Plant biomechanics: an overview and prospectus[1]

Karl J. Niklas,[2,5] Hanns-Christof Spatz,[3] and Julian Vincent[4]

[2]Department of Plant Biology, Cornell University, Ithaca, New York 14853 USA; [3]Institut für Biologie III, Universität Freiburg, Freiburg D-79104, Germany; and [4]Department of Mechanical Engineering, University of Bath, Bath BA2 7AY, UK

We provide a brief overview of the articles appearing in this special issue and place them in the context of the long history of the study of plant biomechanics and what we judge to be the next major intellectual and/or technological challenges in this field.

Key words: algae; biomimetics; cell walls; dynamic wind loads; fracture mechanics; mechanical properties; mechanoperception; static loads; trees; wood.

History shows that engineers and physicists can learn a great deal from studying plants. The use of organisms in general and plants in particular as models to illustrate physical principles or to construct mechanical devices has a long and distinguished history. Galileo Galilei (1638) used the hollow stalks of grass to illustrate his idea that peripheral rather than centrally located construction materials resist bending forces. He also developed his concept of geometric self-similarity (which presaged J. S. Huxley's 1932 study of allometry and biological scaling principles) by comparing the mechanics of small and large oak trees. Leonardo da Vinci's interest in fluid mechanics was inspired by his observation that the cross-sectional areas of tree trunks are roughly equal to the sum of the branch cross-sectional areas distal to any point along a trunk's length, and his drawings of the first parachute and autogyroscopic propeller were based on meticulous examinations of the dandelion pappus and the maple samara (Richter, 1970).

It is also clear that plant scientists have learned much from collaborations with engineers and physicists. While writing the second edition of his *The Anatomy of Plants*, Nehemiah Grew (1682) sought the advice of Robert Hooke (the discoverer of Hooke's law:—*ut tensio sic vis*—"as is the extension, so is the force"). The philosopher and engineer Herbert Spencer first proposed that "internal mechanical stress itself" caused the formation of "strong bonds" in plant cell walls, whereas Robert Culman, the founder of graphical statics, first applied his mathematical methods to the study of plant stems (as well as bones). The Barba-Kick law, which helped Eiffel construct his tower, was essential to the work of A. G. Greenhill, who sought to define mathematically the physical limits to the height of a tree, albeit in complete ignorance of the insights gained from the work of G. Hagen and J. L. M. Poiseuille in 1869 (which figures prominently in current hydraulic theories about the maximum height of trees; e.g., Koch et al., 2004). And, finally,

without the elegant dimensionless equation developed by O. Reynolds in 1885, which permits modeling the complex behavior of fluid flow around miniatures mimicking biological prototypes, the field of bio-fluid mechanics would be impossible (see Vogel, 1981).

It was nevertheless a great but pleasant surprise when the Editorial Board of the *American Journal of Botany (AJB)*, represented by Judy Jernstedt, the *AJB* Editor-in-Chief, approached the three of us to serve as guest editors for a special issue devoted to plant biomechanics to help celebrate the 100th anniversary of the founding of the Botanical Society of America. Invitations to perspective authors were sent out in October 2005, and, with very few exceptions, each was accepted almost immediately. By May 2006, all of the articles appearing in this special issue were reviewed and well into the process of revision and final copy editing. That this special issue appears in print roughly one year after the inception of the project is a testimony to the enthusiasm of the participating authors, the care and alacrity of collegial reviewers, and the dedication, boundless energy, and hard work of the *AJB* Editor and Editorial Staff. We therefore extend our deepest thanks to all of the colleagues and friends who have made this second *AJB* special issue a joy for the three of us to edit and a pleasure to summarize in this overview article.

THE PLANT BIOMECHANICAL LEGACY

Although the first general writings about biomechanics were those of Aristotle, plant biomechanics became a clearly defined field of study with the publication of Simon Schwendener's seminal book *Das mechanische Prinzip im anatomischen Bau der Monocotyledonen* (*The Mechanical Principles of the Anatomy of Monocotyledons*) published in 1874 (Fig. 1), although sporadic writings about mechanical phenomena in plants appeared well before the publication of this seminal book. For example, Du Monceau (1785) compared the skeletons of animals with the wood in trees; Bonnet (1794) drew analogies between the epidermis of herbaceous plants and the exoskeletons of insects; Knight (1811) studied the effects of mechanical perturbation on the growth and morphology of trees; and Sachs (1868) wrote about the role of turgor in stiffening plant tissues and organs. But Schwendener was the first to explore in detail how fundamental engineering concepts could be used to understand the functional anatomy and

DAS

MECHANISCHE PRINCIP

IM ANATOMISCHEN BAU DER

MONOCOTYLEN

MIT VERGLEICHENDEN AUSBLICKEN AUF DIE ÜBRIGEN PFLANZENKLASSEN.

VON

Dᴿ. S. SCHWENDENER,

PROFESSOR DER BOTANIK IN BASEL.

MIT 13 HOLZSCHNITTEN UND 14 LITHOGR. TAFELN IN FARBENDRUCK.

LEIPZIG.

VERLAG VON WILHELM ENGELMANN.

1874.

