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NEWS & VIEWS

ON THE NATURE OF THINGS: ESSAYS
New Ideas and Directions in Botany

Quo vadis plant biomechanics: Old wine in new bottles or an up-and-coming field of modern plant science?

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In this essay, we present a personal view of plant biomechanics today and of the directions in which plant biomechanics will or should move during the next few decades. Biomechanics deals with mechanical investigations on plants, animals, fungi, and bacteria, covering all orders of magnitude—from the molecule to the entire organism—applying methods also used in physics, engineering, and materials sciences. In our opinion, the field of plant biomechanics cannot be considered without mechanically testing, analyzing, and characterizing the underlying structural setup of the hierarchical organization of plant cells, tissues, organs, and organisms. As a consequence, only a thorough analysis of the materials systems of a plant will enable reliable quantitative mechanical investigations. In turn, a quantitative analysis of the form–structure–function relations in plants is only possible if the functional morphology is studied in conjunction with a biomechanical investigation.

PLANT BIOMECHANICS HAS A LONG TRADITION

The mechanical properties of plants and plant structures have been of interest and importance to humans since the very beginnings of humankind. On the one hand, plants always were important parts of the human diet, and the mechanics of plant products influences aspects such as chewability, palatability, and digestibility. On the other hand, the use of plant fibers, wood, and bark for various purposes, e.g., clothing, fishing, hunting, and housing, represents one of the first and most important achievements during the early cultural evolution. In this phase, humans had considerable pre-scientific knowledge concerning the mechanical properties of plants and plant organs, a prerequisite for the meaningful use of plant materials for various purposes. Even during the early phases of modern natural sciences in the 15th to 17th centuries, an interest in the mechanical and structural properties of plants was apparent. Leonardo da Vinci (1452–1519) was fascinated by various aspects of plant biomechanics and in the information that can be gained from plants for technical applications, a field of science that we now term biomimetics. Most notable were his ideas for parachutes inspired by the pappus of anemochorus dandelion fruits (implemented for the first time in a working model by Sir George Cayley [1773–1857]) and for autogyroscopic propellers inspired by spinning samara fruits. Galileo Galilei (1564–1642) found inspiration when considering the physics of tubes in his studies of the bending and buckling behavior of hollow grass culms (Geitmann et al., 2019). At the same time, the scientific exchange between the botanist Nehemiah Grew (1641–1712) and the physicist Robert Hooke (1635–1703) reveals that plant biologists used physical and engineering approaches from the very beginning to better understand certain aspects of plant life, in this case, the hydrostatic (turgor) stabilization of parenchyma cells. By the end of the 19th century, with the publication of Simon Schwendener's book *Das mechanische Princip im*

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anatomischen Bau der Monocotylen mit vergleichenden Ausblicken auf die übrigen Pflanzenklassen (*The Mechanical Principles of the Anatomy of Monocotyledons with an Overview of the Other Plant Classes*) (Schwendener, 1874), plant biomechanics had become a well-defined field of science integrating aspects of biology, physics, and engineering (Geitmann et al., 2019).

