

## What can we learn from nastic plant structures? The phytomimetic potentiality of nastic structures.

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### ABSTRACT

While some researchers see developments on the nanotechnology scale as the major or exclusive biomimetic trend in the 21st century, others insist that the exploration of the biomimetic potentialities of macroscopic systems has hardly been started. On either scale exploration of biological systems and development of engineering materials proceed in parallel and this provides the opportunity to actively search for similar, convergent solutions and designs in both directions. Recent studies of plant motors ranging from rapid calcium-dependent shape changes in plant proteins (forisomes) to the rapid closure of Venus flytraps and the ultra-rapid opening of dogwood flowers attracted the attention of both biologists and engineers. Here we summarize the principal differences of the nanomotors and macromotors that drive plant and animal movements. Then we describe three types of hydration motors that are common in plants: osmotic, colloid, and fibrous. In engineering electroactive polymers (EAPs) have emerged as new actuation materials with large, electrically induced strain and bending capacity. It remains to be seen whether hydrated EAPs with low voltage-actuation have bioconvergent relevance and proximity to biological situations; in particular plant movements. So far we only know that (i) pH-sensitive poly-ionic polymers like pectins are a common occurrence in the primary walls and occasionally some vacuoles of plant cells, (ii), that strong electric field changes also occur in living tissues, and (iii) that some aspects of their action are not understood and remain a matter of further investigation.

### Keyword list (up to 10):

Phytomimetic design – bioconvergent solutions – nastic movements - plant hydration motors – osmotic motors – colloidal or gel motors - fibrous motors

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### BIOMIMETICS AND BIOCONVERGENCE

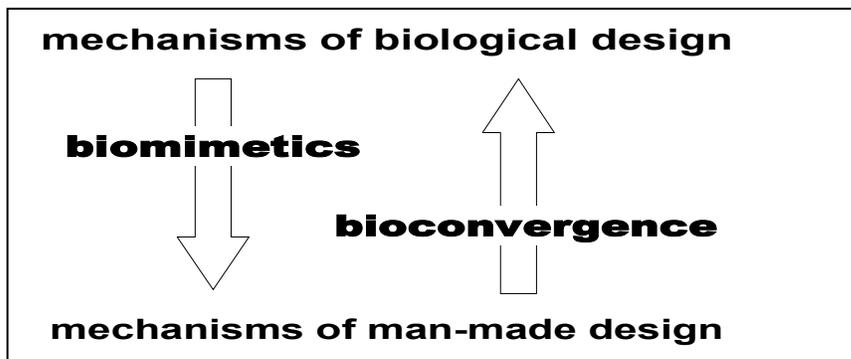
People in our highly specialized modern society and in academia sometimes forget that the separation of the sciences into physics, chemistry, geography, biology, engineering, or molecular biology and functional anatomy, or nano- and macroscale is a matter of human convenience and not of reality. These separations did not exist for plants and animals when they were and are challenged with the opportunity to settle new environments or faced other small to catastrophic

changes in their familiar environment (new predators, new competitors, new climatic factors, human encroachment). For example, plants could not have increased their size and risen from a prostrate to a vertical position if they had not developed a peripheral ring of vascular bundles that served for long-distance water and substance transport as well as for the mechanical enforcement of their stems and if they had not simultaneously experimented with a new phenolic polymer resin (lignin) that would turn the cellulose fibers of their cell walls into a new material (wood, Gordon & Jerominidis 1980) with vastly improved strength.

For the same reason, occasionally a discovery of a specialist has unexpected consequences not only for his own but for other disciplines as well. An example is the physician-biologist L. Galvani who observed the jerking leg movements of dead frogs when they were swinging in the wind on copper hooks and occasionally touched the iron grit of the balcony. Galvani (1791) explained that he had found animal electricity. In this he was opposed by A. Volta who made a model that showed that the frogs were not necessary to generate electricity. His ideas were far from testing Galvani's biological hypotheses about bioelectricity. He got rid of the frogs and created a clean battery made from copper, iron and sulfuric acid as a solvent replacing the wet frog materials. By engineering the portable battery as a source of constant voltage, he prepared the ground for future technical revolutions and established a new scientific discipline – electricity. Using these novel tools, Galvani's biological colleagues later succeeded to understand that indeed an electrical signal in the form of an action potential was necessary to stimulate muscle contraction and so established the new discipline of neurophysiology (Stahlberg 2006). However, physiologists were not trained to prove their theory with working models. In a way this remaining challenge of Galvani's discovery is met only now by those people who attempt the design of artificial muscles on the basis of electro-active polymers (EAPs; Bar-Cohen 2006a). The final outcome will show how practical engineering will fare compared with the original biological design and what muscle physiologists can learn from the workings of this model.