GERMANY

Fig. 1. Title page of Simon Schwendener's 1874 treatise on plant biomechanics entitled *Das mechanische Prinzip im anatomischen Bau der Monocotyledonen mit vergleichenden Ausblicken auf die übrigen Pflanzenklassen* (*The Mechanical Principles of the Anatomy of Monocotyledons with an Overview of the Other Plant Classes*).
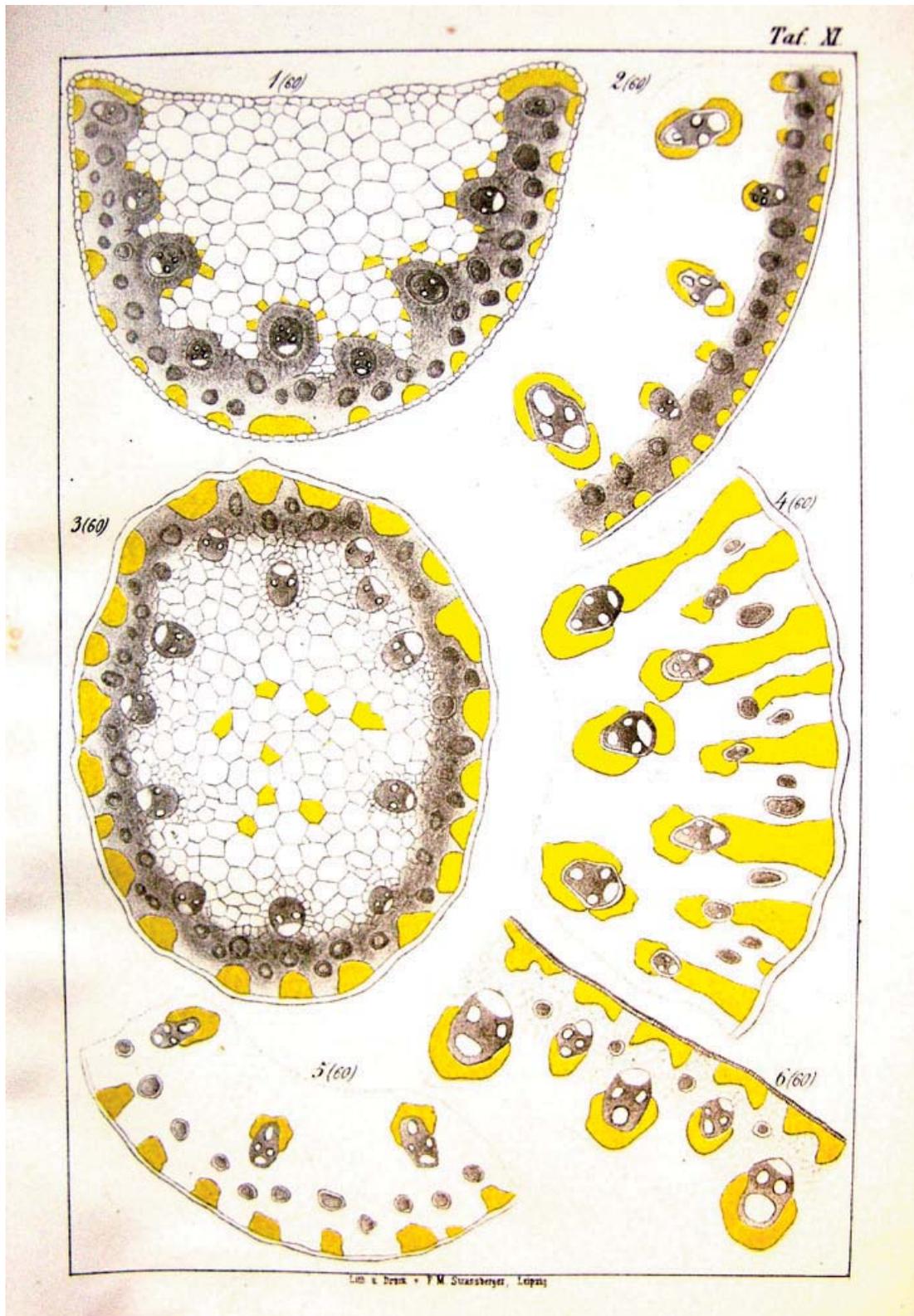
Fig. 2.   Schwendener's (1874) plate XI used to illustrate the presence of I-beam-shaped reinforcing tissues (in yellow). (1) *Fimbristylis spadeacea* leaf, (2) *Cyperus eregius* stalk, (3) *Fimbristylis spadeacea*, (4) *Cyperus conglomeratus*, (5) *Hypolytrum argenteum*, and (6) *Cyperus* sp.

morphology of plants. His book defined and continued to influence the field for the next 40 years. It diminished in importance only after the work of Wladimir Rasdorsky, between 1911 and 1937, which refuted many of Schwendener's earlier theories about the mechanical roles of peripherally located I-beam-shaped strands of rigid stem and leave tissues (Fig. 2).

Most if not all of the concepts first introduced by these and other early plant biomechanicists are re-examined in the articles published in this special issue. The reason is simple: these concepts remain fundamental to our understanding of plant biology and their complexity continues to intrigue theoreticians and experimentalists. For example, between 1874 and 1887, Schwendener provided one of the first comprehensive biomechanical comparisons among fern, horsetail, lycopod, and flowering plant stems, and interpreted correctly the cross-sectional distributions of tensile and compressive stresses in terms of the habitat occupied by each plant. In this sense, he was one of the first workers to see the relationship between mechanical "design" and ecological context, a concept that continues to be important today (see Brüchert and Gardiner, 2006; Read and Stokes, 2006; Sanson, 2006; Sperry et al., 2006). Likewise, Schwendener (1874) and Rasdorsky (1929) argued convincingly that plants are composed of composite materials. Both drew an analogy between reinforced concrete and the anatomical construction of stems and leaves, an idea that was quickly adopted by F. O. Bower (1930, p. 138) who wrote, "Ordinary herbaceous plants are constructed on the same principle. The sclerotic strands correspond to the metal straps, the surrounding parenchyma with its turgescent cells corresponds mechanically to the concrete." This analogy is flawed in many ways, but the notion that plant cells, tissues, and organs can be modeled as (and are in fact) *complex* composite materials remains an important conceptual breakthrough (see Burgert, 2006; Farquhar and Zhao, 2006; Harder et al., 2006; Whitney et al., 2006).