BIOMECHANICS IS A CORNERSTONE OF BIOMIMETICS

These short historical considerations alone indicate that the topic of plant biomechanics was from its very beginning, and still is, an intrinsically interdisciplinary field of science. Today, in addition to the use of a multitude of methodologies typical for biology, plant biomechanics also borrows methods from physics, chemistry, engineering, and materials sciences. This combination is necessary for the study of mechanical properties on and over all relevant length scales and for the analysis of underlying structures at various length scales. However, plant biomechanics is not only interdisciplinary in terms of the methods and approaches used, but also in its impact on other fields of science (Fig. 1). Fields in which biomechanics plays an important role include plant sciences in general (in particular, ecology, physiology, and cell and molecular biology), forestry (tree/wood stability and growth, forest structure), agriculture and horticulture (stability and texture of crop plants, stability of garden plants and cut flowers), paleobotany (size and growth habit of fossil plants), and biomimetics, which encompasses bioinspired materials research, engineering, architecture, soft robotics, and medical devices such as prostheses and orthoses. This knowledge concerning biomechanical functions and their associated underlying structures is the origin of a multitude of bioinspired developments and products, which has already been proven impressively by Leonardo da Vinci and Galileo Galilei. Biomechanics today provides the basis for many aspects of biomimetics, including lightweight constructions and materials, surfaces and interfaces, fluid dynamics, swimming and flying, shape and weight optimization, and architecture and design. Plant biomechanics, in particular, has contributed markedly to some of the most important and visible developments in biomimetics including the Lotus effect® (self-cleaning surfaces inspired by the self-cleaning of leaves, e.g., those of the sacred lotus *Nelumbo nucifera*; cf. Barthlott et al., 2016), the Salvinia effect (air-retaining surfaces that reduce friction in vessels inspired, for example, by the leaves of the waterfern *Salvinia natans*; cf. Busch et al., 2019), shape optimization through computer-aided optimization (CAD) inspired by adaptive tree growth (cf. Mattheck, 1998), the façade-shading systems flectofin® and flectofold (inspired by the movement of the perch of the bird-of-paradise flower *Strelitzia reginae*, and the snap-trapping of the watertrap *Aldrovanda vesiculosa*, respectively; cf. Lienhard et al., 2011; Körner et al., 2018; Westermeier et al., 2018), and the billion-dollar-selling Velcro® (inspired by the attachment of the exozoochorus burdock fruits of, for example, *Actium* spp. to the fur of animals; cf. de Mestral, 1955). Current developments in plant biomechanics, not only in the fields of surfaces, interfaces, and materials systems, but also in morphogenesis and sensing (e.g., mechanoreception), show great potential. They provide not only a better understanding of the functioning of the plant itself (basic research), but also lead to transfer and application in biomimetic research. These research fields are also mirrored in two recently published textbooks on plant biomechanics by A. Geitmann and J. Gril (2018) and K. J. Niklas and H.-C. Spatz (2012), the first approaching the topic more from a biological point of view and the other from a more physical perspective. Furthermore, current special issues of journals highlight the most recent results and most promising developments in plant biomechanics (Geitmann et al., 2019; Geitmann, in press).

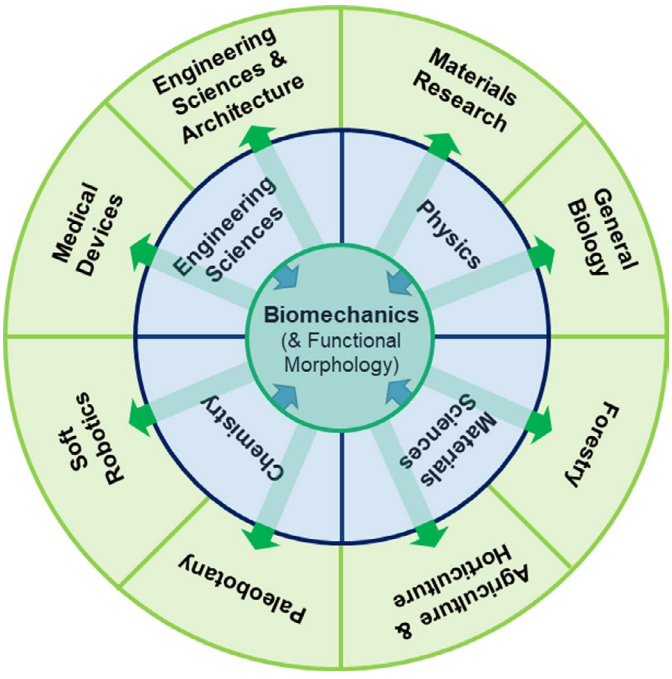


FIGURE 1. Plant biomechanics as a truly interdisciplinary field of science. Schematic drawing highlighting the interdisciplinary import of methodological approaches from the various fields of science to plant biomechanics and the export of knowledge from intrinsically biomechanical research to other fields of science.

