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THEMATIC ARTICLES

Plant Growth—A Biomechanical Perspective

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Growth is one of the most intensively studied topics in plant sciences. It involves numerous processes from gene expression and translation to the formation of materials, tissues, and ultimately the whole plant. The scope of the *Journal of Plant Growth Regulation* predominantly covers topics like gene expression, signal transduction and other molecular interactions. Within this special issue, we would like to shed some light on other aspects of plant growth, the formation of materials and complex structures, their mechanical properties and the mechanical function of individual structural components from the cellular to the organismic level in relation to environmental constraints.

The articles in this special issue are arranged according to the level at which mechanical properties are examined. Starting with the cuticle as an extra-cellular membrane and cell walls, the two following contributions focus on the adaptive growth of plants and the reconfiguration of their shape as a response to external factors such as light or mechanical loads. The final contribution summarizes the mechanical properties of climbing plants from an evolutionary perspective.

The cuticle covers all primary epigean parts of the plant and represents a multifunctional interface between plant and environment. Primarily, the cuticle serves as an effective barrier against uncontrolled water loss. Because very small injuries may result in desiccation of tissues and subsequent necrosis, the integrity of the cuticle is essential for plants. To incorporate material during growth, that is, maintaining the function while the structure is partially weakened, is a highly complex process. This issue has been intensively studied in cell walls, but is virtually unaddressed for cuticles. Tomato fruit belong to the most thoroughly examined objects in terms of cuticle mechanics and we know, that these properties may change considerably during fruit growth. Today, various ripening-impaired mutants exist, that do not show a color change from green to red, which is often related to changes of the elastic modulus. The paper by Bargel and Neinhuis describes the effects of an abandoned ripening process and how this influences cuticle mechanics. Combining tools from molecular genetics and mechanics may be a promising way to understand which regulatory pathways are involved in mechanical optimization during adaptive growth.

One of the most important structural materials is cellulose, the major component of plant cell walls. Although cellulose synthesis and deposition have been extensively studied for quite some time, the mechanism of cellulose fibril orientation is still puzzling. However, the mechanical properties of individual cells and tissues mainly depend on the orientation of fibrils in secondary cell walls. The

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contribution by Burgert and Jungnikl focuses on the influence of structural parameters such as density and the microfibril angle in the S2-layer on the structure-function relationships of the wood of branches in spruce (*Picea abies*) and yew (*Taxus baccata*). Wood samples of different parts of the branches (lateral, ad- and abaxial) subjected either to tension or compression due to the weight of the branch were compared to evaluate the influence of mechanical stresses with respect to adaptive growth.

Different types of wood formation can be a reaction to external factors but may also account for the individual life cycle. Typical examples of changes in plant form during a life cycle are biennials that grow as a rosette in the first year and produce a prominent flower bearing shoot in the second. Similar profound changes are found in lianas. Many species start as self-supporting, freestanding seedlings resembling small tree saplings that later—after being attached to a host tree—produce true climbing, lianescent stems which are no longer self-supporting. This transition is connected to numerous changes at the tissue, cellular, ultrastructural and biochemical level. The most prominent one is the variation of the type of wood that is produced in the two different stages of growth. This transition profoundly changes the stem structure and results in considerably different mechanical properties of the stem as a whole. This variability within an individual life cycle is demonstrated by Gallenmüller and others in the tropical liana *Croton nuntians* (Euphorbiaceae). External factors such as light quantity may be superimposed, and influence via growth processes structure and mechanical properties of the stems, resulting in freestanding plants with stiffer stems in shady places as compared to individuals in more sun exposed habitats. Mechanical adaptation based on external mechanical stresses may not only result in reinforcing of the stressed organ, but can also result in increased flexibility. Flexible structures are advantageous in unstable environments such as wind exposed locations or flow dominated habitats. Such adaptations are addressed by Harder and others in two case studies. Case one deals with the brown alga *Durvillaea* that is exposed to high drag forces on wave swept sea shores, where adaptive growth allowing fast reconfiguration of the lamina is important for survival. The second study was conducted with the giant reed *Arundo donax*, that is temporarily exposed to high wind velocities in its natural habitat. A comparison shows that in both habitats similar passive reconfiguration processes of the plants can result in a reduction of the maximum loads by streamlining of phylloids or leaves and stems.

In the last contribution to this special issue, Rowe and colleagues review the mechanical properties and the underlying structural features of climbing plants representing different systematic groups such as Lycopodiaceae, members of the monocotyledons (climbing palms within the Arecoideae and Calamoideae) and dicotyledons (Apocynaceae, Ranuculaceae) in angiosperms. The adaptations with respect to changes of the anatomical development of the stem during ontogeny, type of attachment to the supporting plant and variation of biomechanical properties of the stem are compared and discussed in the light of the evolution of land plants. The authors point out that the two most important developmental features controlling the biomechanical properties of climbing stems are directly correlated with growth processes and include: (1) the presence or absence of secondary growth, (2) the number, complexity and coordination of development of primary and secondary tissues with different mechanical properties.

The range of articles demonstrates the complexity of biomechanical adaptations of plants on several structural levels. It also demonstrates the intricate growth processes and the regulation by external factors that are involved. The combination and introduction of methods will hopefully stimulate increased interdisciplinary approaches in the field of plant growth regulation.