If such a new interdisciplinary approach is recognized and consciously pursued, this is always reflected in a novel and catchy term and definition. When we make an attempt to simulate a function or structure of animals or plants in technical designs, we call this approach *biomimetics* or *phytomimetics* (Bar-Cohen 2006b). However, if we want to emphasize the other side of the process - i.e. the things that biologists can learn from the technical and artificial models and simulations - we are still at a loss of words. Terms like comparative functionality come to mind but are not likely to catch on. When finding that completely unrelated species developed surprisingly similar phenotypic adaptations (e.g. extinct swimming ichthyosaurs looking surprisingly similar to dolphins), biologists call this phenomenon convergent evolution. So we propose that the intended search for biological parallels to technical solutions should be named *bioconvergence*.

Under bioconvergent designs we then understand a design that fulfils a similar function in man-made and biological structures and follows the same or closely related principles and mechanisms (Fig. 1). This term would also include numerous technical inventions that were developed without the awareness that nature had already developed a



**Fig. 1:** The relationship between biomimetics and bioconvergence.

similar device. Table 1 provides a few examples for truly biomimetic and bioconvergent designs. It emphasizes the point that most technical achievements were made without consideration or knowledge of similar solutions existing in animals and plants. The real story behind the data in the table is, that only the inventions of sonar, infrasound radiation, infrared location, etc. put us in a position to realize how nature operated. Before the development of sonar and radar it was wrongly assumed that bats had especially good night vision. It was a bioconvergent idea to propose that bats

operate a sonar-related echolocation. The approach is to actively search for well-understood and implemented technical solutions in biological structures known or suspected to fulfill similar functions. Under the aspect of convergence engineering and biology look into a bright future of mutual stimulation. This said, it is also high time to acknowledge that this work is already going on for some time.

A clear example for a consequent bioconvergent approach has recently been published under the title “Cells, gels and the engines of life” by Gerald H Pollack. This book attempts to explain many known functions and characteristics of living cells as a consequence of phase transitions and other characteristics of gels. In the final chapter “lessons from biology”, it formulates a guideline for

human made designs	biological designs	relationship	reference
barbed wire	Osage orange shrub	biomimetic	Basalla 1988
elastic wire coils	plant tendrils	biomimetic	
VELCRO	burdock pods	biomimetic	Budde 1995
STOL plane	<i>Zanonia</i> seeds	biomimetic	Etrich 1915
gyro-/helicopter	maple seeds	bioconvergent	
parachute	seeds of dandelions	bioconvergent	
infra-red sensing	IR-sensing pits in vipers & beetles	bioconvergent	
sonar location	sonar in bats and moths	bioconvergent	
infrasound	elephant communication	bioconvergent	
electrolocation	<i>Gymanrchos</i> electrical eels	unresolved	

**Table 1.** *Examples for biomimetic (the intentional mimicking of natural design) approaches and the recognition of bioconvergent designs after a technical innovation.*

biologists on how to apply this principle: “To approach an unknown cell-biological mechanism, the instruction manual states, ‘ look first for some phase-transition and proceed from here’ ” (Pollack, 2001). This approach is based on the idea, hypothesis, or suggestion of a functional similarity or parallel between synthetic and natural gels (i.e. cytosol and contents of certain organelles like chloroplasts, mitochondria but not the water-filled vacuoles of plant cells). Bioconvergent gels are already referred to as biorelated gels (e.g. Okano 1998).

