Botanical ratchets

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Ratcheting surfaces are a common motif in nature and appear in plant awns and grasses. They are known to proffer selective advantages for seed dispersion and burial. In two simple model experiments, we show that these anisotropically toothed surfaces naturally serve as motion rectifiers and generically move in a unidirectional manner, when subjected to temporally and spatially symmetric excitations of various origins. Using a combination of theory and experiment, we show that a linear relationship between awn length and ratchet efficiency holds under biologically relevant conditions. Grass awns can thus efficiently transform non-equilibrium environmental stresses from such sources as humidity variations into useful work and directed motion using their length as a fluctuation amplifier, yielding a selective advantage to these organelles in many plant species.

Keywords: biological ratchets; transport; anisotropic surfaces

1. INTRODUCTION

Motion rectification by ratchets arises repeatedly as a theme with variations in nature to technology on a range of scales, from the molecular (Feynman 1964; Ajdari & Prost 1992; Magnasco 1993; Julicher *et al.* 1997; Reimann 2002; Kulić *et al.* 2005; Galajda *et al.* 2007; Wan *et al.* 2008) to the macroscopic (Bug & Berne 1987; Nordin *et al.* 2001; Mahadevan *et al.* 2003), in both deterministic and stochastic systems. A key ingredient in all ratchets is the presence of a static or dynamic asymmetry that serves to rectify motion, with many convergent solutions seen in nature. For example, ratchet and pawl mechanisms are basic mechanical components in many man-made gadgets and machines. They serve to rectify linear or rotational motions by using a mechanical anisotropy that often takes the form of an asymmetric sawtooth that allows the ratchet to slip in one direction and not in the opposite direction. Their microscopic (thermal) analogues have been intensely studied (Feynman 1964; Ajdari & Prost 1992; Magnasco 1993; Julicher *et al.* 1997; Reimann 2002; Kulić *et al.* 2005; Galajda *et al.* 2007; Wan *et al.* 2008) over the past decades in the context of molecular motors (Julicher *et al.* 1997), where the physical sawtooth is replaced by a potential with a similar property that is periodically switched on and off. On the macroscopic scale as well, nature has stumbled on ratchets repeatedly, and a host of examples exist in the plant world, in particular (Murbach 1900; Peart 1979; Stamp 1984; Garnier & Dajoz 2001; Elbaum *et al.* 2007), where they might proffer selective advantages for seed dispersion and burial. Indeed, the observation that different plant families show the same robust and efficient solution to the problem of dispersion and self-burial is yet another example of convergent evolution driven by a combination of physical

constraints and functional requirements. Here, we use the particular example of the wild foxtail *Hordeum murinum* to study macroscopic natural ratchets that rectify deformation induced by swelling, shrinking and other environmental factors, into unidirectional motion that serves important functional purposes, from the burial of seeds to their transport by animals.

When a *H. murinum* plant awn is placed on a soft, porous or rough material and excited by dynamic macroscopic forces that might be deterministic or random, it generically moves in the direction of its tip. To understand the mechanism of operation of this simple machine, we start with the common observation that sliding one's fingertips over the surface of a foxtail awn is easy in one direction and essentially impossible in the opposite direction. A closer look under a scanning electron microscope (SEM) reveals the reason (figure 1*b*). The awn has a highly anisotropic surface structure with sharp micro-barbs tilted unidirectionally at an angle $\beta \approx 35^\circ$ with the horizontal and a typical length of 50 μm . Such a surface geometry, in combination with the elasticity of the awn, induces a cooperative locking transition of micro-barbs via a progressive bending of the awn towards the substrate (figure 1*d*). This cooperativity of locking increases the number of stress-bearing micro-barbs, and thus reduces the probability of interfacial failure. The tilted barb has a second effect in addition to providing a force parallel to the substrate, since its geometry naturally also gives rise to an effective normal (adhesion-like) force component $F_\perp = F_\parallel \tan \beta$, as shown in figure 1*e*. The combination of a rigid microscopic geometry associated with the barbs and a macroscopic elastic compliance associated with the barb backbone allows the foxtail awn to slide unhindered with respect to the substrate in one direction (figure 1*c*), but efficiently suppresses motion in the opposite direction (figure 1*d*). We now consider two different physical situations in which transport is generically observed.

