



SYMPOSIUM

Mechanics without Muscle: Biomechanical Inspiration from the Plant World

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Synopsis Plant and animal biomechanists have much in common. Although their frame of reference differs, they think about the natural world in similar ways. While researchers studying animals might explore airflow around flapping wings, the actuation of muscles in arms and legs, or the material properties of spider silk, researchers studying plants might explore the flow of water around fluttering seaweeds, the grasping ability of climbing vines, or the material properties of wood. Here we summarize recent studies of plant biomechanics highlighting several current research themes in the field: expulsion of high-speed reproductive projectiles, generation of slow movements by shrinking and swelling cell walls, effects of ontogenetic shifts in mechanical properties of stems, flexible reconfiguration and material properties of seaweeds under crashing waves, and the development of botanically-inspired commercial products. Our hope is that this synopsis will resonate with both plant and animal biologists, encourage cross-pollination across disciplines, and promote fruitful interdisciplinary collaborations in the future.

Plants versus animals

Plant biomechanics is not a new field, but dates back to studies of wood and the impressive stature of trees in the 1700s (see Niklas et al. 2006). Yet, some people are surprised to hear of research on plant mechanics, assume that biomechanists study movement and that plants do not move. This misconception is wrong on two fronts. First, assuming that all biomechanists study locomotion is like assuming that all engineers study cars. Structural engineers who design bridges and materials engineers who develop bullet-proof clothing have much in common with biomechanists studying the stability of redwood trees or the mechanical properties of coconut husk

fibers. Second, although plants lack muscles and are typically considered stationary, they generate a diversity of movements that span a broad range of time scales from hours or days to milliseconds (Skotheim and Mahadevan 2005). Growth and tropisms that allow plants to reach nutrients unfold over periods of hours or days. Included are movements associated with the clasping motion of tendrils that so fascinated Darwin (Darwin 1885, Purdie 2009), the twining of stems (Isnard et al. 2009), as well as sun-tracking and the movement towards light (phototropism) and gravity (gravitropism). In contrast, the dispersal of seeds and spores is often facilitated by rapid movements. Examples are the high-speed pollen release of

the white mulberry (Taylor et al. 2006) or the explosive dispersal of seeds in the Acanthaceae (Witzum and Schulgasser 1995). Indeed, the speed, precision, and efficiency of these rapid plant movements are equal to, or in excess of, those reported for muscle-driven movements in animals.

Animal and plant biomechanists have much in common. Although their frame of reference differs, they think about the natural world in similar ways. Biomechanists who study animal movements are often concerned with the effects of wing or limb morphology on hydrodynamic or aerodynamic performance (e.g., lift, thrust, and drag). Plant biomechanists are often concerned with the same issues, for example studying drag, lift, and survival of tree branches, leaves, or seaweeds in the wind and waves. Whereas zoologists gain biomimetic inspiration from gecko feet and spider silk, botanists explore mechanical properties of woody plants, fruit rind, and gel-forming cell-wall extracts to develop new products for commercial applications.

Across the broad field of biomechanics, opportunities for collaboration and integrative comparisons are many. Although the Society for Integrative and Comparative Biology (SICB) originally developed out of the American Society of Zoologists, SICB has since grown and diversified to include a large number of botanists who share the integrative and comparative mindset of their zoological counterparts. To highlight similarities between plant and animal biomechanics and to encourage interaction and collaboration between the two groups, the authors participated in the Mechanics without Muscle symposium at the 2010 SICB conference in Seattle, WA. In this paper, we summarize a small selection of ongoing research projects that represent different aspects of plant biomechanics, which may dissolve some of the preconceptions held by zoologists. Jacques Dumais and Joan Edwards describe the mechanics (and ballistics) of fast moving plants and fungi. Markus Rueggeberg and Ingo Burgert discuss slow movements of plants, including tropisms and the actuation of plant organs by the swelling or shrinking of cell walls. Nick Rowe explores the ontogeny of mechanical characters in climbing vines that allows them to stay aloft in tropical forests. Michael Boller and Patrick Martone describe morphological and structural adaptations of seaweeds that survive under crashing waves, then Katharine Mach discusses mechanical fatigue of seaweed tissues, which results from repeated loading of fronds by wave-induced forces. Finally, Robin Seidel and Thomas Speck outline the process of biomimetic product development, highlighting the mechanical

inspiration gleaned from ongoing studies of fruit-walls and nutshells. We hope that these studies will resonate with both plant and animal biologists and help integrate plant research into future SICB meetings.

Rapid movements

Lacking muscles, plants and fungi use a variety of energy sources and release mechanisms, many of which have yet to be fully described. Rapid movements have evolved multiple times in a diversity of plant groups, from the airborne sperm of liverworts (Shimamura et al. 2008) and the catapulting spores of the leptosporangia in ferns (Ingold 1965) to the exploding seeds, fruits, and flowers of many angiosperms including monocots (*Catasetum* orchids and *Sucrea* and *Raddia*, two Babusoid grasses), basal eudicots (*Berberis* spp.), rosids (*Geranium maculatum* and *Oxalis* spp.), and asterids (*Cornus canadensis* and *Impatiens* spp.) (Edwards et al. 2005, Romero and Nelson 1986, Sendulsky 1993, Simons 1992). Similarly in fungi, fast movements occur in such diverse groups as the Mucorales (e.g., *Pilobolus*, page 1964; Yafetto et al. 2008), Ascomycetes (Roper et al. 2008), and Basidiomycetes (Money 1998, Noblin et al. 2009). These rapid movements appear to be derived traits with strong selective pressures leading to unique adaptations. Here we focus on three examples of fast motions that facilitate spore/pollen movement to illustrate some of the diverse biomechanical adaptations. We highlight the role these play in increasing plant fitness and how, in some cases, the biophysics parallel movement in animals.

Challenges of being small

The most widespread use of fast motion in plants is in assisting the release of minute spores and pollen grains. The diversity of mechanisms that propel spores and pollen grains is remarkable (Ingold 1939, 1965; Straka 1962) although the ultimate result is the same: permitting small particles to disperse by becoming airborne. To be successfully dispersed, small particles must surmount two challenges: adhesion and drag. Before spores or pollen grains can be released, they must overcome the surface tension that binds them together, which at microscopic scales, can be large compared to the force of gravity. This can be understood from a simple scaling argument. The force of gravity on an object such as a spore is $F_g \sim \rho g R^3$, where ρ is the density of the object, $g = 9.8 \text{ m s}^{-2}$ is the gravitational acceleration, and R is the radius of the particle. On the other hand, the surface tension force is

$F_\gamma \sim \gamma R$, where γ is the surface tension of water ($\gamma = 72 \times 10^{-3} \text{ N m}^{-1}$ for water at room temperature) (de Gennes et al. 2003). Considering the ratio of these forces: $F_\gamma/F_g \sim \gamma/\rho g R^2$; it can be seen that as R gets small, the force of the surface tension becomes increasingly important relative to the force of gravity. This simple phenomenon has profound consequences on the release of spores and pollen grains—these minute particles tend to cling to each other and to the structures that support them. Active ejection of spores and pollen provides a solution to this problem.

The second challenge springs from the fact that wind-borne spores and pollen grains require low terminal velocity so that they can remain aloft and be carried long distances (Vogel 2005a, 2005b). Tall plants, such as wind-pollinated trees, use their stature to release wind-borne spores into the turbulent airflow to be carried vertically and laterally. Ground dwelling plants, however, need to get their spores out of the still boundary layer, which can be as thick as 10 cm (Gregory 1973). Propelling small spores vertically is difficult because the low terminal velocity that keeps them aloft also means that they rapidly decelerate in still air. For example, a single 10- μm spore ejected at a speed of 1 m s^{-1} will travel at most 100 μm before coming to a complete stall. This challenge can be overcome by the collective release of hundreds or thousands of spores in an air mass at high initial velocity. Under such conditions, spores can travel up to 20 cm (see below), well above the boundary layer.