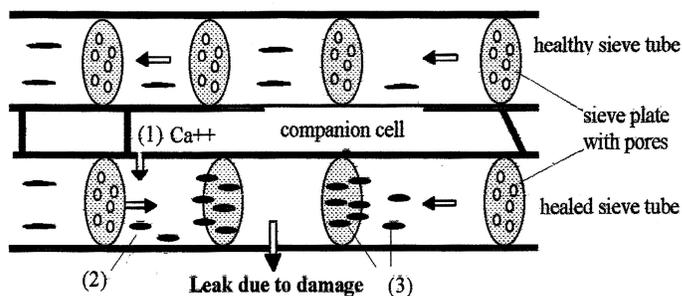
### THE SECRET MATERIAL OF LIFE

Older biology books speak of the cytoplasm as a gel that holds the secrets of life and undergoes gel-to-sol transitions under the influence of external factors like anesthetics. Indeed, cytosolic extracts of both animal and plant cells were often found to form a gel at 25° C and a pH of pH 7 and glucose solution, but reverted rapidly into a more liquid-like hydrosol when cooled to 0 °C. All natural gels are hydrogels with water being dispersed inside the gel. Accordingly, sol-to-gel transitions are modeled as changes in binding sites within a three-dimensional network of fibers; gelation occurs when the affinity for other gel sites becomes higher than for water (with gelation defined as the decrease in gel volume or protein per volume). However, it was soon found out that such gel-to-sol transitions were not a general characteristic of the cytoplasm but associated with specific ATP-dependent motor proteins like actin (Kane 1976; Ishiura & Okada 1979). Similar temperature dependence of gelation at higher temperatures is visible in the fibrous protein collagen (slide). However, not all cell extracts show this behavior and it is not even to be generalized for all fibrous organic molecules; upon warming the fibrous molecule gelatin turns into a liquid hydrosol and returns into a gel-like consistency upon cooling. This is just the opposite of what happens in actin-containing cytoplasm and in collagen.

Following R. Buvat (1969) we can list some interesting characteristics of natural gels:

1. All natural gels are hydrogels. The layers of water on the molecules prevent in hydrogels the strong diffraction of light often found in hydrophobic gels (Tyndall effect).
2. There is no Brownian movement inside the cytoplasm, i.e. there is no thermal agitation of the molecules by their neighbors and diffusion is less than in free solution
3. Cytoplasmic cell extracts show a high surface tension, if cytoplasm exudes from a punctured cell it will assume a spherical shape. This property has been increasingly associated with the cytoskeleton - a contractile fiber matrix near the plasma membrane.
4. Dispersal of colloid particles is enhanced and supported by mutual repulsion by their negative electrostatic charges.

The last point suggests the well-known fact that discharging natural gels near the isoelectric point causes their hydration layers to disappear and the protein to drop out of solution. However, some natural proteins bind more water than others and are therefore able to stay in solution even at their isoelectric point. This certainly applies to super-hydrating mucoproteins that feature a fibrous protein backbone studded with carbohydrate side chains that ensure a high hydration and prevent the precipitation (Wainwright 1995). These proteins are known as mucus in animals and mucilage in plants. These proteogels are the filling material of internal water-storing cells of xerophytic plants from the cactus and lily families (e.g. the medicinal gel of *Aloe vera* – a member of the lily family) that adapted to water storage to survive in very dry habitats (Englmaier 1987). The occurrence and characteristics of natural mucoproteins can teach us a lot from the making of desiccation-resistant hydrogels, natural encapsulation and release of substances (Verdugo & Orellana 1995), synthesis of new reversible and biocompatible adhesives (Yang & Robinson 1998) to the water transport in the vessels of plants where such substances have recently been found (Zimmermann et al. 1994; Pollack 2001; Crews et al. 2003). Many super-hydrating colloids in plants are still unidentified. All we know is that they often contain both carbohydrate and protein polymers and are summed under the name of mucilage (similar to mucoproteins in animals; Wainwright 1995). Although lots of sticky mucogels exist already in many plant seeds to attach them to a wet ground for germination, nothing beats the hagfish that can exude up to 5 liters mucus and fibers in a few seconds. This mixture rapidly hydrates and expands into a protective gel layer that stops the attacker short or even ensnares and suffocates him (Vincent 2006). The biomimetic design of polymers and interfaces similar and compatible to the molecules of life - is one challenge to modern science. Due to huge medical, biotechnological and technological expectations, soft, active materials have quickly established a category of their own. On the other hand, by following the design of natural shells of muscles and nuts, it is also possible to engineer hard materials with hugely superior characteristics relative to the brittle ceramics we are using today.



**Fig. 2.** Self-healing by conformation change of dissolved slim protein bodies (forisomes) into plugs that seal the system at the holes of the sieve plates. Leakage induces (1) calcium influx, (2) inflation of forisomes, and (3) isolation of the leaky element from the rest of the pressurized tubing network.