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Figure 1. (a) Grass species that exhibit ratchet motility (for (i) to (iii)): (i) single spikelet of foxtail grass (*H. murinum*), (ii) green bristlegrass (*Setaria viridis*), and (iii) barley (*Hordeum vulgare*); scale bar, 2 cm. (b) *Hordeum murinum*'s micro-barb surface structure is responsible for the ratcheting effect (SEM); scale bar, 50 μm . (c) A single clamped unstrained *H. murinum* awn (with micro-barbs pointing to the right) glides easily on the substrate moving to the right (paper cover). (d) Awn buckling and progressive micro-barb locking induced by substrate motion to the left (see movie 1 in the electronic supplementary material). (e) A barb-locked awn on the substrate also resists upward lift forces (see movie 2 in the electronic supplementary material).

2. TRANSPORT IN INERTIALLY DOMINATED ENVIRONMENTS

In a first experiment, we placed *H. murinum* spikelets on a horizontal shaker driven sinusoidally with amplitude $A = 3.7$ mm and observed their motion as a function of the driving frequency ω . When $\omega < \omega_c$, a critical frequency, almost no motion is observed, while if $\omega > \omega_c$ we observe that the spikelet drifts in the direction of its tip, as shown in figure 2 (see movie 3 in the electronic supplementary material). The foxtail cannot move unless inertial forces overcome friction, i.e. $\omega_c^2 mA = \gamma mg$, which leads to an expression for the critical frequency $\omega_c = \sqrt{\gamma g/A}$, where m is the mass of the grass; γ is its friction coefficient; and g is the acceleration due to gravity. Above this critical frequency, the mean transport velocity can be derived from the following graphical argument (cf. inset of figure 2b): the grass moves with the shaker up to the point t_1 , where the shaker acceleration $\dot{v}_s(t)$ coincides with the critical slope $-\gamma g$. From this point on, the grass unbinds from the shaker and slides on it, decelerating under the influence of friction with $\dot{v}(t) = -\gamma g$. The free motion ceases when the grass and substrate velocities coincide again at a later time $t = t_2$, and the cycle begins again. In general, the time-averaged grass velocity can be written as

$$\bar{V}_i = \frac{1}{T} \int_{t_1}^{t_2} (v_s - \gamma g t) dt, \quad (2.1)$$

where $T = \omega^{-1}$ and the times t_1 and t_2 need to be determined numerically. Evaluating this expression numerically for a sinusoidal shaker velocity $v_s(t) = A\omega \sin \omega t$ shows that this agrees well with our experimental results, with $\gamma = 0.4$ (figure 2b), the value of which is close to the experimentally measured friction coefficient of $\gamma = 0.46 \pm 0.05$ (from independent inclined plane measurements on

Figure 2. Ratcheting in the inertial regime. (a) Foxtail grass moves unidirectionally on a harmonically oscillating horizontal shaker (see movie 3 in the electronic supplementary material). (b) The mean velocity is shown as a function of the shaker frequency, with error bars from five different foxtail specimens (circles). The best fit to a theoretical model (see text), with $\gamma = 0.4$, is shown as a solid line. Inset: graphical model for ratchet motion on an oscillating substrate. The ratchet leaves the substrate frame when its inertia overcomes the frictional force at $t = t_1$, and it locks and moves with the substrate again when the ratchet and substrate velocities coincide again at $t = t_2$.