PLANT BIOMECHANICS IS A WORLDWIDE TOPIC

To answer questions on the status and future developments of plant biomechanics today, it may be useful to take a look at the scientific topics covered by sessions at the triennial International Plant Biomechanics Conferences (PCB). This conference is the most important "disciplinary" conference in this field of sciences and brings together several hundred researchers from all over the world every 3 years. Having a history of 25 years, with the first PBC taking place in Montpellier (France) in 1994 and the most recent one in Montreal (Canada) in 2018, the PBC sessions mirror, on the one hand, the most exciting research areas in plant biomechanics over the last quarter of a century and, on the other, may help to answer the question "Quo vadis plant biomechanics?" In the following listing, the first number indicates the number of PBCs at which a topic was presented as a session, and the second number represents the number of talks and posters summed up for all PBCs. Appearing at (almost) all PBCs, the sessions Trees & Wood (9/164); Cells, Cell Walls & Tissues (9/160); Ecology & Evolution (9/112); Morphogenesis & Growth (8/97); and Applied Biomechanics & Biomimetics (8/93) can be considered as the core topics that are of ongoing scientific interest for the plant biomechanics community. Special sessions on other topics were only held in some PBCs, such as those on Modeling & Methods (5/93); Fluid Transport (5/64); Mechanosensing (5/63); Plants as

Food and Fiber (3/31); Impact of Wind, Waves & Water Currents on Plants (3/30); Plant Motion (3/28); Roots (3/22); Fracture Mechanics (2/11); and Animal and Fungus Interaction with Plants (1/27). This more limited number of sessions and presentations possibly mirrors the smaller communities working on these topics, a lower scientific interest in these questions in general, and/or the site-specific interests of the PBC organizers. However, to estimate the dynamics in plant biomechanics, we should look at the development of the various topics and the changes in the number of contributions over the years. This analysis shows that, within the range of the regularly presented themes, the topics Trees & Wood and Cells, Cell Walls & Tissues are characterized by a constantly high number of presentations. For the topics Ecology & Evolution, Morphogenesis & Growth, and Applied Biomechanics & Biomimetics, which are about one third smaller than the first two mentioned themes in absolute terms, an increase in the number of presentations is apparent in the last three PBCs. The same applies to the topic Mechanosensors. However, this trend should be interpreted with caution, as many presentations can easily be assigned to two or even three topics.

Forests, trees, and wood and their mechanical properties are of utmost interest not only scientifically but also economically and for local and global ecology, especially as the global climatic changes and droughts and storm events increase (Niklas and Spatz, 2012; Telewski and Niklas, 2017). This interest is mirrored by a considerable number of conferences specifically dealing with tree and forest mechanics (including hydraulics), arboricultural and forestry practices, and tree breeding and selection for improved mechanical stability. Examples include the triennial "IUFRO Wind and Trees conferences", numerous conference of the International Society of Arboriculture (ISA) and many other (inter-)national conferences.