Example 1: The trebuchet mechanism of *Cornus*

Each stamen of the bunchberry dogwood (*Cornus canadensis*) functions like a miniature trebuchet, catapulting pollen into the air as the flower opens explosively (Edwards et al. 2005). High-speed video observations show that the flower opens in $<0.5 \text{ ms}$. As bunchberry flowers burst open, their petals rapidly separate and flip back to release the

stamens (Fig. 1). During the first 0.3 ms, the stamens accelerate at up to $24,000 \pm 6000 \text{ m s}^{-2}$ (2400g), reaching the high speed ($3.1 \pm 0.5 \text{ m s}^{-1}$) necessary to propel pollen, which is light and rapidly decelerated by air resistance [terminal velocity, $0.12 \pm 0.03 \text{ m s}^{-1}$ (mean \pm SEM); $n=7$]. The pollen granules are launched to a height of 2.5 cm where they can be carried by the wind. We note that the hinge mechanism that accelerates pollen grains is surprisingly similar to the way a baseball is accelerated by the sequential deployment of a pitcher's shoulder, elbow, and wrist (Alexander 1991, Whitaker et al. 2007).

The rapid opening of the self-incompatible bunchberry enhances cross-pollination in two ways. First, when insects trigger flower opening, the explosively propelled pollen sticks to their body hairs until it is transferred to an adhesive stigma. Since the force required to open flowers is 0.1–0.5 mN, explosive flower opening favors pollen placement on large pollinators (e.g., the large syrphid fly *Eristalis dimidiata*) that move rapidly between inflorescences and effectively excludes smaller, less mobile visitors such as ants, which rarely carry pollen and move slowly, if at all, between flowers. Second, unvisited flowers eventually explode on their own allowing for wind as a back-up method for pollination (Whitaker et al. 2007).

Example 2: The airgun mechanism of *Sphagnum*

The classic 1897 work of the Russian botanist Sergius Nawaschin still remains one of the best descriptions of the explosive dispersal of spores from capsules of *Sphagnum* moss (Nawaschin 1897). *Sphagnum* spores, which have a low terminal velocity, are propelled as high as 20 cm above the moss (Sundberg 2010). The fresh capsules are spherical but during dehydration the cells of the capsule collapse laterally and not vertically causing the capsule to become cylindrical. This decreases the volume of the capsule and increases the internal pressure to between

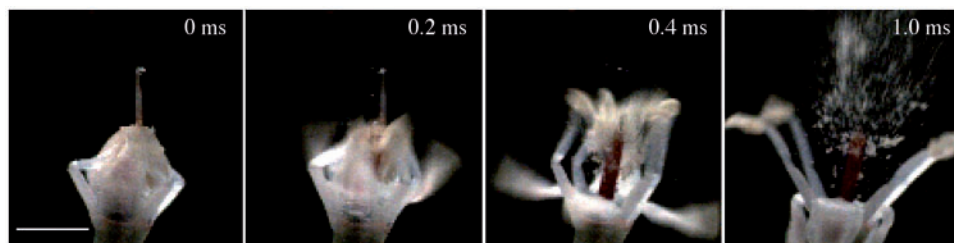


Fig. 1 Bunchberry flower-opening, recorded at 10,000 fps. Time elapsed is indicated. The first frame shows a closed flower with the four petals fused at the tip restraining the stamens, which function like miniature trebuchets. The blur represents the distance moved in 0.1 ms. Scale = 1 mm. From Edwards et al. (2005).

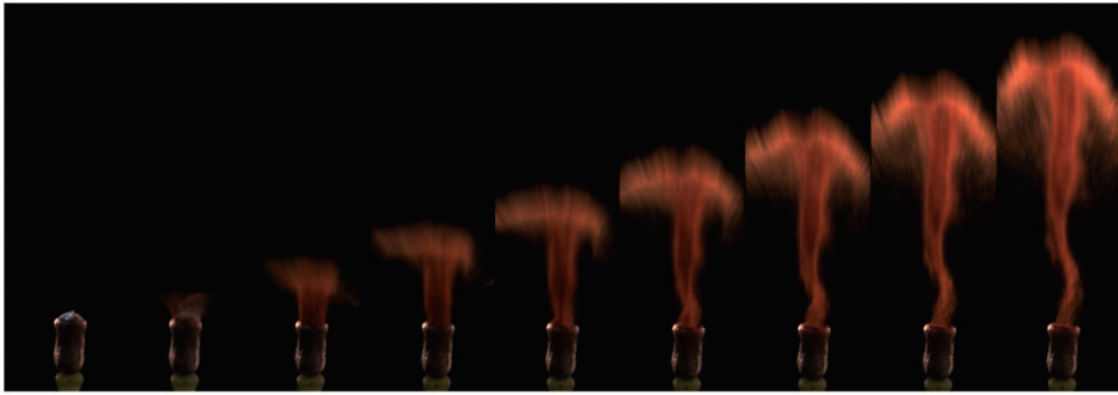


Fig. 2 Successive frames of an exploding capsule of *Sphagnum* moss filmed at 10,000 fps. The capsule is ~ 2.25 mm in height. Note the height achieved by the spores and the formation of a mushroom cloud indicative of turbulent vortex rings.

200 and 500 kPa. Eventually, when the pressure reaches a critical level, the cap breaks free and the spores inside are propelled upwards at high speed (Fig. 2). Critical to achieving heights over 10 cm is that spores are carried upwards in a turbulent vortex ring; spores launched ballistically would only achieve heights of 2–7 mm (Whitaker and Edwards 2010).

Example 3: The surface tension catapults of basidiomycetes

Most basidiomycetes, including many edible mushrooms, actively disperse their spores using the surface tension of water as their only source of energy (Buller 1909–1950; Ingold 1939; Turner and Webster 1991). The spores, known as ballistospores, are borne on the gills of mushroom caps. The ejection process begins with the condensation of a water drop at the proximal end of the spore and the growth of a thin film of water on the spore (Fig. 3A). When the drop reaches a critical size, it touches the water film on the spore surface. At this point, surface tension quickly pulls the drop onto the spore thus creating the necessary momentum to detach the spore from the supporting sterigma and to set it in motion. The freed spore soon emerges from the cap and is carried away by air currents to a distant location where it can germinate to produce a new mycelium and, ultimately, new mushrooms. The use of surface tension to eject spores is a novel mechanism for performing work over small distances. High-speed video imaging and quantitative analyses of ejecting spores in *Auricularia auricula* and *Sporobolomyces* yeasts revealed that the transfer of energy leading to spore ejection has surprising similarities to jumping animals (Noblin et al. 2009). Both processes rely on a “lowering” of the center of mass to allow a reaction force to be created

against a rigid support (Fig. 3B and C). For fungal spores, the growth of the drop brings the center of mass of the spore closer to the end of the sterigma on which it rests. At the start of the coalescence process, the drop and spore exerts on each other forces of equal magnitude but in opposite direction (F_D and F_S). The expected downward displacement of the spore is prevented by the presence of the sterigma giving rise to a reaction force F_{St} acting at the point of contact between the spore and the sterigma. In late coalescence, the momentum of the drop is transferred to the spore which was immobile until then. The transfer of momentum is equivalent to a force F_{SD} applied at the center of mass of the spore complex. This force puts the sterigma under tension, which will resist until the force exceeds the fracture force F_B , leading to release of the spore. Jumping in humans proceeds in the same way (Fig. 3C). First, the center of mass is lowered to allow the legs to do work on the substratum. At this stage, the gravitational force (F_G) and the ground reaction force (F_R) are balanced. Second, as the legs unfold, the moments at the joints (M) are resisted by the substratum thus providing the impulse (I) necessary to accelerate the center of mass. Third, late in the jump, the fast-moving upper body starts to entrain the legs, which to this point were moving slowing upward. Finally, after take-off all body parts are moving at similar speeds and only gravity acts on the body.

