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DOI: 10.1016/j.cub.2009.03.058

Plant Biomechanics: Using Shape to Steal Motion

For grass species to spread efficiently through their environment requires seeds that can disperse over large distances and burrow into the ground. Recent work using awns from *Hordeum murinum* in conjunction with mathematical modelling shows that awn shape leverages environmental oscillations in order to produce these directional translations.

Charles W. Wolgemuth

Vince Guaraldi, the jazz pianist and composer, suggested with a song title that we should cast our fates to the wind. As animals, though, we are typically not so trusting of the benevolence of Nature and, instead, decide where we want to go and expend energy to move there. Many plants nevertheless release their seeds and seemingly hope for the best. A recent paper by Kulic *et al.* [1] shows that some grasses, at least, are not so cavalier and have engineered their seed carrying appendages (spikelets) to increase dispersion and facilitate seed burial by converting periodic or random oscillations in the environment into directed motion.

The spatial extent of a plant population is largely determined by seed dispersal [2]. There are three main mechanisms for seed dispersal: being carried by the wind, water, or an animal. Foxtail grasses employ a spikelet or cluster of spikelets that contains the grass seeds. These spikelets are engineered for hitch-hiking on animals. The more entrapped a spikelet becomes in an animal's fur, the farther the animal can carry the seed, and, therefore, it is beneficial for the spikelet to work its way into an animal's coat. Kulic *et al.* [1] used scanning electron microscopy to show that the awn from an *H. murinum* spikelet has sharp micro-barbs that are angled at roughly 35° with respect to the awn (Figure 1). These micro-barbs produce anisotropic friction with the environment [1]. The awn slides easily when pushed along one direction, but when pushed in the other direction, the barbs catch.

The barbs thus act as ratchets, allowing motion in one direction and preventing the counter motion. If a spikelet is placed on a rough surface that is shaken at a fixed frequency, the barbs slip with respect to the surface when the surface moves one way, but stay stuck to the surface when it moves in the other direction, which leads to net motion of the spikelet (Figure 1). Using a simple mathematical model that incorporates this sticking and slipping, Kulic *et al.* [1] were able to show that anisotropic friction is

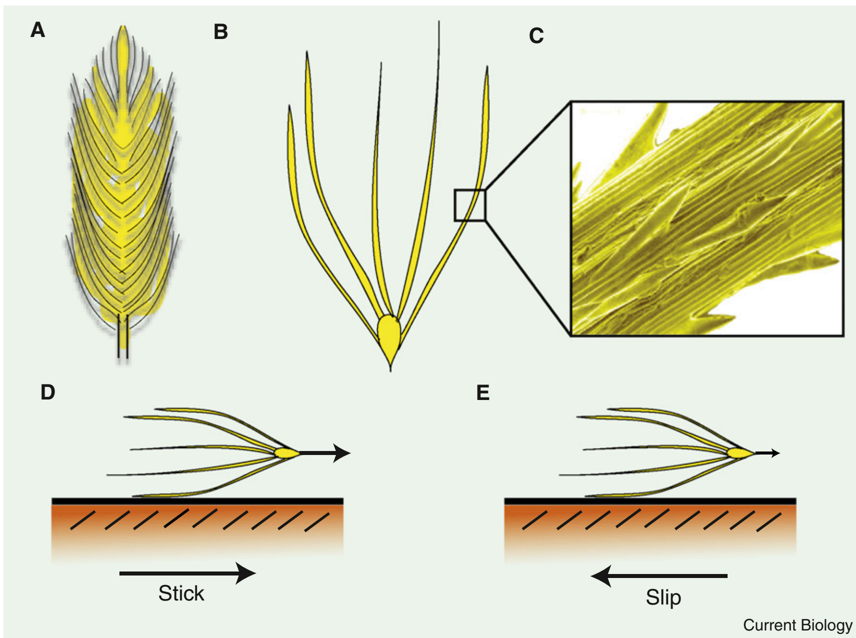

Figure 1. How foxtail grass seeds steal motion from the environment.

