to its height. With *R. fluitans* samples, lateral dimensions varied only slightly, so if flutter was involved one would expect drag to be proportional to the square of its length, rather than to length to the first power. It was found that the linear relationship indicates that the movements of the stem and leaves, observed both in the flow tunnel and in the natural state, are not causing significant flow separation.

Prevention of fluttering may, at least in part, be facilitated by the increased bending rigidity which is seen in the central segments of *R. fluitans*, and which is largely caused by the presence of a central lumen and more peripheral positioning of vascular bundles in these regions. The potential for fluttering is only really a problem at high Reynolds numbers in maintained, turbulent flow, as found in streams and ocean currents, but not as experienced by intertidal macroalgae. The possibility of flutter may explain why the centripetal trend of the structural elements of *R. fluitans* has not continued to produce an arrangement like that seen in *Myriophyllum*, which has a central strand of lignified tissue.

Hinges and fuses

The absence of a central lumen in the basal segments of *R. fluitans*, along with the relatively low bending rigidity, implies that this region may act as a hinge, allowing the body of the plant to swing like a weather vane, with shifting currents. This may, however, simply be a result of the reduced tensile strength found at the base. Despite the reasonable safety factors shown for tensile strength

both with respect to length and drag, coping with washout is still very important. Incidental occurrences such as snagging by high-drag debris or entanglement with neighbouring strands, may produce exceptional loads on a stem, causing it to break, so resulting in the loss of the vegetative growth. Ranunculates have been shown to recover well from this (Dawson, 1989). Whether washout occurs at mid-season or in autumn, the weakness of the base may have adaptive value, since it will protect the root system with a kind of mechanical fuse. It is also possible that detached sections of stem may be able to re-root independently as many nodes are capable of producing adventitious roots. The importance or likelihood of this is probably low compared with the advantage of saving the parental root stock, as *R. fluitans* lives in rivers with high flow speeds and both stems and leaves float.

Implications for management

Management through artificially creating spate conditions is unlikely to prove effective in reducing problem vegetation, as the 'fuse system' will protect the roots, and water buttercups (or crowfoots) grow well if seasonal vegetative growth is removed late in the season. The high safety factors found for plants which are less than fully grown indicate that the more effective pre-emptive control (Westlake and Dawson, 1989) would also be difficult using artificial spate.

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