Slow movements

Of course, not all movements exhibited by plants are rapid. Plants are able to move their organs (i.e., shoots, leaves, and flowers) slowly, often in response to stimuli such as light or gravity. If the direction of

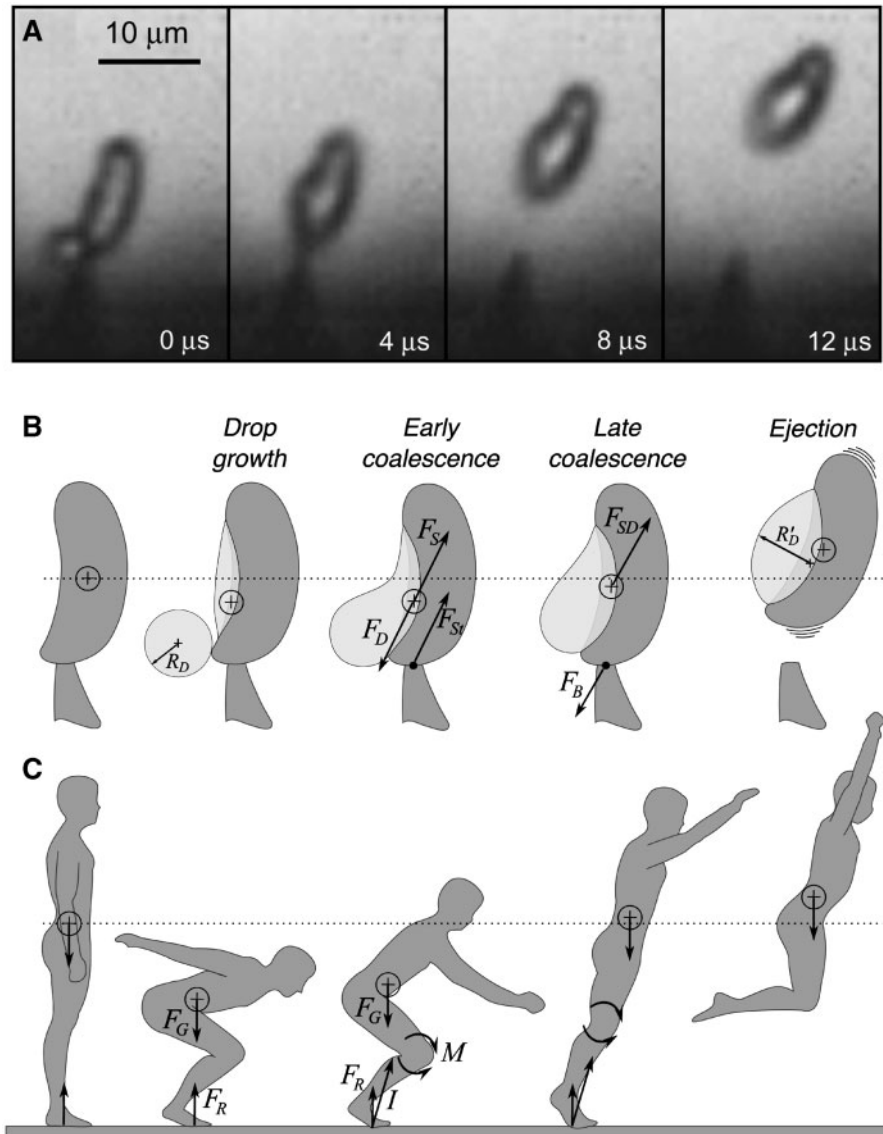


Fig. 3 The surface-tension catapult of basidiomycetes. (A) Ballistospore ejection in *Auricularia auricula* filmed at 250,000 fps. The first frame shows the drop of water at the base of the spore. The second frame shows the spore immediately after fusion of the drop. The following two frames show the spore in flight. (B) The four stages of ballistospore ejection defined with respect to the forces acting on the spore. (C) The corresponding stages in jumping Modified from Noblin et al. (2009).

the stimulus determines the direction of movement, this movement is defined as a “tropism” (Firn and Myers 1989, Braam 2005, Esmon et al. 2005). If these movements are not related to the direction of the stimulus, they are termed “nastic.” Slow movements of plants are mainly due to changes in the water status of cells and cell walls, growth processes and generation of growth stress. Growth-mediated movements naturally occur in living tissues, whereas changes in the water status of cells and cell walls can occur even in dead tissues. In this section, we explain the basic principles of slow movements of plants, using examples of living and dead tissues to

illustrate how the architecture of the cell and cell wall direct the deformation of plant organs.

Slow movements in living plants

In living plants, movements can be mediated by actively varying the internal pressure (turgor) of cells through uptake or loss of water. If changes in volume occur differentially or antagonistically at opposite sides of the plant organ (Firn and Myers 1989), reversible bending and/or rotation of an organ or the whole plant is achieved. The amplitude, speed and frequency of these movements are limited by the number of cells involved, the capacity and rate

of uptake and loss of water (Morillon et al. 2001) and the visco-elastic properties of the cell wall. Macroscopic movements mediated by this mechanism can be completed within $100\ \mu\text{s}$ (Skotheim and Mahadevan 2005).

The opening and closing of stomata for gas exchanges are a well-studied example of reversible changes in turgor leading to movement at the cellular level (Roelfsema and Hedrich 2005). Macroscopic movement of a leaf can be achieved by a pulvinus, a hinge-like structure at the base of the petiole, which consists of specialized motor cells that change antagonistically in turgor pressure (Fig. 4a). According to the nature of the stimulus, the resulting movements are defined as nyctinastic (sleep movements), seismonastic (folding of leaves of *Mimosa pudica*; Datta 1957; Kameyama et al. 2000) or heliotropic (solar tracking; Wainwright 1977; Ehleringer and Forseth 1980).

In other cases, movements are irreversible as the elastic deformation of tissues due to uptake or loss of water is inherently accompanied by differential growth. Phototropism and gravitropism are well known movements caused by differential growth at opposite sides of the shoot: plants bend towards light (Koller 2000; Whippo and Hangarter 2006) and align with the earth's gravitational field (Moulija and Fournier 2009).

Floral heliotropism, which has evolved in a variety of plant species (Kevan 1975, Luzar 2001), has been suggested to be closely related to phototropism (Sherry and Galen 1998). However, the flower stem represents an upright beam, which is fixed at one end, whereas the other end, the flower, tracks the sun over an angle of $\sim 180^\circ$. Motor cells, like those in the pulvinus, have not been identified in flower stems—neither has torsion. One way to elucidate the underlying mechanism of floral heliotropism is to

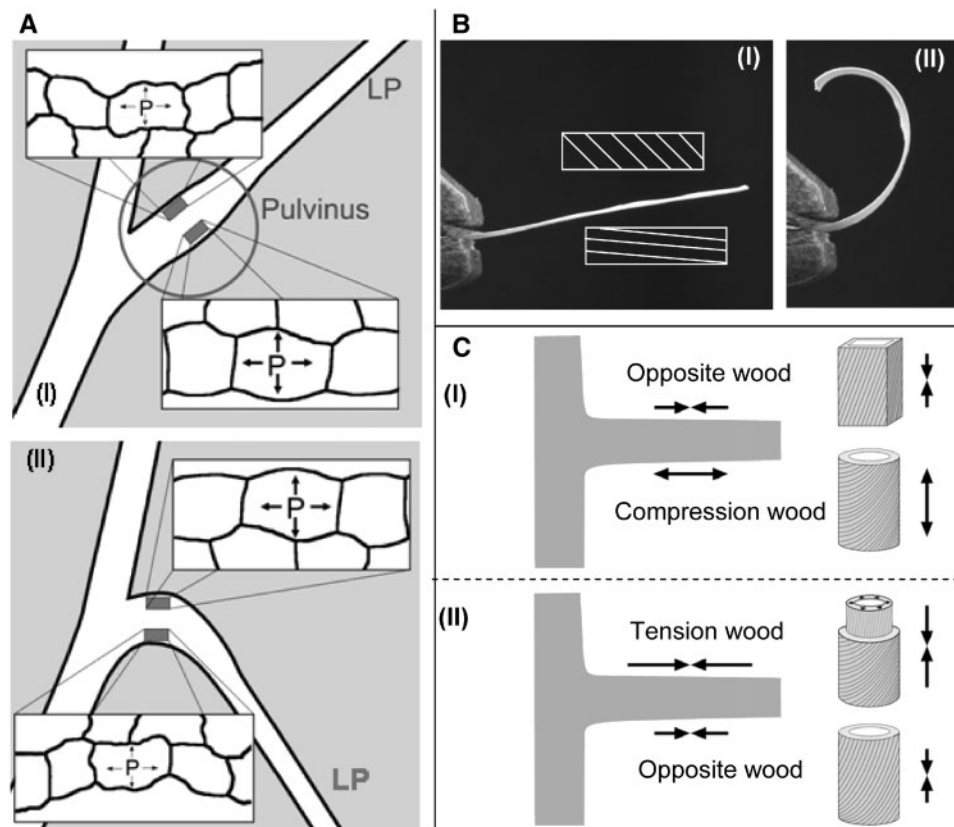


Fig. 4 (A) Schematic drawing of a pulvinus at the base of a leaf petiole (LP) adapted from Kameyama et al. (2000). (I) Inclined state with insets showing cells of the upper side with a low turgor (P) and cells of the lower side with high turgor; (II) declined state with turgor distribution reversed. (B) Drying experiment with a bi-layer containing regular spruce wood (small microfibril angle) at the underneath side and compression wood (high microfibril angle) at the upper side; (I) wet bi-layer straight, (II) dry bi-layer curved, illustrating the working principle of various seed-dispersal systems upon drying, such as those of pine cones or wheat awns. (C) Schematic drawing of the stress-generation principle in reaction wood of trees and the role of microfibril orientation in the cell walls, (I) compression wood in gymnosperm trees (II) tension wood in angiosperm trees; arrows indicate sense and magnitude of stress generation.

track the 3D-movement of the stem to distinguish between irreversible movements caused by differential growth and reversible movements caused by changes in turgor.