Finally, Oltmanns (1923) working with algae and Rasdorsky (1930) working with terrestrial plants drew sharp attention to the fact that plants must be flexible as well as rigid to deal with fluid-induced drag forces as well as their own weight. Both argued cogently that the "architecture" and growth of aquatic and terrestrial plants are adaptively responsive to dynamic and static forces. This concept remains as important today as it did in the formative years of plant biomechanics (see Harder et al., 2006; James et al., 2006; Moulia et al., 2006; Peltola, 2006; Telewski, 2006).

A FEW WORDS ABOUT JARGON AND MATHEMATICS

Before we present our overview of the articles in this issue, we believe a few comments are in order regarding vocabulary and equations.

Like the physical sciences, biomechanics is terminologically and mathematically rich. It needs to be, because it draws heavily on the concepts and tools developed and used in a broad spectrum of physical sciences, each of which has its own terminology and all of which rest on mathematics. In addition, it draws on biology, which is no less rich in terminology and every bit as dependent on the quantitative approach as any of the physical sciences. But the juxtaposition of jargon and mathematical tools evident in many biomechanical studies can be irksome, perhaps particularly to a biologist, because some technical words have colloquial meanings (e.g., stress, strain, and compliance) and because some mathematical tools may be so unfamiliar as to suggest "smoke and mirrors" to the uninitiated (e.g., second order tensors and elliptic integrals of the first kind).

Indeed, problems about terminology and even mathematics were pitfalls in the development of biomechanics many centuries ago. Had Aristotle not confused "density" with "viscosity," we might be talking about "Aristotlian" rather than "Newtonian" fluids (Scott Blair, 1969). Had Robert Hooke's first publications not been so "eccentric" terminologically, many of his contemporaries in the Admiralty would have understood the importance of *ut tensio sic vis*. Similarly, much confusion in the biomechanical literature would have been avoided during the beginning of the 20th century had authors not conflated the technical meanings of "stiffness," "rigidity," and "bending strength" with the more common meanings of these words (Nachtigall, 1994).

Mathematical obfuscation was also a problem, albeit to a lesser degree than the confusion revolving around word usage. Consider that there are two ways to calculate what we now call normal strain (i.e., the Cauchy or "conventional" strain and the Henchy or "true" strain), each of which can give a different absolute numerical answer depending on the magnitude of strain (even for the same material tested in the same way). Many workers in the 19th and early 20th century failed to report how they calculated strain (perhaps because the distinction between the two kinds of strain was unknown to them), which resulted in profoundly vitriolic debates in the literature about the elastic properties of certain cell or tissue types.

Naturally, some areas of research rely heavily on a quantitative approach and cannot eschew comparatively complex mathematics (see Farquhar and Zhao, 2006). Other areas of enquiry must cope with biological systems so large and complex that mathematics currently provides little or no help (see Read and Stokes, 2006; Sanson, 2006). Fortunately, all of the authors whose works are presented here are particularly sensitive to the issues of jargon and mathematics. Each has made every attempt to be terminologically concise, and, for those readers who are less mathematically inclined, each has tried to minimize the use of complex equations wherever possible.

THE ORGANIZATION OF ARTICLES IN THIS ISSUE

One of the great goals during early plant biomechanical research was to understand the internal structure and material properties of plant tissues and organs, to link these features to the mechanical configuration of the whole organism, and, in turn, to link both of these to the manner in which the external environment affects the organism. This goal—to understand and relate "internal" levels of biological organization to "external" levels of organization—served as the basis for arranging the articles in this issue. Papers dealing with methodological issues or the material properties of cell walls and tissues or the dynamics of cell growth precede articles dealing with organs or the entire plant body; and thus the special issue ends with papers discussing the mechanical interplay of the organism with its abiotic or biotic environment.

As in any collection of papers, some of the articles presented here are highly taxon-oriented or focus on a particular, albeit

important, biomechanical phenomenon. The article by Harder et al. (2006), for example, centers on the "adaptive" mechanical behavior and the material properties of brown algal macrophytes (thus carrying on the early work of Oltmanns). In contrast, Farquhar and Zhao (2006) present a detailed and highly mathematical treatment of plant fracture mechanics (which historically resonates with F. O. Bower's speculations about leaf margin venation patterns; see Bower, 1925). Other articles defy a clear classification, but are nevertheless highly informative. For example, the treatment of the delightfully unique mechanical and acoustical properties of wood by Wegst (2006) could find a comfortable place anywhere within the papers assembled in this issue.

Additionally, biologists know full well that the distinction between "internal" and "external" is neither clear-cut nor even realistic in most cases. Many of the physical and biological properties of cell walls and tissues are physiologically adjusted in response to external environmental factors. Indeed, this is the focus of much of the research devoted to understanding mechanoperception and thigmomorphogenesis (see Telewski, 2006). By the same token, the manner in which a plant responds to its physical environment depends on the physical attributes and behavior of its constituent parts. It is almost tautological to say that the physical and biological linkages among the various levels of biological organization, from the subcellular and cellular to the supercellular and ecosystem levels, are so extraordinarily complex that their elucidation presents the greatest challenge we face as biologists.

Nevertheless, each of the 17 articles appearing in this issue has an emphasis or perspective that permitted us to arrange the entire collection of papers into a series that moves along the "internal" to "external" continuum of plant biomechanical topics. For this reason, we believe that it is advisable for the reader to "begin at the beginning and end at the end," particularly since some of the phenomenology treated in earlier articles resurfaces in later articles.