(A) A cluster of spikelets has the appearance of a foxtail. (B) Schematic of a single spikelet from *H. murinum*. The long arms that project off the base are known as awns. (C) Scanning electron microscopy shows that the awn surface is covered with angled micro-barbs. (D) When a spikelet is placed on a shaking surface, the barbs catch when the surface moves in one direction, and the spikelet moves with the surface. (E) When the surface moves in the other direction, the spikelet continues moving in the original direction, but slows due to friction with the surface.

sufficient to explain the net translation of the spikelet as a function of the applied frequency. So when the spikelet is in contact with an animal's fur, random motions of the animal can lead to the ratcheting of the spikelet further into the animal's coat.

Spikelets also use this mechanism to facilitate burying themselves into the ground, which acts not only to plant the seeds, but also to protect the grass species during fires [3]. Periodic variation in humidity causes soil swelling and leads to changes in awn shape [4]. To model how the anisotropic friction of grass awns couples to soil swelling, Kulic *et al.* [1] inserted grass spikelets into a rubber tube. The tube was then slowly stretched and relaxed and the motion of the spikelet with respect to the tube was measured [1]. Kulic *et al.* [1] developed a mathematical model that describes how these changes in environmental strain — the 'stretching' of the environment — can interact with the spikelet in order to bury the seeds. The model predicts that the burial rate should increase with environmental strain and with awn length. This latter prediction is in good agreement with measurements of the burial depth of *Stipa somata* awns as a function of awn length [3]. Some awns also have a twisted shape at the end, which can facilitate burying [4].

Grass awns are not the only place where biology has found a use for coupling anisotropic friction to undulatory motion in order to create net translation. Another prime example of this mechanism is the motility of snakes and earthworms. Snake skin has slanted 'micro-hairs' [5], analogous to the micro-barbs observed in awns, and these micro-hairs lead to significant frictional anisotropy between forward and backward motions [6]. Contraction and extension of the snake musculature produces an oscillatory motion of the snake skin against the surface, and the combined effect gives a slithering snake.

An interesting difference between the snake and the awn is that the snake relies on its own power, while the awn effectively steals energy from the environment. Biology has figured this strategy out in other arenas, too. Inside cells, some proteins can do work. A myosin molecule walks to pull on actin and contract muscle. Actin, itself, can polymerize and push. The flagellar motor and ATP synthase rotate. For all of these examples, the molecules ratchet random motions from thermal fluctuations and thereby drive many processes in our cells. New work also suggests that jelly fish and some bugs may be able to steal motion from undulating water or air currents: Spagnolie and Shelley [7] have shown that if a swimmer, such as a jelly fish, changes its shape out of step with a periodic flow, it can swim.

Biology has thus repeatedly found ways of producing net work by rectifying fluctuations with ratchets, and it is interesting to speculate on other areas where this mechanism may play a role. Evolution is one directly analogous system and a comparison between it and Brownian ratchets has been drawn previously [8]. Clearly, random mutations in an organism's genome lead to fluctuations in phenotype. Reproduction can lock in these variations, and natural selection then acts as a ratchet, reducing the likelihood of maintaining a population that is less competent at reproducing while increasing phenotypic populations that are fitter. A more tenuous comparison, though, comes to mind when I consider my own thoughts, which all too often seem quite random. I must consciously work to rectify these thoughts, plucking out the good ones and discarding the bad, in an attempt to construct an understanding of the world about me. Could my own thinking be working by trapping useful ideas from a pool of noise? One of the not-so-useful ideas, right? But, it has been suggested that certain nuclei in the basal ganglia act as a random motor pattern noise generator [9]. If our brains can create noise, maybe they can ratchet it too.

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DOI: 10.1016/j.cub.2009.03.052

Nuclear Envelope: Membrane Bending for Pore Formation?

Membrane-shaping proteins known as reticulons help to sculpt the endoplasmic reticulum; recent findings indicate that they also play a role in the formation of nuclear-pore-complex-associated pores in the nuclear envelope.

Wolfram Antonin

In eukaryotic cells, nuclear pore complexes (NPCs) in the nuclear envelope mediate transport between the cytoplasm and the nucleoplasm. These are huge macromolecular assemblies of about 65 MDa in yeast and up to 120 MDa in vertebrates. Although most, if not all, components of NPCs are known [1,2], it is not fully understood how these large structures are formed from their individual proteins. Nevertheless, significant progress in understanding the protein interaction network in the NPC has been made in recent years [3,4]. NPCs are embedded in the membrane of the nuclear envelope, but how insertion is achieved is not known [5]. An inspiring new study [6] suggests that the membrane bending proteins of the endoplasmic reticulum (ER) play a role in this process.