Stress generation and slow movements by swelling/shrinking

Some plants utilize the orientation of cellulose microfibrils in their cell walls to actuate organs by swelling or shrinking and to generate growth stresses (Burgert and Fratzl 2009). The underlying principles can be nicely illustrated for dispersal systems in a variety of plant species, which can be actuated by changing the hydration status of their cell walls. In several of these systems, bending is accomplished by bi-layered structures consisting of two distinct tissue types. Cells from one part of the bi-layer have cellulose fibrils oriented almost parallel to the cell axis, whereas cellulose fibrils in the opposite layer are oriented randomly or perpendicular to the cell axis. Upon drying, the hygroscopic matrix polymers between the cellulose fibrils shrink, and the tissues deform mainly perpendicular to the cellulose fibril orientation, since deformation parallel to the fibril axis is largely restricted due to their high stiffness. As a consequence, one layer shrinks more than the other along the longitudinal axis, resulting in a bending of the bi-layer upon change in moisture (Fig. 4b). This deformation principle can be found in several dispersal systems, including pine cones and wheat awns (Dawson et al. 1997, Elbaum et al. 2007, Reysat and Mahadevan 2009).

The orientation of cellulose fibrils also plays an important role when tensile or compressive stresses are generated in woody tissues to support leaning stems and branches (Donaldson 2008). In so called “reaction wood” tissues of trees, the orientation of cellulose fibrils in the cell wall is adjusted to generate stresses and change the direction of growth. The reaction wood of gymnosperms, called compression wood, is formed on the underside of leaning stems and branches and generates compressive stresses. It has a much greater cellulose microfibril angle than regular woody tissues, which typically generate moderate tensile stresses (Fig. 4c). According to calculations by Yamamoto (1998) a microfibril angle above $\sim 30^\circ$ is needed to generate compressive stress. Further evidence for an important role of cellulose orientation has been shown in a recent study in which an additional swelling of already wet cell walls by salt treatment led to longitudinal shrinkage of regular cells but to longitudinal elongation of compression wood cells (Burgert et al. 2007).

The reaction wood of angiosperm trees, called “tension wood,” develops on the upper side of leaning stems and branches and generates high tensile stresses. Tension wood produced by approximately half of the species consists of an additional cell-wall layer. This “G-layer” consists of almost pure cellulose, oriented parallel to the cell axis. Although the specific function of the G-layer in the generation of stress is still debated (Clair et al. 2008, Goswami et al. 2008, Mellerowicz et al. 2008), it is well established that the parallel orientation of the cellulose fibrils plays a crucial role and that very high tensile stresses in tension wood are associated with formation of the G-layer (Fang et al. 2008) (Fig. 4c). Interestingly, fibers containing a G-layer have been found also in other species that generate relatively slow moving organs, such as tendrils (Bowling and Vaughn 2009) or contractile roots of perennial plants (Fisher 2008, Schreiber et al. 2010), possibly pointing to a general principle of tensile stress generation by this stiff and highly expansible inner cell-wall layer (Goswami et al. 2008).

Indeterminate growth and ontogenetic mechanical shifts

There is an aspect of the great animal-plant divide that is probably crucial for understanding differences in evolutionary process and ecology between the two groups. It concerns the generally determinate growth pattern of animals and the generally indeterminate growth pattern of plants. Plants, for sure, develop a lot of determinate organs such as leaves, flowers and seeds, but in many plants, overall form and size is indeterminate. Big changes in form and size engendered by simple changes in growth of primary meristems, such as the apical meristem or secondary meristems such as wood-forming tissue, can produce profound differences in size and shape that are not generally feasible with the developmental plan of many animals. A baby rhinoceros will develop more-or-less to the size and shape of an adult rhinoceros whatever the prevailing ecological conditions. Heaven help rhinoceroses if environmental change dictates that large body size no longer fits into the new state of things. A fig seedling, on the other hand, can grow, flower and survive as an environmentally challenged shrub or, under ideal conditions, as a big tree by relatively simple changes in height, diameter and branching.

We are increasingly of the opinion that this developmental plasticity of size and form in plants is widespread in evolutionary contexts via heterochrony (Gould 1977). Ancestors may produce derived forms

that differ considerably in size and shape via a simple change in developmental rate or limit. When we talk about size and form in plants, biomechanics can play an important part in comprising some of the traits that distinguish growth forms such as trees, shrubs, climbers, and herbs and their appearance or disappearance across phylogenies. Recent studies combining phylogenetic and biomechanical analyses have shown that during radiation in a non-forested region, plants can escape from the specialized developmental constraints characterizing highly flexible lianas merely by retaining juvenile biomechanical characters, such as stiff early wood, in shrub-like descendants (Lahaye et al. 2005).

Growth forms and physical complexity in the ecosystem

Plants constitute the physical and structural complexity of many ecosystems, particularly tropical rain forests. Trees, climbers, epiphytes, hemi-epiphytes and herbs are major players in producing the three-dimensional structure that provides the niches for other plants and animals. This complexity is not only three dimensional but fractal: trees may host big woody vines, called lianas, big lianas may host lesser vines, vines may host small epiphytes, and so on. Different growth forms can have very different self-supporting, climbing, attaching, dangling—sometimes even strangling—biomechanical requirements (Rowe and Speck 2005). Here we discuss some recent approaches in the biomechanics of plant growth form with reference to the diversity of growth forms in the tropical rain forest.

Early growth

Forest trees have entirely different mechanical requisites compared with the slender climbers that attach to them. Trees need to be self-supporting throughout their entire life history and must remain stable in terms of their own static loading as well as any dynamic forces produced by their environment. Many climbers need to be initially self supporting in order to reach supports but then they need to develop flexibility and toughness in their relatively slender stems to survive excessive mechanical stresses when host trees sway or are buffeted by the wind. Early development of seedlings and saplings in the understory is constrained by availability of light. For trees, the ability to remain upright and reach maturity depends on developing sufficiently rigid and stiff stems when faced with limited light. Current studies are uncovering how young woody plants manage to retain an upright orientation via fine-tuning stem

biomechanics, gravitropic responses, and formation of reaction wood in the forest's understory (Alméras et al. 2009, Jaouen et al. 2007). For lianas, eventual success depends on efficient attachment to hosts after which extension growth towards light can be prioritized over growth in diameter and the need for stability (Isnard and Silk 2009). Tropical tree species have recently been shown to possess several distinct types of reaction wood, with and without specialized cells containing a G-layer (Clair et al. 2006). Tropical climbers show a dazzling range of attachment mechanisms that vary from twining stems, tendrils, roots and a wide variety of hooks, spines, and adhesive structures, all having their own biomechanical novelties. Ongoing studies are showing how diverse modes of attachment are linked with different kinds of stem biomechanics: species that attach quickly and rapidly by stem-twining, usually develop highly flexible stems rapidly, whereas species that attach via loose hooks only develop highly flexible stems after an extended “stiff” phase of growth (Rowe et al. 2006). Some climbers rely on a large number of relatively weak attachment organs that can pull off or detach without damaging the slender climbing stem. Other climbers produce very strong, tough points of attachment such as thickened hooks that will only fail after many kilograms of equivalent force and many times the weight of the climbing stem. Yet other climbers do not really have any specialized attachment organs but finally secure highly flexible stems when specially angled branches are engaged in the surrounding vegetation (Gallenmüller et al. 2000, Ménard et al. 2009).