Another interesting mixture of slimy proteins has been discovered in the sugar-conducting phloem tubes of plants. These P-proteins or forisomes are a coherent mixture of proteins with an elongated shape. Under the simple influence of calcium ions these elongated bodies contract undergoing a conformation change from slim and elongated to short and bulky (Knoblauch et al. 2003, Mavroidis & Dubey 2003). These devices are currently tested as potential micromotors that have the unique characteristic not to require ATP. Their role in the plant is that of a self-healing agent. The sugar-conducting phloem tubes are under high pressure and wounding would therefore lead to the rapid depletion of resources. Wounding, however, goes along with a massive influx of calcium ions from the surrounding cell walls and under this influence the forisomes transition into bulky plugs that are carried with the pressure-driven mass flow towards the wound site. Since they now no longer fit through the holes of the sieve plate walls between phloem

elements they plug them up and so prevent further flow towards the injured phloem site (Fig. 2). This, the biological use of forisomes, is only one of the many possibilities that arise once a promising protein or mucilage has been identified. This example shows that simple microscopic screening for larger protein or mucilage bodies can identify potential candidates for micro- and nanomotor action as a first step. These should be replaced by constructs that mimic the original function but allow other characteristics to be optimized. A good example for such an approach is the semi-synthetic production of a protein-polymer mix that simulates the properties of mucoproteins. Using recombinant DNA, Petka et al. (1998) created artificial (i.e. modified natural) proteins that underwent reversible gelation in response to pH and temperature. The combination of the intended coiled protein aggregates with water-soluble poly-electrolyte polymers prevented the precipitation of the protein by creating a three-dimensional gel net that could be dissolved by small steps of elevated pH or temperature; an ideal encapsulation device for the delivery of drugs. Hence this artificial combination simulates properties of natural mucoproteins.

## THE MOTORS BEHIND PLANT MOVEMENTS

When the journal *Science* published an interesting set of papers on “Movements: molecular to robotic” in the year 2000, two plant scientists pointed out that the editors completely forgot the movements of plants (Leopold & Jaffe 2000). Such incidents show that the plants’ potential for bioconvergent technical designs has been explored superficially at the most. In the past only a few conspicuous plant structures have served as the basis for the successful phytomimetic design of structures (see Table 1). While it was sometimes very easy to proceed from the natural design to a phytomimetically inspired concept (barbed wire, gyrating and gliding seeds), current and future efforts require much more work and interdisciplinary effort to fully understand, mimic and modify the time-tested structures and machines plants developed and perfected over millions of years of evolution.

Life originated in water. Plants as well as their hydraulic motors are optimized to use the unique characteristics of this solvent. It is rewarding to study the multiple examples for solutions plants found to convert hydraulic pressure or dehydration-mediated tension into various types of movements. Although plants possess similar molecular motors as animals (cytoplasmic streaming and pollen tube movement use actin-based myosin motors while cytokinetic chromosome movements use microtubule-based kinesin motors), these remain confined to movements inside cells and do not play a causal role in the macroscopic movements as they do in animals (Asada and Collings 1997, Shimmen et al. 2000). It appears that only animals have adopted linear molecular motors for macroscopic cell contractions as the unique basis of their macro-movements. Animal locomotion involves long fiber cells with the ability to contract. On the nanoscale this contraction involves actin-based myosin motors. Only animals have adopted linear molecular motors like myosin to drive their macro-movements by cell contraction. To drive their macro-movements plants use hydration motors that are an internal part of the moving structure. Different from the myosin nanoengine of muscles, these macromovements are based on an ATPase – a rotary nanomotor whose working has only recently been understood (Boyer 1998, Walker 1998). The important role of nanomotors for bio-nanorobotics has been recently described by Ummat et al (2006). Here we just want to emphasize that the differences between plants and animals are on both levels: nanomotors and macromotors

Although the basis of all hydraulic motors is a change in hydrostatic pressure plant motors differ from muscles and related technical designs in how they generate it. Animals and human-made designs use compressors in the form of heart muscles and mechanical pumps. Both the vertebrate heart and lower aquatic animals with a hydrostatic skeleton (soft-bodied invertebrates such as annelids and cnidarians) use inflation driven by the contraction of muscles around one part of a water-filled cavity. Through the contraction of sphincter muscles earthworms generate a hydrostatic pressure increase to expand their segments as a means of locomotion. However, rather than compressing the water directly, plants generate hydrostatic pressure by injecting solutes into a confined space that is surrounded by a membrane that retains the solutes but allows water to permeate freely into this space with the result that the subsequent hydration of these solutes increases the hydrostatic pressure inside these compartments. Plant cells use the uptake and release of water as the basis for the movement of their organs. The three major hydration mechanisms that plants use are the osmotic, colloid and fibrous motors. Each type of motor will be discussed, in turn.