Finally, the reader familiar with the field of plant biomechanics will undoubtedly perceive some areas of interest that are only lightly touched upon or that are treated not at all. As in any scientific discipline, it is almost impossible to cover all topics, even in a large textbook (but especially in a journal issue, which is limited by space and economics). Additionally, some topics, like plant evolution and plant hydraulics, are not extensively represented (but see Sperry et al., 2006), because summaries of these topics have appeared recently in print (e.g., Holbrook and Zwieniecki, 2005). Despite these gaps in topics, we believe that the articles assembled here provide an excellent representation of the depth, breadth, and vigor of the large field called plant biomechanics.

AN OVERVIEW OF THE ARTICLES IN THIS ISSUE

Cell walls and plant growth—Although Henshaw's drawings of the vessels in wood are credited as the first published treatment of cell walls (cited by Preston, 1974), Nehemiah Grew in *The Anatomie of Plantes* (1682) arguably presents the first detailed treatment of the plant cell wall. Despite the optics of his times, Grew believed that the plant cell wall was composed of exceedingly thin fibers, and by emphasizing the chemistry and physics of the plant "infrastructure," he set the stage for some of the very first biomechanical enquiries (see Preston, 1974). It therefore seems only fitting that this collection of papers should begin with articles devoted to the study of the plant "endoskeleton."

Geitmann's (2006) article begins this topic. She reviews the experimental methods used to quantify the physical properties of plant and fungal cell walls at the subcellular level as well as the techniques available to study the structure and physical properties of the cytoskeleton. Many of these techniques have been used primarily to study animal cells; their applicability to studying plant cells is critically evaluated by Geitmann. Burgert (2006) continues on with a discussion of the range of experimental approaches used to examine the mechanical properties of cells isolated from wood and other plant tissues, both in their natural state and after enzymatic treatments designed to explore the mechanical roles of specific cell wall constituents. His review, which cautions against inferring the behavior of a tissue from the behavior of a few isolated cells, reinforces the view that interconnected cells in tissues as well as individual cell walls must be viewed as "composite" materials.

In their review of the cellulose–xylogucan cell wall framework, Whitney et al. (2006) carry on the theme of "cell walls as composite materials" by exploring the mechanical properties of artificial bacterial cellulose constructs differing in their xyloglucan composition. Using this simple model, Whitney et al. (2006) show that, regardless of its molecular length, xyloglucan binds to cellulose and perturbs its crystallinity. High molecular xyloglucans combined with cellulose yielded centimeter-scale homogeneous composites with extensive cellulose cross-linkings, whereas lower molecular weight xyloglucans yielded heterogeneous composites with a range of microscopic structure. Comparisons between the structure and mechanical properties of these artificial constructs with their biological counterparts provide insights into the molecular organization of plant walls.

In conventional solid mechanics, a curved form is thought to be produced by something like a bimetallic strip model, wherein one side of the form expands (grows) more than the other side. Indeed, Darwin's seminal experiments with decapitated coleoptiles rested on this mechanical model and provided the basis for explanations of plant tropisms (Darwin, 1880). However, Silk and Erickson (1979) showed that the curved form of a seedling hook was produced by a procession of tissue elements, each of which curves and then straightens, by their application of continuum fluid mechanics to understand changing cellular elements that are displaced through a growing form. The article by Schopfer (2006) addresses some of these concepts in the context of the mechano-hydraulic process attending irreversible cell expansion and the roles played by manifold internal and external signals (e.g., hormones and light, respectively). He concludes that anisotropic cell expansion is the result of these signals indirectly altering the molecular structure and spatial organization of cell wall polymers rather than as a result of the intensity and distribution of mechanical stresses resulting from turgor.

Tissue mechanical properties—Although it is extremely difficult to separate the physical behavior of individual cells from that of the tissue in which they are embedded, the papers grouped under this topic focus on the physical properties of tissues rather than isolated cells.

We begin with a treatment of the biomechanical properties of algal macrophytes, which have received far less attention than those of vascular plants for a number of reasons.

Nevertheless, the few workers that have focused on these organisms have shown that the allometry and mechanical behavior of algal macrophytes are remarkably complex (e.g., Koehl and Wainwright, 1977; Koehl, 1979; Holbrook et al., 1991). The article by Harder et al. (2006) compares and contrasts the mechanical behavior and adaptive nature of the material properties of four wave-swept brown macrophytes and thus adds new insights at several structural levels of algal organization. Their work reinforces the general impression that the algae rely more on complex species-specific functional modifications of tissue behavior and organ geometry to cope with different wave energy regimes (e.g., viscoeleastic behavior and twist-to-bend ratios) than on modifications of individual structural or tissue material properties.

The mechanical properties of individual xylary elements and wood as a tissue have long interested biomechanicists, both for theoretical and practical reasons (Greenhill, 1881; Mark, 1967). Despite intensive study, however, debates about the roles played by lignin in wood continue even today. In this special issue, Koehler and Telewski (2006) review the mechanical properties of wood isolated from genetically transformed trees that differ structurally or chemically from their wild-type counterparts.

The science of acoustics is discussed in terms of the physical properties of wood by Wegst (2006) who explores why different wood species are preferred by musicians for the construction of different parts of their instruments.

Fracture mechanics is a complex but biologically important phenomenon, which is well illustrated by Farquhar and Zhao (2006) who, using the perspectives gained from the study of engineered materials, review this topic as it applies to turgid and woody plant structures as well as the behavior of soils when penetrated by growing roots (or stems). As will be seen, the "classic" theory for fracture developed by Griffith leads to substantial underestimates of the fracture strength of biological materials, particularly those of interest to botanists, because plant tissues are composite structures whose constituents behave as nonlinear viscoelastic materials. In contrast to metals and many plastics whose mechanical behavior motivated key developments in the theory of fracture mechanics, plant "materials" also tend to be highly deformable and anisotropic—features that limit the applicability of theory as it currently stands and provide fertile grounds for future research.