six different *H. murinum* samples). Near the transition frequency ω_c , it is possible to obtain analytic results by noting that both critical times t_1 and t_2 will be close to the zero-velocity crossing point $t = T/2$. In this limit, we can use a Taylor series expansion of the shaker velocity $A\omega \sin \omega t$ to the third order around $T/2$ to determine expressions for the unbinding time $t_1 \approx T/2 - \sqrt{2}\alpha/\omega_c$ and the rebinding time $t_2 \approx T/2 + 2\sqrt{2}\alpha/\omega_c$, with the small parameter $\alpha = \sqrt{1 - \omega_c^2/\omega^2} \ll 1$, leading to

$$\bar{V}_i = \frac{1}{T} \int_{t_1}^{t_2} (v_s - \gamma g t) dt \approx \frac{9}{2} \Theta(\omega - \omega_c) A \omega (1 - (\omega_c/\omega)^2)^2, \quad (2.2)$$

with Θ being the Heaviside function. In the limit of strong forcing corresponding to large frequencies $\omega \gg \omega_c$, and the grass moves almost freely being impulsively driven by the shaker during a very brief locking phase, we expect an asymptotic mean velocity

$$\bar{V}_i \approx A\omega. \quad (2.3)$$

In summary, in the frictional-inertial regime, the transport velocity is independent of the mass and length of the grass spikelet, but has a nonlinear dependence on the driving frequency at the onset of motion,¹ which eventually transitions to a simple linear relation far from the threshold.

3. TRANSPORT IN CONTINUOUSLY DEFORMING ENVIRONMENTS

We now turn to the second, biologically more relevant, situation in which net transport is observed: continuous deformation of the substrate along which the grass is moving. Two important examples for such deformations are (i) deformation of the skins of animals (naturally dispersing the foxtail) and (ii) diurnal and seasonal soil swelling and shrinkage driven by humidity and temperature variations (Iwata *et al.* 1988; Marshall *et al.* 1996). The first process is believed to be responsible for the dispersal of foxtail over large distances. It poses a potential hazard to animals if the foxtail is trapped in nostrils or ear channels, as it can ratchet into tissue to cause infection, and possibly death. The second process is a potential mechanism for the seed and awn burial into the soil (Murbach 1900; Peart 1979; Stamp 1984; Garnier & Dajoz 2001; Elbaum *et al.* 2007), an important precursor of germination. In general, in addition to substrate deformation, the contour length of the ratchet grass itself can actively vary as well. For example, relatives of the foxtails such as *Stipa somata* show a hygroscopically driven coiling and kinking of their awns to vary the effective contour length of awns (along the direction of motion), which yields linear strains of up to 20 per cent (Murbach 1900). In either case, these strain variations may be rectified in the direction of the grass tip. To understand the minimal properties of ratchet propulsion in this case, we consider the combination of a time-periodic hygroscopic strain of the grass awn $\varepsilon_g(t)$, and that of the surrounding substrate (soil/animal fur) $\varepsilon_s(t)$. Then, on dimensional grounds, we expect a simple scaling relation of the mean propulsion velocity of the awn,

$$\bar{V}_g \sim aT^{-1}f(\varepsilon_s, \varepsilon_g), \quad (3.1)$$

where a is the awn length; T is the period of the soil and awn strain variation; and $f(\varepsilon_s, \varepsilon_g)$ is a dimensionless

functional. To complete this analysis, we parametrize the grass using its unstrained arc length $s_g \in [-a/2, a/2]$, with $s_g = 0$ corresponding to its centre. In response to internal and substrate strain, each point along the grass moves so that its position is $x_g(s_g, t) = X_g(t) + s_g(1 + \varepsilon_g(t))$ and its velocity is $v_g(s_g, t) = \dot{X}_g(t) + s_g \dot{\varepsilon}_g(t)$, with $X_g(t) = x_g(0, t)$ and $v_g(s, t) = \dot{x}_g(s, t)$. The substrate (soil tube) can be parametrized in a similar manner via its unstrained arc length coordinate s_s , so that material points along it have a position $x_s(s_s, t) = (1 + \varepsilon_s(t))s_s$ and velocity $v_s(s_s, t) = s_s \dot{\varepsilon}_s(t)$. At a given instant of time t , the grass is in contact with the soil over the interval $x_s \in [X_g(t) - (a/2)(1 + \varepsilon_g(t)), X_g(t) + (a/2)(1 + \varepsilon_g(t))]$. Then, the relative velocity between the grass and the substrate parametrized in terms of the grass material parameter s_g is $V_{\text{rel}}(s_g, t) = v_g(s_g, t) - v_s(s_g(s_g, t), t)$. We assume that the grass acts as an ideal ratchet, i.e. no part of it can move in the *negative* direction (that of the micro-barb sharp tip orientation) with respect to the contact points with the substrate. Then, the relative velocity must satisfy the following condition:

