Plant biomechanics in the 21st century

Living beings obey physical laws, and this applies at all scales of the organism, from the interaction of the whole organism with its environment to subcellular processes. Biomechanics research enhances our understanding of the manner in which biological organisms cope with and exploit physical principles and how the functional design of cells, tissues, and processes involves not only biochemical but also mechanical concepts. Neither the cell biologist nor the ecologist can afford to ignore mechanical aspects when investigating the relationship between genotype and phenotype. As we continue to decipher the physical and engineering principles that determine plant structure and function, engineers and architects continue to be inspired by and mimic these to let human-created design benefit from structural and organizational principles that have proven their efficiency through their evolutionary survival.

Interdisciplinarity is a term that must, without fail, appear in any 21st century grant proposal to demonstrate that the proposed research program is at the leading edge. Yet, disciplinary silos that characterized much of the research done during the 20th century started emerging less than a couple of hundred years ago. For example, the investigation of the physical underpinnings of plant life and inspiration from plants for engineering design have a venerable history. Galileo's concepts concerning the mechanics of tubes emerged from his studying how grass stems deform when bent, while da Vinci's drawings of the first parachute and autogirosco propeller are reportedly based on his observations of the dandelion pappus and maple samara. Inversely, it is also clear that plant biologists have learned from studying engineering principles and physics. While writing the second edition of his The anatomy of plants, Nehemiah Grew (Grew, 1682) sought the advice of Robert Hooke about how plant cell walls could hydrostatically resist compression; A.G. Greenhill, who wanted to calculate the maximum height of trees (Greenhill, 1881), studied engineering as a student; hydraulic theories about plant vessels often turn to the insights of G. Hagen and J.L. Poiseuille's equation concerning the hydraulics of tubes (Niklas, 1992); and the elegant dimensionless equation developed by O. Reynolds in 1885 (Reynolds, 1885) permits many plant biologists to model the complex behavior of cumbersomely large or microscopically intractable plants, organs, and cells.

The intellectual marriage of the physical and mathematical sciences with botany can be traced to the writings of Aristotle, which are sadly lost to us and only mentioned by Aristotle's student Theophrastus (Encyclopaedia Britannica, 1911). However, plant biomechanics became a clearly defined field of study upon the publication of Simon Schwendener's seminal book Das mechanische Prinzip im anatomischen Bau der Monocotyleden (Schwendener, 1874), although scattered writings about mechanical phenomena in plants appeared well before the publication of Schwendener's book. For example, Du Monceau compared the skeletons of vertebrates with the wood in trees (Du Monceau, 1785); Bonnet drew analogies between the epidermis of herbaceous plants and the exoskeleton of insects (Bonnet, 1760); while Sachs wrote about the role of water pressure in the stiffening of plant cells, tissues, and organs (Sachs, 1868). However, it is not unfair to say that the discipline of biomechanics did not achieve full status until the latter part of the 20th century with the publication of two seminal books: Mechanical design in organisms by Wainwright et al. (1976) and Life in moving fluids by Vogel (1981). These two books, more than any others, merged the physical and biological sciences and illustrated how the conceptual reciprocity between the two Weltanschauungen (world views) could illuminate every aspect of biology.

This reciprocity is especially evident in plants owing to their structural simplicity and their photosynthetic physiology, which is tightly coupled to abiotic environmental variables. It is not surprising, therefore, that the field known as plant biomechanics has evolved as a vibrant area of study bringing together scientists from all over the world and a multitude of disciplines to share ideas about every level of biological organization, ranging from the molecular structure of cell walls and the viscoelasticity of protoplasm to the hydraulic architecture of trees to the dynamics of forest canopies experiencing gale force winds. The breadth and depth of plant biomechanics, now fully ushered into the 21st century, is nowhere better illustrated than in the papers collected in this special issue of the Journal of Experimental Botany.

Plant biomechanics: a truly interdisciplinary community

Plant biomechanics, according to today's understanding, is a field of research that not only combines physics, engineering,
mathematics, and chemistry with botany and forestry science, but also includes diverse aspects of plant physiology, cell biology, biochemistry, ecology, as well as developmental and molecular biology. It is also a very important component of many aspects of biomimetics. This merger of multiple disciplines is not without challenges, as students entering this field must rapidly get a grasp on a wide range of concepts ranging from molecular biology to the physics of non-linear viscoelastic materials, and tools as diverse as confocal laser scanning microscopy, tensile testing, and finite element modeling. An important role for the community over the past 25 years has therefore been a dedicated international conference series on this topic: the Plant Biomechanics Conferences. The first of these meetings, which have been held every 3 years since, took place in 1994 in Montpellier (France) and was initiated by Bernard Thibaut. Since then, eight more conferences have attracted an ever-growing number of scientists and an increasing diversity of disciplines: Reading (UK, 1997), Freiburg-Badenweiler (Germany, 2000), East Lansing (USA, 2003), Stockholm (Sweden, 2006), Cayenne (French-Guyana, 2009), Clermont-Ferrand (France, 2012), Nagoya (Japan, 2015), and finally the 9th Plant Biomechanics Conference, in Montreal (Canada, 2018). These conferences not only bring together the scientific community working on plant biomechanics but continue to widen and sharpen the scientific context in which plant biomechanics is embedded.