The last paper in this section, deals with examples of biomimetics, whereby structural features observed for cells, tissues, organs, or entire plants are redacted to their basic engineering principles and the lessons thus learned are used to construct engineered artifacts. Velcro, which mimics the properties of cocklebur fruits, is perhaps the best-known example. This area of research is covered in the article by Milwich et al. (2006), who briefly review the history of plant biomimetics and illustrate its potential with the "technical plant stem"—an engineered product inspired by the structural properties of stems such as those of *Arundo donax* and *Equisetum hyemale*. Although these taxa could never hybridize, the ability of engineers and botanists to "synthesize" and blend the features of widely different plants holds the potential to benefit industry, commerce, and medicine.

Mechanoperception and posture control—The ability of plants to perceive and respond to gravity, touch, or wind-induced mechanical stimulation has fascinated biologists for well over a century (see Vöchting, 1878; Hegler, 1893).

Externally applied mechanical forces (such as those produced by touch, water spray, or wind-induced flexure) are perceived and used by plants to alter their development and the physical properties of cell walls and tissues. More recent work indicates that the response mechanisms provoked by mechanical disturbance are only part of a much more extensive, complex, and perhaps very ancient "stress-response system" (Albrecht et al., 1993; Braam et al., 1997; Jaffe et al., 2002; Braam, 2005).

In this issue, Telewski (2006) reviews this extensive topic and discusses two competing models for plant mechanosensory perception: a plasmodesmatal-based, cytoskeletal–cell membrane–cell wall network and a stretch-activated, mechanosensory, calcium-selective ion channel system. Currently, neither of these models explains how plants are able to differentiate between different mechanical signals (e.g., gravity, wind-induced stem flexure, and vibration). It is also obvious that the roles of plant growth regulators, such as auxin and ethylene, in post-mechanoperception responses are poorly understood. For example, textbooks invariably mention that ethylene is produced when plant organs are mechanically disturbed. Yet, ethylene-deficient mutants respond morphogenetically when touched or caused to sway in the same manner as control plants.

During the 18th century, a discussion began on whether the supporting structures of plants were comparable to animal skeletons. Du Monceau (1785) argued for a functional analogy between wood and endoskeletons; Bonnet (1782) drew an analogy between the epidermis of herbaceous plants and the exoskeletons of insects. This functional analogy is taken up by Moulia et al. (2006) who argue that mechanoperception and the "motor functions" of plants are functionally equivalent to the active postural and equilibrium control of animals. By recognizing two kinematic designs—plants with localized movement (or an articulated construction) and plants with continuously distributed active movements, Moulia et al. (2006) advocate the need for new biomechanical models for plant architecture, which can cope with the mechanics required by indeterminate growth in a low density and highly turbulent fluid (air). Like many other authors in this special issue, Moulia et al. (2006) believe an integrative multidisciplinary approach will be required to construct models for plant growth and mechanical stability.

Hydraulics and wood anatomy—The height of self-supporting stems ranges well over six orders of magnitude, and an individual plant may span this size range as it grows from a seedling to an old tree. One obvious result of this growth in size is a dramatic increase in the root-to-leaf hydraulic pathway. Another is a concomitant increase in the resistance of water flow through this pathway. As a consequence, vascular land plants have evolved a broad spectrum of functional anatomical adaptations to cope with this increasing resistance and with the potential for the catastrophic and irreparable interruption of water flow through xylary elements (Carlquist, 1975). Sperry et al. (2006) describe just one of these adaptations by comparing the hydraulics of conifer torus-margo pits and flowering plant vessels. Perhaps contrary to our general perceptions about the "efficiency" of these two different anatomical configurations, Sperry et al. (2006) show that conifer sapwood has lower wood-area resistivity than does angiosperm sapwood with the same average conduit diameter. Although vessels are significantly longer than tracheids of the same diameter, they appear to lack the low end-wall resistance of

THE HOOKER OAK, 101 FT. HIGH. ESTIMATED AGE 1000 YEARS. BIDWELL PARK, CHICO, CALIFORNIA   J-260

Fig. 3.   The "Hooker Oak" tree, named by Annie Bidwell to honor Sir Joseph Dalton Hooker on the occasion of his visit to Chico, California in 1877. The tree, which fell during a windstorm in 1977, was estimated to be a thousand years old. It was nearly 30 m in height and had a basal circumference of 2.4 m. The largest branch measured 33.6 m from trunk to tip.

tracheids conferred by the presence of torus-margo pits. These findings, in tandem with the physical constraints imposed by mechanical and hydraulic multifunctionality of wood, led Sperry et al. (2006) to suggest that the evolution of vessels in angiosperm wood may have required ancient angiosperm species to survive and pass through a phase of mechanic-hydraulic instability.

Tree biomechanics—Perhaps because of the size and eco-logical importance of trees, no plant growth habit has received more attention than that of arborescent species (Fig. 3). Early workers interested in the mechanical "design" of arborescent species focused on how trees supported their own weight and what physical factors limited tree height. Only comparatively recently has the focus shifted to understanding the effects of dynamic wind-loading on the mechanical stability of leafy stems and anchorage roots.

In three interrelated articles, Peltola (2006), Brüchert and Gardiner (2006), and James et al. (2006) devote their attention to both static and dynamic loadings. Peltola (2006) takes a practical approach to the topic by considering how experimental data and mechanistic models can be used to estimate the risk of tree failure and to predict the effects of different management tactics on tree stability and stand productivity. A detailed review of the literature leads Peltola (2006) to conclude that models designed to understand the effects of static loads are insufficient to assess the mechanical stability of trees, which can fail under dynamic loads that are much smaller than those predicted by static tests.