### **Osmotic motors.**

The basis of hydraulic motors is a change in hydrostatic pressure. In animals and human-made designs, this is achieved by muscles and mechanical pumps that subject water to pressure. Plant osmotic motors are different; they generate

pressure by uptake of water through osmosis. Rather than compressing the water directly, plants generate hydrostatic pressure by injecting solutes into a confined space that is surrounded by a membrane that retains the solutes but allows water to permeate. Osmosis therefore requires three components: (i) a nanomotor of the ATPase-type to concentrate solutes, (ii) a semi-permeable membrane in which solutes are concentrated and (iii) a restraining, but elastic and expandable wall outside to prevent the compartment from bursting when water is taken up. If the concentration of the solutes inside is greater than outside, water will enter by diffusion and expand the volume of the compartment, and exert pressure on the surrounding wall, which will be stretched elastically. When incubated in solutions with an osmotic pressure equal or higher than their own, cells lose their internal pressure and their membrane is no longer closely pressed against the cell wall but separated from it, a visible process called plasmolysis.

The accurateness of this principle was first demonstrated by a phytomimetic model ingeniously devised by the engineer Traube; an artificial cell consisting of a porous clay cylinder covered with a copper ferrocyanide membrane that turned out to be permeable for small water molecules but not the larger, hydrated ions. This device was instrumental for a major breakthrough in biology. Combining it with a simple manometer allowed to determine the osmotic pressure values for physiological concentrations and solutes and also to predict the existence and measure properties of membranes too thin to be visible in the light microscopes of his time (Pfeffer 1873). Little known is that precipitation membranes could also be formed with biological polymers like mucilage precipitated with tannins (Pfeffer 1880/1897; 1890, 1921).

Internal cell pressures can reach up to 5 MPa in storage roots of sugar beets and in the shoots of some halophytic and xerophytic desert plants (Walter 1950). As in human-made inflatable structures (e.g. sleeping pads) pressurization of the cells leads to increased stiffening and hydrostatic stabilization of the cells, tissues or organs (Niklas 1989). To prevent an explosive rupture of the membranes, the pressures have to be counterbalanced by strong cell walls made of cellulose and other polymers. However, under the influence of decreasing pH young walls also have the ability to transition to a state where they yield to the pressure by allowing plastic and elastic expansion.

Some plant species can also use osmosis to pump water and solutes into the upper shoot. Membrane-based ATPase pumps are used to pump ions into the xylem vessels of the lower end of the root stele; roots generate a local pressure increase of up to 0.1 MPa sufficient to push a water column 9-10 m above the ground. This so-called root pressure is more prominent in some plant species than in others. It is apparent in such phenomena as guttation (the appearance of droplets at the leaf periphery of grasses and broad-leafed plants and the so-called bleeding of decapitated stumps (Stahlberg & Cosgrove 1997). Root pressure is required when humid air or lack of leaves in the spring prevents normal water and ion transport by transpiration-driven tension in the vascular bundles.

Osmotic motors have the disadvantage to depend on the intactness of a very thin, fragile membrane that also must be permeable only to the small water molecules. Freezing and subsequent thawing destroys these membranes and with it all osmotic mechanisms. Structural deformation of tissues parallels the shrinking of osmotically operating vacuoles that often occupy more than 90 % of the cell volume. This is harmful to most plant cells and structures. However, some plants (e.g. in the genus *Selaginella*) can repeatedly dry and rehydrate without structural damage. They avoid critical cell deformations during the severe dehydration by using vacuoles of smaller size that are filled with colloids instead of ions (Walter 1950). Nature itself shows an interesting alternative.