$$\min_{s_g \in [-a/2, a/2]} V_{\text{rel}}(s_g, t) = 0. \quad (3.2)$$

Using the fact that $x_s(s_s, t) = x_g(s_g, t)$ and $\min_{s_g \in [-a/2, a/2]} (s_g C) = -(a/2)|C|$ (for any value C), the previous condition can be recast as an equation of motion for the position of the awn centre,

$$\frac{d}{dt} \frac{X_g}{1 + \varepsilon_s} = \frac{a}{2} \frac{|(1 + \varepsilon_s)\dot{\varepsilon}_g - (1 + \varepsilon_g)\dot{\varepsilon}_s|}{(1 + \varepsilon_s)^2}. \quad (3.3)$$

Integrating the previous expression yields $X_g(t) = (a/2)(1 + \varepsilon_s) \int_0^t (1 + \varepsilon_s)^{-2} |(1 + \varepsilon_s)\dot{\varepsilon}_g - (1 + \varepsilon_g)\dot{\varepsilon}_s| dt'$. To determine the mean velocity of the awn in a simple yet realistic case, we assume that both $\varepsilon_s(t)$ and $\varepsilon_g(t)$ are periodic functions with a single minimum and maximum, with the same period T , and that ε_s satisfies $\varepsilon_s(0) = \varepsilon_s(T) = 0$. Then, the velocity averaged over a complete cycle $\bar{V}_g = (X_g(T) - X_g(0))/T$ is

$$\bar{V}_g = \frac{a}{2T} \int_0^T \frac{|(1 + \varepsilon_s)\dot{\varepsilon}_g - (1 + \varepsilon_g)\dot{\varepsilon}_s|}{(1 + \varepsilon_s)^2} dt. \quad (3.4)$$

There are two interesting limiting cases worth considering.

Case I. Negligible substrate strain. In this case, $\varepsilon_s = 0$, so that equation (3.4) simplifies to $\bar{V}_g^I = (a/2T) \int_0^T \dot{\varepsilon}_g dt = (a/2T) (\int_0^{T_{\text{max}}} \dot{\varepsilon}_g dt - \int_{T_{\text{max}}}^T \dot{\varepsilon}_g dt)$, yielding the expressions

$$\bar{V}_g^I = \frac{a}{T} \varepsilon_{\text{max}}, \quad \Delta_g^I = T \bar{V}_g^I = a \varepsilon_{\text{max}}, \quad (3.5)$$

for the velocity and displacement per cycle, where T_{max} is the point at which ε_g attains its maximum and $\dot{\varepsilon}_g$ changes sign from positive to negative and ε_{max} being the maximal strain during a single strain cycle.

Case II. Negligible plant awn strain. In this case, we have $\varepsilon_g = 0$ and $\bar{V}_g^{\text{II}} = (a/2T) \int_0^T [|\dot{\varepsilon}_s|/(1 + \varepsilon_s)^2] dt$. Splitting the integral as in the previous case, and integrating over a full cycle, yields

$$\bar{V}_g^{\text{II}} = \frac{a}{T} \frac{\varepsilon_{\text{max}}}{(1 + \varepsilon_{\text{max}})}, \quad \Delta_g^{\text{II}} = a \frac{\varepsilon_{\text{max}}}{1 + \varepsilon_{\text{max}}}. \quad (3.6)$$

In summary, we see that the speed and displacement per cycle in both cases scale linearly with the grass length a , showing that longer grasses pick up and rectify