Brüchert and Gardiner (2006) focus their attention on experimental data from the study of a wind-exposed Sitka spruce stand of 60 trees exposed to four different average wind speeds. They report that wind-exposed trees at the edge of the stand were smaller, more tapered, and more flexible than their counterparts growing in the middle of the stand—phenomena that correspond well with the mechanical responses of most plants to chronic stem flexure (see Telewski, 2006). Brüchert and Gardiner (2006) demonstrate that a combination of tree-form characteristics and stem mechanical properties combine to influence the ability of trees to cope with wind-induced, harmonic swaying—a conclusion that is strikingly similar to that reached by Harder et al. (2006) in their study of wave-swept brown algal macrophytes.

James et al. (2006) present a new model for the dynamic damping of tree motion induced by wind, one that incorporates the dynamic structural properties of branches as well as the trunk. These authors conclude that branches greatly influence the dynamic sway motion of the tree by means of mass damping (masses swaying counter to one another in a complex manner that acts to reduce the potentially dangerous harmonic sway of the trunk). James et al. (2006) conclude their article by considering the mechanical significance of the evolution of branches (and we note in passing that mass damping can occur for nonbranched tree-sized monocots whose compound leaves mimic the mechanical effects of branches).

Ecology—This special issue concludes with two papers devoted to the topic of ecobiomechanics—one dealing specifically with the biomechanics of browsing and grazing (from the perspective of both prey and predator) and another that tackles the topic synoptically.

Sanson (2006) points out that animals mechanically process leaves (and tender stems) to maximize the production of new surface area by promoting elastic fracture, which is resisted by a number of mechanisms operating at the molecular, cell, tissue, and entire organ level. Drawing on the many differences between di- and monocotyledonous leaves (and relying on the principles of fracture mechanics discussed by Farquhar and

Zhao, 2006), Sanson discusses how these two leaf types resist the mandibles of small insects and the teeth of small and large mammal herbivores and provides us with a fascinating treatment of how the scale of feeding relates to the scale of defense.

Read and Stokes (2006) draw on the insights gained from a diverse and highly scattered literature relating plant form and function to local environmental conditions to inform ecologists about the importance of the quantitative biomechanical perspective and to advise biomechanicists to carefully consider ecological context when inferring an adaptive form–function relationship. Their first message seems particularly timely in light of recent theories about plant allometry, which purport to explain virtually all physiological and ecological scaling relationships, including biomechanical phenomena. Their second message is as true today as it was when Gould and Lewonton (1979) enjoined against spinning "adaptationist scenarios" in the absence of fastidious experimentation or with disregard of the importance of "phyletic legacy."

A PROSPECTUS FOR THE FIELD

Predicting the future for any discipline or suggesting which among many potential research goals should be given preference is not without considerable risk. Nevertheless, past developments in the field of biomechanics and the insights provided by the articles presented here give us all some guidance.

Consider the mechanical behavior of the plant cell wall, which has long interested botanists and physical scientists. Despite well over a century of enquiry, until recently, a mechanistic explanation for the complex behavior of the plant cell wall has remained elusive at best. Today, we have the ability to construct artificial biocomposites that, when used with genetics to develop different mechanical phenotypes, have opened the door to understanding cell biomechanics at the molecular level. When juxtaposed with recent advances in molecular biology, we are also in the enviable position of comprehending the interactions between the cytoskeleton and its "ergastic" envelop during growth and development.

On a related topic, mechanoperception and its attending signal transduction are also fertile and active areas of research, both at the level of individual cells and at the level of the entire plant body. Competing models for thigmomorphogenesis can now be studied experimentally at a very sophisticated level of understanding. Recent developments in genomics, such as the elucidation of how DELLA proteins permit flexible modulations of growth in response to changes in the environment, are shedding light on how plants may be able to differentiate between different external signals and how the same signal can evoke different morphogenetic responses (see Achard et al., 2006). The application of molecular methods, such as microarrays and bioinformatics, will undoubtedly further help us to identify the different physiological responses that occur after the mechanoperception cascade is initiated (see Braam, 2005).

New technologies and approaches in tandem with nanofabrication also allow us to learn from nature and to construct biomimetic materials, devices, and structures, fashioned at the molecular level of organization, that can have diverse industrial or medical applications (see John et al., 2005). For example, Shahinpoor and Thompson (1995) developed a molecular model with sensors and actuators based on the mechanical design of the Venus-flytrap (*Dionaea muscipulata*); Valtchev et al. (2004) used the silicified epidermis of *Equisetum arvense* as a template for constructing zeolite beta-macrostructures; and Sieber (2005) draws upon plant based micro- and macroporous structures to develop methods of manufacturing ceramics and ceramic composites.

Other areas of rapid or great potential growth are obvious. The interface between biomechanics and allometry, which was initiated by Galileo Galilei in 1638, is now a fully developed field of enquiry, one that promises to shed light on the scaling relationships between plant body size and a host of physiological, developmental, ecological, and evolutionary phenomena, ranging from respiration and growth rates to biomass partitioning patterns and the evolution of organ types (see Brown and West, 2000). Computer programs are now capable of modeling complex dynamic processes, such as the effects of weather in tree stands and the seemingly chaotic sway of branches during violent storms. Biomechanics is also shedding light on the ability of some species to become invasive (e.g., Spector and Putz, 2006).

Additionally, there are sufficient data with which to construct "mechano-morphospaces" in which mechanical performance is calculated and mapped onto a space representing all morphological possibilities (e.g., Skotheim and Mahadevan, 2005). By superimposing those phenotypic variants that actually exist onto those that are functionally conceivable, we can see graphically life's "periodic chart" of mechanical design and ponder how and possibly why plant evolution followed the historical trajectories it did. The reconstruction of life's past as well as present-day diversity is also possible. Using data from the fossil record and the tools of engineering theory, it is now possible to calculate with reasonable accuracy how ancient calamites and lepidodendrids swayed in the wind and dispersed their spores or seed-like propagules into the air (e.g., Mosbrugger and Roth, 1996; Ackerman, 2000; Rowe and Speck, 2005).