Trees and climbers probably carry out biomechanical battles in terms of wood production. In some cases, twining stems or clasping and coiling attachment organs might suppress the production of wood and secondary phloem by the host; in other cases growth of wood by trees appears to inhibit growth of wood by twining lianas facing the trunk.

Mature growth

Stiffness, flexibility and toughness are also important during mature growth after the establishment of different growth forms. Tree-falls and occupation of the gaps that form are an important aspect of tropical forest dynamics. Flexible and tough stems and roots of growth forms that can survive the mechanical stresses during tree-falls are more likely to thrive in the light gap that forms. Ongoing studies investigating “a year in the life” of liana seedlings and reiterative shoots suggest that in the subsequent race for

light after trees fall, reiterative shoots developing from stems surviving tree-fall gaps may grow more vigorously and faster than seedlings. Toughness and resistance to failure in stems of diverse tropical growth forms is little studied. Lianas are famously capable of surviving extreme stresses and strains and have evolved anatomical organizations capable of surviving extreme bending, shear, and torsion as well as preventing complete fracture via derived anatomical variations of secondary growth (Fisher and Ewers 1991). Such forms often involve radically derived developmental modification of wood, phloem, cortex and periderm. Compared to most self-supporting plant stems, these modified forms are highly heterogeneous structures, which are flexible and may divide or compartmentalize when submitted to overwhelming mechanical strains, thereby saving at least part of the hydraulic supply and functionality of the stem.

Our understanding of how different tropical rain forests modify their growth forms in response to mechanical perturbation is only beginning. Clearly, different growth forms show different mechanical architectures and likely respond to mechanical stresses differently. Part of the problem in determining how plants respond to mechanical perturbation is in controlling or dosing comparable amounts of mechanical strain under experimental conditions, which are difficult to replicate in the field. Recent studies suggest that an experimental woody liana shows different thresholds in response to mechanical perturbation, measured in terms of growth in diameter and length, compared to tree saplings (Coutand et al. 2010). Unraveling how different parts of the plant respond to mechanical perturbation in different ways and produce the appropriate mechanical properties in adjacent, but functionally different, organs (e.g., a tough woody attachment hook borne on a flexible segment of a climbing liana) is a fascinating aspect of how developmental patterns either interact or are isolated from environmental factors.

Comparative biology

Diversity of growth forms in rain forests has an important comparative component; size, shape, form and mechanical properties all result from the diverse phylogenetic histories of trees, lianas, and epiphytes. Angiosperms (monocotyledons and dicotyledons), ferns and gymnosperms possess different organizational plans and develop different growth forms with differing phylogenetic constraints. These can radically influence the ways biomechanical traits are combined to produce trees, lianas or epiphytes

(Niklas 2000), and can also lead to highly divergent and sometimes bizarre growth forms. Palms, for example, are common in many tropical ecosystems and include both tree palms and climbers. However, palms are not able to develop wood as can dicotyledonous trees and climbers. Some of the climbing palms from Southeast Asia, known as rattans, are among the longest plant stems known, reaching lengths of up to 200 m (Tomlinson 2006). Studies on the biomechanics of rattans have shown that over 90% of the stem's rigidity is lost in the transition from young, support-searching stems to flexible old stems. High flexibility is necessary for many slender climbers so as to survive movement and swaying of the canopy. Whereas most woody lianas (dicots) develop highly flexible wood, palms cannot produce wood at all but develop the required flexibility by shedding the stiff fiber-rich leaf sheath (Isnard and Rowe 2008). Since the essential attachment hooks are lost along with the leaf sheath, climbing stems of rattans must continue to produce more searching stems—along with additional hooks—just in order to stay attached to the canopy (Putz 1990). Evolution of climbing in palms resulted in a novel way of producing stem flexibility that in turn resulted in a kind of “Red Queen” dynamic: in order to stay attached to the forest canopy, the plant stem has to keep growing in length. The extreme length of rattan stems therefore resulted from a combination of phylogenetic constraint (absence of wood) and novel integration of biomechanical traits (stiffness, flexibility, hook attachment) necessary for the climbing habit.

Clearly, biomechanical approaches are just one feature of the plant's life history that has an important impact on tropical plant diversity. These approaches should ideally be integrated with other approaches including phenology, developmental plasticity, ecophysiology, and in particular the functionally related approach of plant architecture—the development and organization of organs on the plant's body (Barthélémy and Caraglio 2007).

Mechanical adaptations to hydrodynamic loading

Wave-swept rocky shores present some of the most physically demanding conditions on the planet. At low tide, intertidal organisms experience terrestrial stressors: large temperature fluctuations, desiccation, and increased insolation (Denny and Wethey 2001, Tomanek and Helmuth 2002, Denny et al. 2009). At high tide, waves breaking over the rocks impose extreme water velocities, often in excess of 10 m s^{-1}

(Gaylord 1999, Denny and Gaylord 2002, Denny 2006). Despite these physical rigors, wave-swept environments host diverse and productive assemblages of life (e.g., Leigh et al. 1987, Paine 2002), the ecology and physiology of which have long been the focus of research (e.g., Paine 1966, Wolcott 1973, Somero 2002, Harley and Helmuth 2003).

Plants and seaweeds on wave-swept shores face a particular challenge: they are attached to the substratum. Whereas intertidal animals such as crabs and snails can, for instance, retreat to sheltered crevices and avoid the full brunt of low-tide temperature increases or high-tide wave action, intertidal macrophytes and macroalgae must endure the vagaries of climate and waves in place, tethered to the rock.

Here we focus on physical adaptations of macroalgae in response to the intertidal hydrodynamic environment. Macroalgae have largely adapted to the violent motions of water on wave-swept shores through increased flexibility and extensibility, allowing them to bend, reconfigure, and generally “go with” wave-induced flows (Vogel 1984, Koehl 1984, 1986, Denny and Gaylord 2002). We describe recent findings on three fronts. First, we describe insights into the ways in which macroalgae reconfigure, or change shape when subjected to flow, and thereby reduce wave-imposed forces. Second, we profile investigations at cellular and molecular levels that have revealed surprising adaptations of segmented calcified algae. Finally, we detail a novel understanding of the mechanisms by which repeated wave-induced forces can cause macroalgae to break and dislodge from the substratum.

Reconfiguration of wave-swept seaweeds

Intertidal macroalgae reduce hydrodynamic forces through reconfiguration: they passively bend and change shape and size when subjected to flow (Vogel 1994). For these seaweeds, reconfiguration has been characterized as a “prerequisite for survival” (Harder et al. 2004) because wave-swept macroalgae cannot re-locate to avoid the high velocities generated by breaking waves. Thus, macroalgae serve as excellent model organisms for understanding how morphology and structural properties alone influence hydrodynamics. Furthermore, resulting insights may elucidate the fluid dynamics of animals, since passive aspects of lift and drag in animals may be governed by similar principles.

Hydrodynamic and solid-mechanical processes function simultaneously during reconfiguration of macroalgae (Vogel 1994). When subjected to flow, flexible macroalgae bend and change shape, and the

associated process of reconfiguration has been quantified through a number of methods (e.g., Vogel 1994, Gaylord and Denny 1997, Sand-Jensen 2003, Boller and Carrington 2006b, Statzner et al. 2006). Two morphological shifts influence drag during reconfiguration: algal area projected into flow is reduced and algal shape, quantified by the drag coefficient, changes (Boller and Carrington 2006b, 2007) (Fig. 5). Through these changes, reconfiguration reduces drag forces imposed on macroalgae, compared to forces imposed on rigid bodies. The morphological changes involved in reconfiguration point to alternate strategies: similar reductions in drag-force can be achieved either through reduction in projected area or through reduction in drag coefficient, which accompanies a change in shape (Boller et al. in preparation).

Data on flexibility and reconfiguration may provide insight into the evolution of morphological diversity in intertidal macroalgae. Reconfiguration in fast-moving water reduces morphological variation as flexible algae are compressed into similar shapes (Boller and Carrington 2007). Convergence in shape may, in large part, release macroalgae from the selective pressures applied by drag, allowing fronds to develop myriad flexible morphologies and perhaps allowing other selective processes, such as light interception (Stewart and Carpenter 2003), reproduction (Parker 1981), or space competition (Carpenter 1990), to dominate. Reconfiguration may similarly factor into the evolution of intertidal animals with sessile, flexible body forms, such as cnidarians and bryozoans.