In this context, it is appropriate to remember a personality who has accompanied and helped shape plant biomechanics and the Plant Biomechanics Conferences since their inception in 1994: Hanns-Christof Spatz, who sadly passed away in August 2017. Hanns-Christof had been trained as a physicist and, after his PhD from Göttingen on the kinetic behavior of protons and deuterons in ice crystals, he worked for several years on the genetics of bacteria. After an appointment to a chair of biophysics at the Albert-Ludwigs-University of Freiburg, he changed his research topic again and worked for nearly 20 years very successfully in neurobiology with a main emphasis on molecular mechanisms of learning and memory in *Drosophila*. In the late 1980s, he became increasingly interested in plant biomechanics and founded, together with Thomas Speck, the Plant Biomechanics Group at Freiburg. Since that time, he devoted his scientific life to this field and contributed many publications on various topics of plant biomechanics, including the local buckling of hollow stems, the static and dynamic loading of trees, damping, the mechanics of plant tissues, and even the mechanics of fossil plants. His main interest was always on the theoretical description of plant mechanical behavior based on sound experimental data. He was a regular contributor to the Plant Biomechanics Conferences, attended all but one, and organized, together with Thomas Speck, the third iteration of the series in Freiburg-Badenweiler, Germany. Hanns-Christof Spatz supervised several PhD theses on plant biomechanics topics and was scientifically active during his entire life (the last paper he co-authored dates from 2016). In 2012, he published, together with Karl Niklas as his ‘opus max-imus’, the book *Plant physics* (Niklas and Spatz, 2012), which is a must read for everybody interested in biomechanics and biophysics of plants. His work and career were honored at the Montreal conference during a special session dedicated to his memory.

**From cells to trees, from fluid mechanics to non-linear viscoelasticity**

Mechanical principles govern processes at all scales relevant to the biological organism. How entire plant organs optimized their architectures to survive in the ever-moving waters of an ocean or the turbulence of wind is summarized in two papers in the present issue. Gosselin (2019) provides an overview of the physical framework that can be used to calculate the forces to which plants are exposed by water flow or wind movement. Drag forces and the different types of organ deformation are discussed, and particular attention is given to seaweeds upon exposure to wave action and surface friction. Whether plants grow in a fluid environment or in a gaseous one, the acting forces have the potential to cause them to vibrate. Vibrations can occur at various size scales ranging from the wind-induced swaying of trees to the bumble-bee-triggered motion of anthers resulting in pollen release. The analysis of such oscillatory motions requires a detailed understanding of the plant’s tissue or organ structure and biomechanics as discussed by de Langre (2019). More dramatic forces have the potential either to damage plants or to dislodge them. Stubbs et al. (2019) provide an overview of the different design strategies that have evolved to ensure that root architecture stabilizes plants in a manner that is optimized with respect to the typical growth substrate and habitat.

Plants not only respond passively to motion-triggering forces, but are also able to actively execute movement. This occurs in the absence of actin–myosin-regulated muscles, and is instead driven by the controlled interaction of turgor, osmotically driven uptake of water, and the cell wall (Geitmann, 2016). In their review, Morris and Blyth (2019) describe the mechanism of various plants or plant organs that are able to change shape in a reversible manner. The authors base their discourse on the fact that the physical principles underpinning such movement include osmosis, elastic instabilities, and cell wall mechanics. The authors provide an overview of the mechanisms that govern the movements of carnivorous plants such as the Venus flytrap and bladderworts. Motion in plants is not limited to the organ level but also occurs at the cellular scale. Arguably the most consequential cellular motion is exerted by the guard cells forming stomata. Their controlled swelling and relaxation regulate the gas exchange between the internal leaf tissues and the outside, and thus influence photosynthesis, respiration, and transpiration. How the architecture and mechanical properties of individual guard cells ensure efficiency in this motor function is elaborated in detail by Yi et al. (2019).