A PARADIGM SHIFT BY MOLECULAR APPROACHES

In recent decades, the dominant molecular approaches in biology have undoubtedly brought about a paradigm shift in the subject and enabled a previously unimaginable in-depth understanding in many biological areas, including botany. During this time, the subject areas of biomechanics and functional morphology as part of organismic biology have sometimes been underestimated and regarded as "old-fashioned". However, they have a value of their own, and new approaches and methods from molecular biology may help to answer interesting questions in plant biomechanics and functional morphology extending far beyond obvious mechanical testing on the molecular scale. To understand the full potential of combining molecular approaches with functional morphology and biomechanics, we need to consider the importance of an organism's phenotype, which is the basis of all functional morphological and biomechanical analyses. All organisms interact via their phenotype with their biotic and abiotic environment, and the phenotype is crucial for niche formation and the evolutionary success of an organism. A good example is the lianescent growth habit, which has evolved more than 100 times independently in unrelated evolutionary lineages of plants (Gentry, 1991; Schnitzer et al., 2015). Our analyses suggest that some (simple) basic mechanical constraints exist that are crucial for a successful lianescent climber. These include young searcher twigs and reiterative axes that are stiff in bending and torsion and thus can bridge gaps between old and new supporting host trees. After secure attachment by such different means as tendrils (with or without adhesive pads), twining stems, or roots and root hairs, lianas develop increasingly compliant stems with high bending and torsional flexibility that allow the swaying movement of a host tree to be followed and that sometimes even lead to the survival of the liana stem after the breaking off and falling down of a supporting branch (Rowe and Speck, 1996, 2015). The increasing flexibility in older liana stems is always achieved by the production of a less-dense, flexible secondary wood with huge-diameter vessels that additionally enable sufficient water conduction within the slender liana stems, which are often several hundreds of meters long (Fig. 2). However,

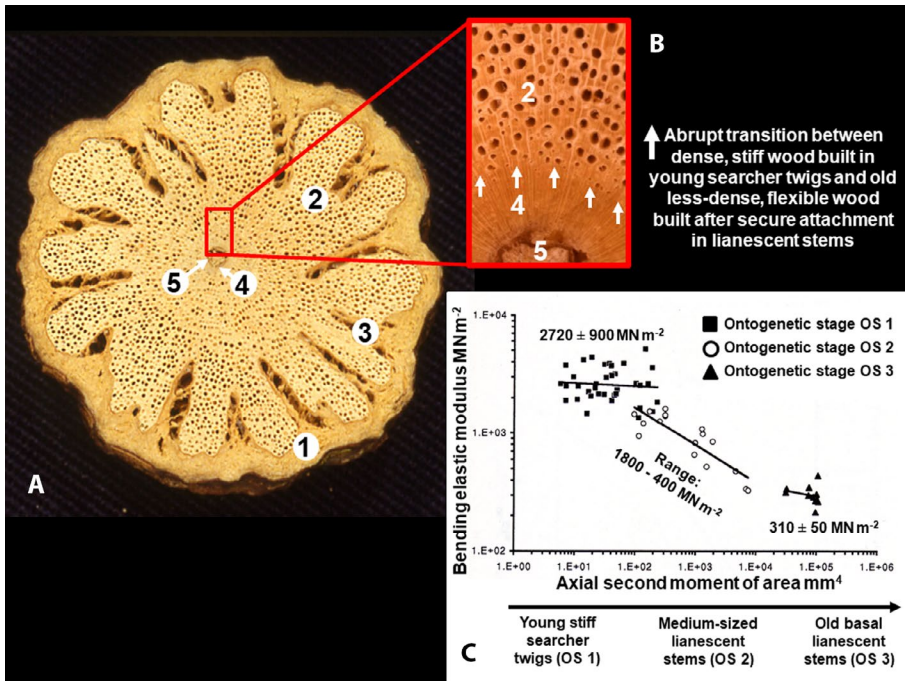


FIGURE 2. Anatomy and biomechanics of the tropical twining liana *Condylocarpon guianense*. (A) Cross section of an old, highly flexible stem with (1) a thick, damping, flexible cortex and bark; (2) a wide cylinder of star-shaped flexible wood (density: 430 kg m^{-3} / bending modulus: 750 MN m^{-2} / torsional modulus: 200 MN m^{-2}) with huge-diameter vessels, few wood fibers, high cellulose microfibril angle (44°), and lignin with a high sinapyl to coniferyl ratio of ca. 0.5; (3) huge parenchymatous wood rays; (4) a small cylinder of dense, stiff wood (density: 560 kg m^{-3} / bending modulus: 4200 MN m^{-2} / torsional modulus: 450 MN m^{-2}) built during the juvenile growth phase with small vessels, many thick-walled wood fibers, a low cellulose microfibril angle (30°), and lignin with a low high sinapyl to coniferyl ratio of ca. 0.2; and (5) a tiny pith (cf. Hoffmann et al., 2003). (B) Detail of the transition between dense, stiff wood built in the young searcher phase and less-dense, flexible wood built after secure attachment in older lianescent stems. (C) Diagram showing the relation between the bending elastic modulus and the axial second moment of area of stems of different ontogenetic stages (cf. Rowe and Speck, 1996).