Structural adaptations of segmented seaweeds

Although flexibility is central to the survival of most wave-swept seaweeds, rocky coastlines around the world are prime habitats for calcifying coralline algae, which fortify their cell walls with calcium carbonate (Borowitzka 1977, Johansen 1981). How can we reconcile the importance of flexibility with the abundance of rigidly-calcified algae in the intertidal zone? Whereas many coralline algae grow prostrate along the substratum, forming crusts that avoid the brunt of wave forces and use the rock for mechanical support, other corallines grow complex upright fronds that bend in the surf by virtue of articulations that separate calcified segments (Fig. 6). Thus, the paradigm of flexibility even extends to many calcifying algae.

Segmentation permits calcified coralline fronds to bend (Martone and Denny 2008a), to reconfigure (Boller et al. in preparation), and to resist breakage

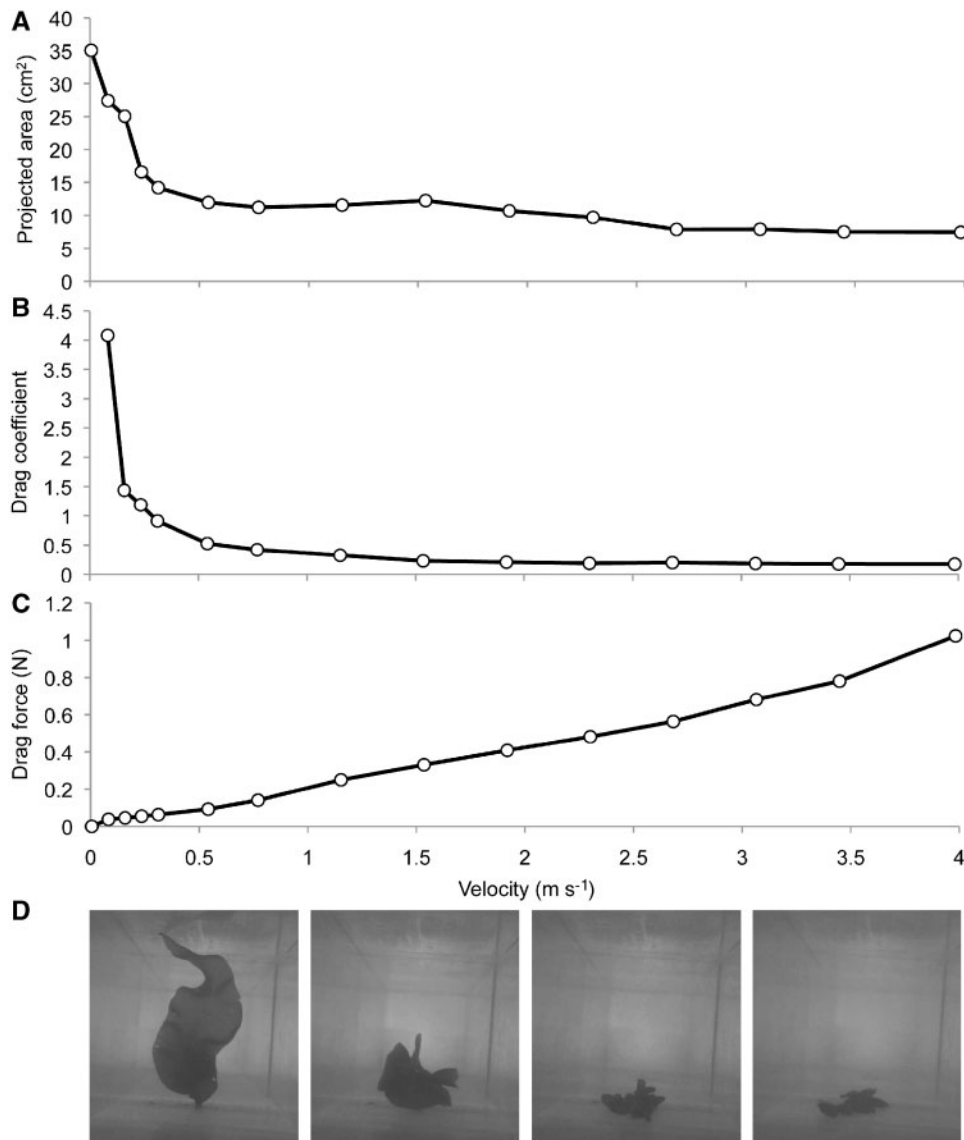


Fig. 5 Reconfiguration and drag force experienced by the macroalga *Mazzaella*. As water velocity increases, (A) frond area projected into the flow decreases, (B) drag coefficient—a measure of shape—decreases, while (C) drag force increases. (D) Changes in shape and size can be documented by photographing seaweeds upstream during reconfiguration.

(Martone and Denny 2008b) much as do fleshy seaweeds. However, the details are quite different. Unlike fleshy seaweeds, which are generally flexible along their entire length, articulated coralline algae are flexible only at discrete joints along their otherwise rigid thalli (Fig. 6A and B). Recent studies of the articulated coralline *Calliarthron* have shown that articulations have distinct morphological and mechanical properties that maximize flexibility, reduce the risk of breakage, and permit fronds to thrive—and sometimes outperform—their fleshy counterparts.

Using a computational model, Martone and Denny (2008a) demonstrated that basal segments of

the articulated coralline *Calliarthron*, which experience the greatest bending moments in flowing water, have a near-optimal morphology that maximizes bending and minimizes amplification of stress. For example, basal joints are longer and are more closely spaced than are joints positioned near the apices of fronds. Furthermore, basal joints resist significantly more force than do apical ones (Martone 2006), which likely contributes to the survival of fronds under breaking waves, since basal joints must resist drag forces experienced by entire fronds in flowing water whereas apical joints only need to support a few distal segments. *Calliarthron* joints are significantly stronger, tougher, and more extensible

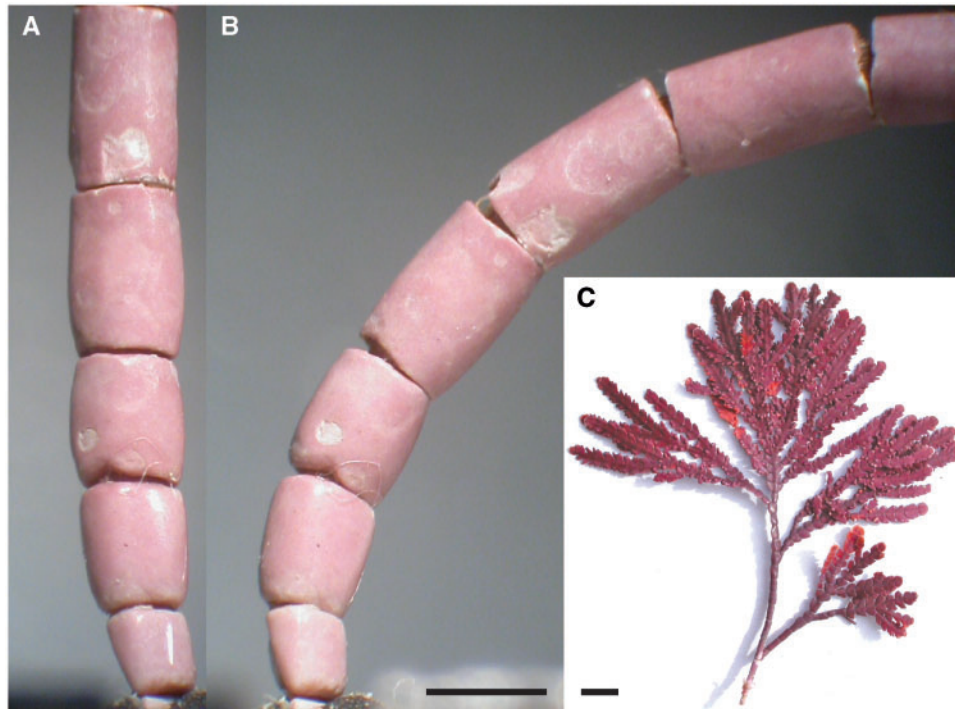


Fig. 6 Morphology of the articulated coralline alga *Calliarthron*. (A) Calcified segments, called intergenicula, are separated by flexible joints, called genicula, which allow articulated corallines to (B) bend and (C) produce complex erect fronds even in hydrodynamically stressful environments. In A and B, scale represents 2 mm; in C, scale represents 10 mm.