#### **Colloid- or gel-based motors.**

Colloids are much larger hydrating particles than ions and many natural polymers like starch, pectin, proteins, nucleic acids, latex etc. belong here. Colloids with fiber-like molecule chains can form gels while others can be diluted infinitely and finally form true solutions. One molecule of gelatin binds 30 000 to 100 000 water molecules (Walter 1950). The high degree of hydration is not osmotic but due to the presence of adsorptive forces called adhesion or imbibition that can equal and exceed the pressure of osmotic systems by reaching values of up to 100 MPa. Hence colloid or gel motors can potentially develop more power and more volume increase per weight than reversible osmotic motors. Szent-Gyorgyi (1951) showed that ATP-induced shrinkage of actin gels parallels a radical switch from water: protein-ratio of 50:1 to 1:1.

Although colloid-containing vacuoles have been described in plants (including the rapidly moving *Mimosa*), their role is not understood. A sudden expansion of a gel forming colloid inside a vacuole would rapidly bind water and cause a rapid water influx into the vacuoles together with a temporary dehydration of the cytoplasm. Compared with osmotic mechanisms we would have an unusually quick mechanism for changing the hydration of enzymes. Unfortunately it is also true that most of the scant information about such phenomena dates back a long time and similar studies do not find financial backing.

Seeds are known to contain colloids of pectin and protein character (albumins and globulins) with a high capacity to bind water. Seed hydration is also easy to follow since the seeds are big and their expansion can be measured macroscopically (Kuhne & Kausch 1965, Larson 1968). The imbibition pressure of hydrating seeds is considerable and many students have witnessed how hydrating pea or bean seeds crack easily and effectively bottles and skulls by what can be considered a slow, and silent “explosion”.

Mucilage is known to swell perceptibly in water and can be precipitated (dehydrated) with alcohol. Plants in highly dehydrating environments have lots of mucilage in their cells (Englmaier 1987; Clifford et al. 2002). Interesting are recent findings of mucilage in the water-transporting xylem vessels of halophytes where it might have an unknown role in water transport (Zimmermann et al. 1994). An increase in xylem-bound mucilage was found after mechanical wounding and might also have a blocking function for pathogens (Crews et al. 2003). A recent review (Shepherd et al. 2004) about the giant alga *Valonia* showed that it has intracellular and extracellular layers of mucopolysaccharides, which have surprising consequences for ion transport. In conclusion one may say that the knowledge about the role of gels in plants is elementary.

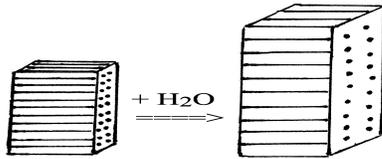
Electroactive phase transitions in ionic polymers are not requiring excessive electrical voltages and it is therefore legitimate to ask whether plants or animals have come up with convergent designs or structures. Stems and leaves contain small, valve-like openings (stomata) that are made up of a pair of bean-shaped guard cells and used to facilitate gas exchange for the purpose of respiration and photosynthesis. Polyionic polymer gels are a major constituent in the primary cell walls of guard cells, which contain polygalacturonic acid or pectin (Raschke 1975). When treated with pectinase, stomatal pores show unnaturally wide apertures. Under natural circumstances stomatal opening parallels the activation of  $H^+$ -ATPase motor that acidifies the cell walls and so increases their expandibility and releases potassium counterions bound to the pectinate. Similar cases exist in other nastic plant structures that often feature primary walls with high contents of polygalacturonic acid (Stahlberg and Taya 2006). This consideration suggests that pH-sensitive polymers do exist in plants, but that electric fields and voltages as in the case of EAPs may not cause the pH shifts. However, considerable electric fields do occur in plant tissues. First there is the large potential drop plant cells show at the plasma membrane. It can reach up to -200 mV or a field strength of  $2 \times 10^6 \text{ V m}^{-1}$ . Sudden large changes (like action spikes) in this membrane potential are certainly of a size that could cause similar changes as in EAPs and might have a role in channel gating and ATPase function. Second, a large depolarization of a plant cell with such a large membrane potential (e.g. by an action spike) would lead to the sudden establishment of an electric field towards a neighboring cell that did not undergo depolarization. With a depolarization by 100 mV and a cell wall thickness of 100  $\mu\text{m}$  such an intercellular potential could temporarily reach a field strength of  $10^3 \text{ V m}^{-1}$ . As far as known to us, nobody has yet looked for such a possibility, but the fact remains that the pectin polymers in the cell wall proteins are exposed to such field changes and that this may have effects that are still to be found.