But technological advances are only as good as the conceptual environment in which they are conceived and put to use. Who can predict what breakthroughs might emerge from a few equations scribbled on the back of an envelope by friends nurtured by a fine single malt Scotch or the sound of a good jazz band? For this reason, the most exciting development in the field of plant biomechanics is the conceptual confluence among workers in so many diverse disciplines, ranging from the study of molecular biology and genetics to that of ecology and evolution. The academic interests and expertise of the authors contributing to this special issue, all of whom share an interest in biomechanics, attest to this convergence, and suggest to us that the future for the discipline will develop in ways that are impossible to foresee.

It is our sincere hope that this special issue will inaugurate new collaborative ventures and help to solidify old ones. We also hope that the papers in this special issue will inspire the next generation of plant biologists to take up the study of plant biomechanics, because the future of any discipline is written by its newest devotees. And it is to this new generation as well as to those that have come before that we respectfully dedicate this special issue of *American Journal of Botany*.

LITERATURE CITED

ACHARD, P., H. CHENG, L. DE GRAUWE, J. DECAT, H. SCHOUTTETEN, T. MORITZ, D. VAN DER STRAETEN, J. PENG, AND N. P. HARBERD. 2006.

Integration of plant responses to environmentally activated phyto-hormonal signals. *Science* 311: 91–98.

ACKERMAN, J. D. 2000. Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. *Plant Sytematics and Evolution* 222: 167–185.

ALBRECHT, T., B. GROTH, Z. Q. XIA, M. LUXEM, H. LISS, L. ANDERT, AND P. SPENGLER. 1993. Evidence for the involvement of jasmonates and their octadecanoid precursors in the tendril coiling response of *Bryonia dioica*. *Phytochemistry* 32: 591–600.

BOWER, F. O. 1925. Plants and man. Macmillan, London, UK.

BOWER, F. O. 1930. Size and form in plants. Macmillan, London, UK.

BRAAM, J. 2005. In touch: plant responses to mechanical stimuli. *New Phytologist* 165: 373–389.

BRAAM, J., M. L. SISTRUNK, D. H. POLOSENSKY, W. XU, M. M. PURUGGANAN, D. M. ANTOSIEWICZ, P. CAMBELL, AND K. A. JOHNSON. 1997. Plant responses to environmental stress: regulation and functions of the *Arabidopsis TCH* genes. *Planta* 203: S35–S41.

BROWN, J. H., AND G. B. WEST [EDS.] 2000. Scaling in biology. Oxford University Press, Oxford, UK.

BRÜCHERT, F., AND B. GARDINER. 2006. The effect of wind exposure on the tree aerial architecture and biomechanics of Sitka spruce (*Picea sitchensis*, Pinaceae). *American Journal of Botany* 93: 1512–1521.

BURGERT, I. 2006. Exploring the micromechanical design of plant cell walls. *American Journal of Botany* 93: 1391–1402.

CARLQUIST, S. 1975. Ecological strategies of xylem evolution. University of California, Berkeley, California, USA.

DARWIN, C. 1880. The power of movement in plants. John Murray, London, England.

DU MONCEAU, D. 1785. La physique des arbes, [etc.] I. Paris, France.

FARQUHAR, T., AND Y. ZHAO. 2006. Fracture mechanics and its relevance to botanical structures. *American Journal of Botany* 93: 1449–1455.

GALILEI, G. 1638. Discorse e dimonstrazioni matematichi, intorno a due nouvo scienze. Leida.

GEITMANN, A. 2006. Experimental approaches used to quantify physical parameters at cellular and subcellular level. *American Journal of Botany* 93: 1380–1390.

GOULD, S. J., AND R. C. LEWONTON. 1979. The spandrels of San Marco and the Panglossian paradigm. *Proceedings of the Royal Society of London, B, Biological Sciences* 205: 581–598.

GREENHILL, A. G. 1881. Determination of the greatest height consistent with stability that a vertical pole or mast can be made, and of the greatest height to which a tree of green proportions can grow. *Proceedings of the Cambridge Philosophical Society* 4: 65–73.

GREW, N. 1682. The anatomie of plantes [etc.] 2nd ed. London, England.

HARDER, D., C. HURD, AND T. SPECK. 2006. Comparison of mechanical properties of four large, wave-exposed seaweeds. *American Journal of Botany* 93: 1426–1432.

HEGLER, R. 1893. Über den Einfluss des mechanischen Zugs auf das Wachstum der Pflanze. *Beiträge zur Biologie der Pflanzen* 6: 383–432.

HOLBROOK, N. M., M. W. DENNY, AND M. A. R. KOEHL. 1991. Intertidal "trees": consequences of aggregation on the mechanical and photosynthetic properties of the sea-palms *Postelsia palmaeformis* Ruprecht. *Journal of Experimental Marine Biology and Ecology* 146: 39–67.

HOLBROOK, N. M., AND M. A. ZWIENIECKI. 2005. Vascular transport in plants. Elsevier, Amsterdam, Netherlands.

JAFFE, M. J., A. C. LEOPOLD, AND R. C. STAPLES. 2002. Thigmo responses in plants and fungi. *American Journal of Botany* 89: 375–382.

JAMES, K., N. HARITOS, AND P. K. ADES. 2006. Mechanical stability of trees under dynamic loads. *American Journal of Botany* 93: 1522–1530.

JOHN, G., D. CLEMENTS-CROOME, AND G. JERONIMIDIS. 2005. Sustainable building solutions: a review of lessons from the natural world. *Building and Environment* 40: 319–328.