than are tissues produced by fleshy algae (Martone 2006, 2007, and unpublished data). These distinct material properties have led to several ongoing studies of cell-wall structure and chemistry that underlie mechanical performance. Histological studies have shown that *Calliarthron* joints are composed of long cells surrounded by cell walls that thicken over time; mature tissue is more than 50% cell wall in cross-section, which likely contributes to its great strength (Martone 2007). Further study has demonstrated that cell-wall thickening represents the addition of secondary walls, structures that had never before been described in seaweeds and were thought to develop only in the xylem tissue of terrestrial plants (Martone et al. 2009). This exciting example of convergent evolution extends even to chemical composition. In terrestrial plants, secondary cell walls contain lignin and cellulose, which lend mechanical support to upright stems and, when present in abundance, form “wood.” Recent studies have now demonstrated that secondary walls in the coralline *Calliarthron*, which lend mechanical support to coralline algae in the surf, also contain lignins (Martone et al. 2009) and crystalline cellulose (Martone unpublished data). Such profound similarities in cell-wall structure and chemistry among terrestrial plants and this highly derived group of

marine coralline red algae have raised new questions about the evolutionary history of lignin biosynthesis and of the development of secondary cell walls (Martone et al. 2009).

Together, these studies of biomechanical, structural, and chemical adaptations of segmented coralline algae have paved the way toward future studies exploring the evolution of flexible articulations in other groups of calcifying algae. For example, phylogenetic analyses suggest that, even among the red algae, articulated corallines evolved from crustose corallines three separate times (Bailey and Chapman 1998)—a result that is strongly supported by structural and developmental differences in their joints (Johansen 1969, Johansen 1974). Furthermore, calcifying green algae, such as *Halimeda*, also produce articulated thalli with flexible joints, which are completely distinct from those produced by the corallines. In other words, flexible joints are nonhomologous structures that evolved independently in several lineages of segmented calcifying algae—a common solution to the biomechanical constraints of calcification. Future studies will reveal whether joints in each lineage of segmented algae contain lignins, develop secondary walls, and have distinct material properties like the intriguing coralline *Calliarthron*.

Failure by fatigue in wave-swept seaweeds

Full understanding of macroalgal adaptation to the extreme hydrodynamic environment of wave-swept shores requires knowledge of the mechanisms of macroalgal breakage and dislodgment; when do wave-imposed forces exceed macroalgal strengths and result in failure? The question suggests a straightforward approach. First, determine the nature of loadings imposed by waves. Second, measure strengths of seaweeds in this mode of loading and compare them to the largest wave-imposed forces. This approach has been pursued repeatedly. Biomechanical studies have established that, for the many seaweeds that reorient nearly completely in the direction of flow, wave-induced water velocities primarily exert drag force in tension (Gaylord et al. 1994, Gaylord 2000, Boller and Carrington 2006a). In laboratory and field experiments, tensile “pull-to-break” strengths of macroalgae have been measured, along with strengths in other loading modes when relevant (e.g., Hale 2001, Carrington 1990). A problem, however, then arises. Comparison of measured strengths and drag forces imposed by the largest wave-associated water velocities suggests that macroalgae should rarely break, often under-predicting observed rates of breakage (e.g., Koehl and Alberte 1988, Friedland and Denny 1995, Utter and Denny 1996, Denny et al. 1997, Kitzes and Denny 2005).

To address this discrepancy between prediction and reality, an alternative mechanism of breakage has been recently assessed. As mentioned, wave-imposed water velocities can be extreme. In addition, wave-induced flows are repeated, with more than 8000 waves striking shore each day. Given repeated imposition of force on seaweeds, failure may occur by fatigue, with damage accumulating over the course of repeated loadings (Hale 2001, Mach et al. 2007a, 2007b). Laboratory tests on the red macroalga *Mazzaella* have shown that this seaweed breaks by fatigue, much like other engineering and biological materials such as elastomers and bone (Mach 2009). In conditions of repeated loading, small cracks eventually form in seaweed tissues and then grow in length until rupture occurs. Extrapolation from the laboratory-measured fatigue behavior indicates that *Mazzaella* blades in the field likely fail by fatigue, with large fronds more susceptible to breakage than small fronds and with the female-gametophyte phase most vulnerable to fatigue failure (Mach 2009). Additionally, laboratory studies suggest costs of endophyte infection and specific tradeoffs between reproduction and breakage (Mach 2009). Fatigue cracks, the initial points of failure in

the fatigue process, often form in association with endophytes and with reproductive structures in female-gametophyte blades.

Many organisms, plant and animal, terrestrial and marine, experience repeated loadings from waves, wind, and locomotion. Nonetheless, much biomechanical investigation in all these contexts has focused on single applications of force. Recent findings about fatigue in *Mazzaella* provide a reminder of the utility and perhaps necessity of considering repeated forces when investigating the performance and evolution of organisms.

Biomimetic inspiration

Biological structures are ideal role models for the development of bio-inspired technical packaging and containments. The best-known example is the large egg of the ostrich, *Struthio camelus*, which is referred to as one of the most prominent examples of natural multifunctional packaging (Küppers 2004, 2008, Bappert and Hacker 2005). These functions include mechanical stability, controlled gas exchange, protection against bacterial invasion and passive temperature control by surficial reflection of UV-radiation—all of this with a very limited amount of overall material necessary. In terms of sustainability, natural packaging leads the way as it is always biodegradable with a lifespan regulated by the organism. A second well-known example of biological packaging is the coconut, *Cocos nucifera*, which is typically referred to as a nut even though, from a strict botanical perspective, it belongs to the drupes with a triple layered fruit wall, composed of exocarp, mesocarp and the typical hard pit called endocarp. The composition of the fruit's wall is highly shock-absorbing and accounts for the robustness of the coconut. During ripening the thick wall of the fruit is fully hydrated, insulating the kernel from heat and protecting the young embryo from mutagenic radiation. At the same time the fruit's wall allows for gas exchange. Once the coconut has been shed and the wall's function as an impact resistant layer has been fulfilled the middle layer of the wall starts to dry out leaving behind loosely attached bundles of fibers, which increase buoyancy. The kernel survives for several months in salt water until it eventually washes up and germinates on the beach of a new island (Küppers and Tributsch 2002, Nachtigall 2002, Küppers 2004, 2008, Bappert and Hacker 2005).

Very surprising is the fact that, even though these multifunctional properties provide a high potential for biomimetic applications, biological models have

hardly been studied quantitatively in terms of their form-structure-function relationship in order to transfer this knowledge into a technical product (Küppers and Tributsch 2002, Nachtigall 2002, Küppers 2004, Speck et al. 2009).

Biomimetic approaches: bottom-up versus top-down

Biomimetics is a young discipline that combines Biology and Engineering. The goal of biomimetics is to solve technical problems by abstracting, transferring and applying the underlying principle of a biological phenomenon. The transfer is hardly ever a direct copy of the biological solution but rather the transfer of new insights about the biological solution. The transfer into a technical solution therefore must be seen as a creative process, a nature-inspired “reinvention” that generally accounts for multiple steps of abstraction and modification. Biomimetics is highly multidisciplinary, bringing together the expertise of biologists, physicists, chemists, mathematicians, architects and designers. The biomimetic approach can be subdivided into two categories: (1) “Bottom-Up-Process” (Biology Push) and (2) “Top-Down-Process” (Technology Pull) (Speck and Speck 2008).

The “Bottom-Up-Process” starts from results obtained from basic research and is therefore usually initiated by biologists. Once the basic underlying biological and physical principles are understood, engineers and researchers from other disciplines start to enter the process. A typical example of the “Bottom-Up-Process” is the development of self-cleaning technical surfaces which are nowadays available as materials with Lotus-Effect®, originally inspired by superhydrophobic plant surfaces (Speck et al. 2004, Cerman et al. 2005).