the structural changes occurring at the different hierarchical levels of secondary wood markedly differ within the various evolutionary lineages. The arrangement of the flexible secondary wood segments in old liana stems, for example, shows a plethora of patterns ranging in cross sections from star shapes, to isolated concentric rings, to various arrangements of isolated wedges, but always with huge parenchymatous inclusions that further increase bending and torsional flexibility (Hoffmann et al., 2003; Rowe and Speck, 2015). These data reveal that only a few basic mechanical requirements must be met for the successful establishment of a climbing liana and that these constraints can be met within various evolutionary lineages in completely different structural ways and on different genetic backgrounds. Molecular approaches will help not only to deepen our understanding of the form–structure–function relations in lianas and of the switching from the self-supporting juvenile state to the flexible nonself-supporting adult state, but also (via molecular systematics) will help to decipher the independence or not of shifts in growth habit within the various evolutionary lineages of plants.

PERSPECTIVES OF PLANT BIOMECHANICS IN THE ANTHROPOCENE

One goal of this essay is to inspire new studies in plant biomechanics and to "infect" young researchers from various disciplines with the plant biomechanics "virus". Plant biomechanics, with its highly interdisciplinary character, will benefit markedly from novel inspiration coming from young scientists educated in different fields contributing to plant biomechanics. In particular, we wish to inspire molecular biologists to join the bandwagon of biomechanics and to converge the newest molecular approaches and results with questions concerning (whole plant) organismic botany as addressed in biomechanics. In our opinion, this combination holds great promise and will mark a new level of research in plant biomechanics. Indeed, the expected results will not only contribute to a better understanding of many aspects of plant ecology, physiology, and evolution, but also add to more applied questions concerning, for example, tree growth and wood quality, or stem stability in many nutrient plants such as corn, wheat, and rice increasingly important in an era of climatic change and open up new vistas in the up-and-coming field of molecular biomimetics. One area of plant biomechanics that should especially benefit from novel molecular approaches is the field of mechanoreception and morphogenesis. Our personal "favorites" include work aimed at understanding the stimulus–sensor–reaction cascades in self-repair processes in plants (Speck O. and Speck T., 2019) and the processes leading to the entirely different wood type produced in liana stems after they established secure attachment (Hoffmann et al., 2003). These studies would not only help to answer fascinating questions about immediate individual responses and evolutionary adaptations of plants, but might also act as the basis for a novel group of adaptive, decision-making, and trainable materials systems that are high ranked on the to-do list in bioinspired materials research (*liv*MatS, 2019). Additionally, a deeper comprehension of the adaptive (growth) processes and attachment modes in climbing lianas may help in the development of an entirely new group of climbing soft robots able to explore complex unknown 3D environments and to establish themselves therein (GrowBot, 2019).

To conclude, biomechanics has without doubt the potential to become an up-and-coming field of modern plant science and might contribute to solving some challenging questions in the Anthropocene (Crutzen, 2002). The importance of the protection of biodiversity should be considered here. Of the ca. 10 million species (among them around 500,000 plant species) dwelling on our planet today, only 10,000–15,000 have been analyzed with respect to their biomimetic potential. Thus, the drastically increased extinction rate that is occurring during the Anthropocene not only impacts our ecosystem and its stability, but also substantially reduces the number of role models for biomimetic developments based on plant biomechanics research. Such a consideration adds an economic aspect to the argument for the conservation of species, which is typically based on ecological and moral points of view, as each vanishing species might make—via novel also economically interesting biomimetic products—a contribution to the solution of the urgent problems that face humankind.

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