Cellular shape changes such as those in stomata are reversible processes that rely on the elastic deformation of the cell wall. However, the cell wall can also undergo significant plastic (irreversible) deformations. These are typically associated with developmental processes. During cell growth and differentiation, plant cells increase in size, in some cases multiplying their volume up to several thousand-fold, and they change their
shape from the simple brick-shape of the meristematic cell to the intricate shapes that characterize various tissues. These growth and shape changes involve the stretching and deformation of cell wall material whose mechanical properties in turn control the process (Bidhendi and Geitmann, 2018a). Cell growth, combined with cell division, is therefore a key process giving rise to new organs, a complex process that is discussed by Echevin et al. (2019). Mathematical simulation of growth processes has enabled researchers to rapidly evaluate different biological hypotheses in silico. The formal representation of plant shape, and biomechanical and biochemical signaling treats plants as organized systems of information processing and can be done in a variety of ways, as illustrated by Palubicki et al. (2019). While a wealth of information is available about the signaling processes associated with biochemical cues, knowledge of the molecular underpinnings of the perception and processing of biomechanical cues is only emerging. Landrein and Ingram (2019) provide a summary of the state-of-the-art and emphasize how crucial the integration of biochemical and biomechanical signaling processes is for many developmental steps as it allows cells to coordinate their behavior. One of the ubiquitous biomechanical signals is the one caused by gravity as it enables plants to orient the growth efforts of their organs (Nakamura et al., 2019). The review by Nakamura et al. focuses on the regulatory mechanisms underlying amyloplast sedimentation and the ensuing signaling cascade that mediates differential growth responses. The resulting orientation of the root (in the direction of gravity) and the shoot (generally opposite to gravity) arise from a complex integration of signals that combine the information provided by gravity with that resulting from proprioception, as elaborated by Moulia et al. (2019).

The biomechanical structure whose properties govern both internally driven processes such as cell growth and the behavior of plant organs upon external load application is the cell wall (Chebli and Geitmann, 2017; Bidhendi and Geitmann, 2018b). The primary cell wall must be deformable to enable cell growth and morphogenesis (Bidhendi and Geitmann, 2016), whereas the secondary cell wall renders plant tissues rigid in ways that fit the lifestyle of the plant. Certain habitats such as those of lianas require stability combined with flexibility. The strategic alternation of rigid and softer tissues in the stems of lianas ensures an architecture that is able to provide resistance of tree architectures, from subcellular signaling processes to macroscopic organ function, from molecular biology to fluid mechanics. It is a unique field that benefits from the synergy arising through interdisciplinary approaches, and from technological development that enables unprecedented investigation into biological structures and processes.

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References
Bidhendi AJ, Geitmann A. 2016. Relating the mechanics of the primary plant cell wall to morphogenesis. Journal of Experimental Botany 67, 449–461.
Bidhendi AJ, Geitmann A. 2018a. Finite element modeling of shape changes in plant cells. Plant Physiology 176, 41–56.
Bidhendi AJ, Geitmann A. 2018b. Tensile testing of primary plant cells and tissues. In: Geitmann A, Grill J, eds. Plant biomechanics – from structure to function at multiple scales. Cham: Springer Verlag, 321–347.

Plant biomechanics research relies on an integration of biological studies with engineering technology and physical and mathematical modeling. The tool kit of a plant biomechanics lab is, therefore, diverse, and the expertise required to perform the research generally requires collaboration between members of various disciplines. Mathematical and computational modeling forms an essential component of plant biomechanical research as it enables researchers to do two fundamental things: develop new hypotheses based on predictive models and extract quantitative information from complex experimental data based on reverse engineering. Growth processes represent an intriguing subject for predictive modeling exercises, and several papers in this special issue address the challenges associated with this in silico approach to biology (Echevin et al., 2019; Smithers et al., 2019). Reverse engineering, on the other hand, is required to extract useful parameters from micro- and macro-mechanical studies. Bidhendi and Geitmann (2019) assess how modeling allows the extraction of elastic moduli such as Young’s modulus for the cell wall from experiments that deform the cell wall, cells, or tissues in various ways. The same paper also provides an overview of the various experimental strategies and set-ups that have been developed to execute these experiments on samples that consist of the primary cell wall, a rather soft material that is not easy to handle. This paper and that by Nelson et al. (2019) address the fact that the best practices in plant biomechanics are still lacking and that a significant amount of work will need to be invested to ensure reproducibility of experiments performed on diverse sample types and tissues. Finally, a necessary complement to mechanical testing is the investigation of the 3D structure of specimens, and recent technical developments enable this to be done in a non-invasive manner. Hesse et al. (2019) compare different imaging methods targeted at large and opaque plant specimens for which, until recently, the only way to visualize the inner structure was destructive.

Combined, the papers in this special issue illustrate the breadth of biomechanics research which ranges from the growth mechanism governing leaf development to the wind resistance of tree architectures, from subcellular signaling processes to macroscopic organ function, from molecular biology to fluid mechanics. It is a unique field that benefits from the synergy arising through interdisciplinary approaches, and from technological development that enables unprecedented investigation into biological structures and processes.