The “Top-Down-Process” begins at the engineering side. Usually the starting position is an existing technical product that may be already established on the market, but needs to be improved. Due to the clear conceptual formulation the “Top-Down-Process” usually yields lesser potential for highly innovative leaps than do the “Bottom-Up-Process,” but has the advantage that the development time scale is much shorter. Successful examples of the “Top-Down-Process” are the profile of tires, produced by Continental AG, that was inspired by the foot structure of tree frogs, cats and polar bears, and shock-absorbing pallets that were inspired by hedgehog spines, bamboo, and the morphology of buttress roots produced by tropical trees. These innovations were developed by the Plant Biomechanic Group Freiburg in cooperation with the Institute for

Textile and Process Technology (ITV) Denkendorf, the Institute for Technology-Orientated Design Innovation, Hochschule für Gestaltung Offenbach and Rittal GmbH & Co. KG (Herborn) as industrial partners (Masselter et al. 2008).

Fruit-walls and nutshells

The fruit-walls of nuts and drupes are of special interest for the development of impact-resistant and puncture-resistant materials. As humans have to protect themselves from large amounts of energy freed instantaneously (e.g., during a car crash), some fruits must cope with the impact on the ground after being shed. Understanding how various hierarchical combinations of structures and materials yield fully functional protective layers will permit the construction of new lightweight bio-inspired materials with great resistance to impact and puncture. Current biological role models are the tough seed coat of the *Macadamia* nut, which from a strict botanical perspective is a follicle, the large spongy mesocarp of *Citrus maxima*, and the combined fibrous mesocarp and tough endocarp of the above-mentioned *Cocos nucifera*. All fruit-walls are organized according to at least five hierarchical levels: integral, macroscopic, microscopic, ultrastructural and biochemical. Furthermore, unlike most technical materials used today, the different hierarchical levels usually exhibit gradients within material and structure.

According to the work by Jennings and MacMillan (1980) and Wang and Mai (1995a, 1995b) the structure of the *Macadamia* seed coat is highly optimized for toughness. Due to the relative low density of the seed coat, *Macadamia* even outperforms ceramics and glass when compared on the basis of specific strength and toughness (strength or modulus divided by density) (Wang and Mai 1995a, 1995b). The fruit-wall of *Cocos nucifera* has been mainly analyzed with respect to the mechanical properties of dry coir fiber bundles and dry single coir fibers as they are used in carpets, ropes (Varma et al. 1984), and cushions and seat covers in the automotive industries (Goulart et al. 2000). The Young’s moduli of single dried fibers are in the range of 3–6GPa and the fracture strains in the range of 15–47% when tested under tension (Kulkarni et al. 1981, Goulart et al. 2000). However, neither the entire hydrated mesocarp of *C. nucifera* nor the mechanical properties of the exocarp and mesocarp of *Citrus maxima* have yet been investigated as potential biological materials that withstand impact.

The fruit-wall of *Citrus maxima* is divided into three parts: the exocarp comprising epidermis and

multiple underlying layers of cells, the thick and spongy mesocarp with a large voluminous fraction of intercellular space, and the endocarp consisting of small dense layers of cells that also produce the juice vesicles. Most interesting are the gradual changes in intercellular space in the mesocarp. At the peripheral region the amount of intercellular space gradually increases to ~65% of the total volume. This contribution remains constant within most of the mesocarp except near the endocarp where the amount of intercellular space rapidly decreases. The cell walls that form the spongy mesocarp have a fibrous composition, which is visible even at low magnifications. This non-homogeneous structure of the fruit-wall seems, to a great extent, to control its biomechanical behavior.

The fruits of *Citrus maxima* and *Cocos nucifera* are relatively heavy with typical weights >1 kg. Both lack any aerodynamic adaptation and share the same challenge of having to withstand impact from heights of more than 10 m. Conducting high-speed camera-controlled experiments on *Citrus maxima* freely falling from a height of 6 m and comparing the potential energy of the fruits before and after impact ($n=13$) shows that a high proportion of the energy, possibly up to 90%, is dissipated by the fruit-wall and pulp. Only after several free-fall tests the samples started to display visible outer damage of the fruit-wall. Compressing the fruit-wall in a quasi-static test to 40% of its original thickness yields 50–70% energy loss during one hysteresis cycle. The immature fruit wall of *Cocos nucifera* shows a benign failure behavior with a bell-shaped stress-strain-curve having its maximum stress around 15% strain and failure only at up to 40% strain when loaded in tension nearly parallel to the main orientation of the fibers (Seidel et al. 2009).

The Young's modulus of *Citrus maxima* is surprisingly low with values ranging from 0.14 to 0.45 MPa when tested in compression along the radial axis of the fruit and 0.39–0.98 MPa when tested in tension normal to the radial axis of the fruit (Seidel et al. 2009). The Young's modulus of the immature *Cocos nucifera* mesocarp, obtained from specimens loaded in tension nearly parallel to the orientation of the fibers lies in the range of 10.4–14.6 MPa. The difference between these values and the values reported in the literature (Kulkarni et al. 1981, Goulart et al. 2000) are most likely due to the low lignification and cross-linking of the fiber matrix as the maturation of the tested coconut had only just started. The tensile tests of *Citrus maxima* samples all ended in an abrupt rupture whereas the samples of *Cocos nucifera* showed benign failure behavior with fiber bundles

and fibers breaking in series. The fruit-walls of *Citrus maxima* and *Cocos nucifera* both exhibit properties that are of high interest for the development of biomimetic impact-resistant structures: *Citrus maxima* shows very high deformations of up to 60% strain until failure when tested under tension, and large energy-dissipation during compressive loading and unloading, combined with a high resistance to impact when dropped from significant heights. The fruit wall of *Cocos nucifera*, having a fibrous matrix in contrast to the spongy mesocarp of *Citrus*, also allows for large deformations of up to 40% strain but reveals a benign failure behavior due to the successive rupture of single bundles of fibers. From a structural point of view both fruits achieve their special mechanical properties by hierarchical structuring and using gradients within the material. As the composition of the seed core of *Macadamia* and the endocarp of the *Cocos nucifera* are very similar, we hypothesize that the endocarp of the latter is also optimized for toughness; this will be the subject of further studies.

Future applications

In the future, bio-inspired materials that resist impact and puncture may combine the extraordinary protective properties of fruit-walls and nutshells, including high energy-dissipation, benign failure behavior and almost full recovery from large deformations. A sandwich material consisting of a high energy-absorption outer layer in combination with a very tough puncture-resistant inner layer is most likely. *Cocos nucifera* appears to be the best natural role model for man-made impact-resistant structures but, as impressively shown by *Citrus maxima*, multiple pathways can be used to achieve high energy dissipation. The transfer of the naturally-occurring, organic materials into technical materials like metallic cast alloy and fiber-reinforced composite materials with a matrix made of metal, glass, ceramics or various polymers will be one of the major challenges in the technical transfer.

Potential applications for biomimetic impact-resistant fiber-reinforced materials are vessels for transportation of dangerous goods, e.g., explosives or hydrofluoric acid, helmets and other protective wear, protection of vehicles during impact, and fortification of space stations against meteoroids.

The above examples of bio-inspired impact-resistant materials suggest that there may be many more cases in which animals and plants will both offer innovative solutions for technical problems. With its multidisciplinary approach, biomimetics

also allows students to quickly enlarge their background knowledge and enables them to communicate across borders of scientific fields. Plant–animal interactions, such as insect adhesion on plant surfaces, provide yet another promising field for biomimetic applications, which will undoubtedly require both botanical and zoological perspectives. Collaborators will need to connect their research tightly from the beginning to ensure success.

Outlook

Since its inception, the field of plant biomechanics has grown and blossomed into a diverse discipline exploring all levels of mechanical performance, from the effect of cell-wall chemistry on material properties to the effect of macroscopic structure on higher-order interactions with the environment. In recent years, studies of plant biomechanics have led to the development of biologically-inspired commercial products. Biomechanical studies of new organisms have revealed a broadening range of movements, materials, and structures among diverse taxa, including aquatic algae, fungi, and higher plants. This striking botanical diversity provides a renewed evolutionary perspective on mechanical characters and raises questions about selective pressures that have given rise to organisms that grow, reproduce and, in some cases, move, without muscle. The time is ripe for like-minded plant and animal biomechanists to share ideas and cross-pollinate. We believe that the Society for Integrative and Comparative Biology is an ideal forum for such fruitful collaborations.

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