### **Fibrous motors**

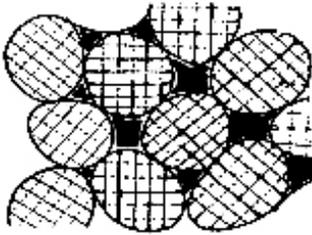
A third type of hydration motor is based on the adhesive absorption of water into the internal capillary spaces of parallel-arranged fibers. Fibers are used as reinforcing elements against tensional stress in both technical and biological designs. Their additional ability to function as hydration motors identifies them as multifunctional materials. The most common natural fibrous material is cellulose. Cellulose fibers are made of long chains of glucose molecules twisted together in a micellar bundle. These bundles are often found in a parallel arrangement to increase the breaking strength of the material. Unlike isometrically expanding colloids, such parallel fibers swell in a diametric fashion, i.e. they expand only in the two directions that are orthogonal or perpendicular to the direction of the fibers (Fig. 3). Diametric expansion occurs when water enters the inter-fibrillar spaces where it pushes the fibers apart without altering their length (Fig. 3 and 4). The space between the microfibril bundles resembles small-sized capillaries and is large enough (about 10nm diameter) for water to move and to be adsorbed (Frey-Wyssling 1959). These spaces can be filled with the polyphenolic resin lignin instead of water (Fig. 4; Brett and Waldron, 1996). This process changes the cellulose properties completely. It turns a water-permeable, hydrating and swelling net of cellulose microfibrils into a non-expandable, water-repelling resin-fiber composite called wood. By combining swelling, modestly swelling and non-hydrating cellulose layers plants generate a diverse multitude of actuators.

Botanists were among the first who studied and correctly explained the movements of dead fibrous hydration motors as actuators consisting of two (or sometimes more) layers with different hydration-mediated expansion characteristics. The encountered plant movements were modeled with paper laminates in the form of two joined paper strips (each with a different orientation of the fibers (Jost 1933). The simple combination of a modestly or non-swelling layer (random orientation of the fibers) and a swelling layer with parallel fibers generates a simple bending when the laminate is hydrated. A combination of two swelling layers with a perpendicular orientation of their parallel aligned

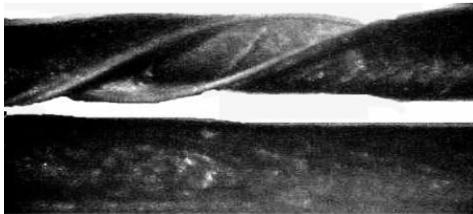
fibers adds a rolling movement to the simple bending. Finally, with a 45° angle between the parallel oriented fibers of the two strips, hydration subjects the laminate to twisting and torsion (for the paper models see Stahlberg & Taya 2006). The paper models differ from the natural design of a pea pod only by the fact that they are glued together when they are straight and that they therefore twist upon hydration rather than upon dehydration as seed pods (Fig. 5).



**Fig. 3:** Unequal or diametric expansion of hydrating fibrous motors confines their expansion to the two directions perpendicular to the orientation of the fibers.



**Fig. 4:** Capillary spaces of a few nanometers exist between microfibril bundles (black areas) of elongated cellulose fibers that allow the adhesive absorption of water molecules. Alternatively these spaces can be filled with the hydrophobic, waterproofing resin lignin.



**Fig. 5:** Dehydration twists the halves of a legume pod (top) while hydration straightens them. The torsion movement occurs because the wall consists of two layers with a different orientation of their fibers.

One can safely predict that the biomimetic use of fibrous hydration will not stop with the development of blotting paper that is essentially a lignin-free sheet with a loose and random orientation of the fibers. A major disadvantage of cellulose fibers is their strong hold on water molecules. The design of shorter fibers with a quicker water release and larger relative volume change (side chains) and force development than the original cellulose fibers of plants are a useful step on the way to a new generation of fibrous actuators. The long-known reconstitution of cellulose in the form of semi-synthetic Rayon or cellulose acetate fibers shows one direction of manipulation, the combination of fibers with synthetic polymer gels another.

In conclusion, one can see that plants polymers show a largely unexplored potential for biomimetic applications. The theoretical lead biology once had over engineering, however, has largely disappeared. This creates the not quite so new situation in which interdisciplinary learning must operate in both directions, a situation in which the search for biomimetic solutions by engineers will be equally profitable as the search for techno-convergent solutions in organisms by biologists.

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