Figure 3. Ratcheting in a continuously deforming environment. (a, b) Experimental set-up: foxtail spikelets are placed inside a 4 mm inner diameter rubber tube that is periodically strained (see movie 4 in the electronic supplementary material). Spikelets move in the direction of their tips (stained black for video analysis) with an efficiency that varies with their length. The distance between marker lines on the tube is 2.54 cm. (c) An intensity line scan (kymograph) corresponding to the time dynamics in (a) shows the periodic tube motion and the average propulsion of the spikelet over the time course of 60 s (x -axis). (d) Propulsion distance per strain cycle versus maximal rubber tube strain for four spikelets of various lengths: experimental points with error bars from seven to nine measurements and best fits to $\Delta_g^H = a\epsilon_s^{\max}/(1 + \epsilon_s^{\max})$ (solid lines). Inset: the fitted effective contact length (y -axis, centimetre units) versus the measured length of the longest awn (x -axis, centimetre units) of individual spikelets. While the effective lengths show a good correlation with the measured lengths, they are slightly smaller due to occasional awn buckling and imperfect tube–awn contact.

larger fluctuations in proportion with their length. Therefore, longer grass awns act effectively as better ‘fluctuation amplifiers’.

4. COMPARISON WITH OBSERVATIONS AND EXPERIMENTS

Although the results of equation (3.5) were not directly tested experimentally, they are consistent with the previously measured linear relationship between the awn length and burial depth of *S. somata* (Garnier & Dajoz 2001). This provides some evidence for a selective advantage of larger awn lengths in the contractile awn case as well. More generally, for hygroscopically driven awns, equation (3.4) predicts a non-trivial interaction between soil strain and awn strain contributions to the rectification of motion. Indeed, the two effects act in concert or ‘resonate’ for oppositely phased strains but can cancel each other for in-phase strains.²

To test the behaviour of a ratcheting awn in contact with the soil, as described by equation (3.6), awns and single rachis spikelets of various grasses of different lengths and diameters (figure 1a) were placed inside a rubber tube (inner diameter of 4 mm). The tube was then subjected to slow periodic strains with maximal strains ranging from

$\epsilon_{\max} = 0.01$ to 0.4. All the grasses rectified the oscillatory strain, with the *H. murinum* spikelets showing the most robust and reproducible behaviour (figure 3d). At very small sub-hertz frequencies at which the rubber tubes were strained (0.3 Hz), the ratchet displacements per cycle were independent of both frequency and the direction of gravity. The experimental results for the propulsion displacement Δ_g , as a function of the length of *H. murinum* spikelets, show good agreement with the theoretical prediction from equation (3.6) with a single fitting parameter per specimen—the effective contact length a , which is itself proportional to the actual awn length (figure 3d, inset). For longer awns, the fitted length shows, however, a systematic 20–40% reduction relative to the measured length consistent with our observations of occasional awn buckling and imperfect tube–awn contact of longer spikelets; this effect is less pronounced for shorter spikelets (figure 3d, inset).

Grasses and plant awns have long been known to have anisotropically barbed microstructural elements that are able to lock directionally into virtually any soft natural material, such as soil, animal fur and skin. Our theoretical and experimental study shows how the asymmetry of these surface structures enables them to rectify external

environment fluctuations that have functional consequences for dispersal and anchoring. In particular, in the context of seed dispersal, longer awns lead to a selective advantage to those seeds, since they can move further and thus disperse more efficiently than their shorter competitors. Our results also point the way for technological designs that might mimic this simple but robust motif.

ENDNOTES

¹We note that the transport behaviour at the critical frequency ω_c is non-universal and depends on the differentiability of the excitation signal. A symmetric sawtooth shaker velocity leads to a jump of the mean velocity slope $\partial \bar{V}_i / \partial \omega$ at $\omega = \omega_c$.

²In general, the ratchet motion will be dominated by the strain contribution with the larger value of the product of the strain and frequency. For similar but incommensurate oscillation frequencies $\omega_g \approx \omega_s$, the mean velocity displays an intermittent switching between periods of large and small mean velocities on time scales $T \approx 2\pi/|\omega_g - \omega_s|$, but saturates to a value $\bar{V}_g \sim a(\omega_s + \omega_g)(\epsilon_s^{\max} + \epsilon_g^{\max})$ at large times.

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