KOCH, G. W., S. C. SILLETT, G. M. JENNINGS, AND S. D. DAVIS. 2004. The limits to tree height. *Nature* 428: 851–854.

KOEHL, M. A. R. 1979. Stiffness or extensibility of intertidal algae: a comparative study of modes of withstanding wave action. *Journal of Biomechanics* 12: 634.

KOEHL, M. A. R., AND S. A. WAINWRIGHT. 1977. Mechanical adaptations of a giant kelp. *Limnology and Oceanography* 22: 1067–1071.

KOEHLER, L., AND F. TELEWSKI. 2006. Biomechanics of transgenic wood. *American Journal of Botany* 93: 1273–1278.

KNIGHT, T. A. 1811. On the causes which influence the direction of the growth of roots. *Philosophical Transactions of the Royal Society of London* 1811: 209–219.

MARK, R. 1967. Cell wall mechanics of tracheids. Yale University Press, New Haven, Connecticut, USA.

MILWICH, M., T. SPECK, O. SPECK, T. STEGMAIER, AND H. PLANCK. 2006. Biomimetics and technical textiles: solving engineering problems with the help of nature's wisdom. *American Journal of Botany* 93: 1455–1465.

MOSBRUGGER, V., AND A. ROTH. 1996. Mechanics in fossil plant biology. *Review of Palaeobotany and Palynology* 90: 195–207.

MOULIA, B., C. COUTAND, AND C. LENNE. 2006. Posture control and skeletal mechanical acclimation in terrestrial plants: implications for mechanical modeling of plant architecture. *American Journal of Botany* 93: 1477–1489.

NACHTIGALL, W. 1994. On the research history of plant biomechanics. *Biomimetics* 2: 87–107.

OLTMANNS, J. 1923. Morphologie und Biologie der Algen. Jena, Germany.

PELTOLA, H. 2006. Mechanical stability of trees under static loads. *American Journal of Botany* 93: 1501–1511.

PRESTON, R. D. 1974. The physical biology of plant cell walls. Chapman and Hall, London.

RASDORSKY, W. 1929. Über die Baumechanik der Pflanzen (Teil I–III). Biologia generalis. *Internationales Archiv für allgemeine Fragen der Lebensforschung* 5: 63–94.

RASDORSKY, W. 1930. Die Lehre von den Biegungsfedern im Dienste der Pflanzenmechanik. *Berichte der Deutschen Botanischen Gesellschaft* 48: 253–275.

READ, J., AND A. STOKES. 2006. The ecology of plant biomechanics, from individual to ecosystem. *American Journal of Botany* 93: 1546–1566.

RICHTER, J. P. 1970. The notebooks of Leonardo da Vinci (1452–1519), compiled and edited from the original manuscripts. Dover, New York, New York.

ROWE, N., AND T. SPECK. 2005. Plant growth forms: an ecological and evolutionary perspective. *New Phytologist* 166: 61–72.

SACHS, J. 1868. Lehrbuch der Botanik. Engelmann, Leipzig, Germany.

SANSON, G. 2006. The biomechanics of browsing and grazing. *American Journal of Botany* 93: 1531–1545.

SCHOPFER, P. 2006. Biomechanics of plant growth. *American Journal of Botany* 93: 1415–1425.

SCHWENDENER, S. 1874. Das mechanische Prinzip im anatomischen Bau der Monocotylen mit vergleichenden Ausblicken auf die übrigen Pflanzenklassen. Engelmann, Leipzig, Germany.

SCOTT BLAIR, G. W. 1969. Elementary rheology. Academic Press, London, UK.

SHAHINPOOR, M., AND M. S. THOMPSON. 1995. The Venus-flytrap as a model for a biomimetic material with built-in sensors and actuators. *Materials Science and Engineering C (Biomimetic Materials, Sensors and Systems)* 2: 229–233.

SIEBER, H. 2005. Biomimetic synthesis of ceramics and ceramic composites. *Materials Science and Engineering A (Structural Materials, Properties, Microstructure and Processing)* 412: 43–47.

SILK, W. K., AND R. O. ERICKSON. 1979. Kinematics of plant growth. *Journal of Theoretical Biology* 76: 481–501.

SKOTHEIM, J. M., AND L. MAHADEVAN. 2005. Physical limits and design principles for plant and fungal movements. *Science* 308: 1308–1310.

SPECTOR, T., AND F. E. PUTZ. 2006. Biomechanical plasticity facilitates invasion of maritime forests in the southern USA by Brazilian pepper (*Schinus terebinthiformis*). *Biological Invasions* 8: 255–260.

SPERRY, J., U. HACKE, AND J. PITTERMANN. 2006. Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany* 93: 1490–1500.

TELEWSKI, F. 2006. A unified hypothesis of mechanoperception in plants. *American Journal of Botany* 93: 1466–1476.

VALTCHEV, V. P., M. M. SNAIHI, A. C. FAUST, AND L. VIDAL. 2004.

Equisetum arvense templating of zeolite beta-macrostructures with hierarchical porosity. *Chemistry of Materials* 16: 1350–1355.

VÖCHTING, H. 1878. Über Organbildung im Pflanzenreich. Max Cohen, Bonn, Germany.

VOGEL, S. 1981. Life in moving fluids: the physical biology of flow. Willard Grant Press, Boston, Massachusetts, USA.

WEGST, U. 2006. Wood for sound. *American Journal of Botany* 93: 1439–1448.

WHITNEY, S. E. C., E. WILSON, J. WEBSTER, A. BACIC, J. S. G. REID, AND M. J. GIDLEY. 2006. Effects of structural variation in xyloglucan polymers on interactions with bacterial cellulose. *American Journal of Botany* 93: 1402–1414.