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THEMATIC ARTICLES

Plants and Gravity

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Gravity is a constant factor on Earth and has been ubiquitous throughout the evolutionary history of our planet. Thus, gravity has had a profound impact on the form, structure, and function of plants. This issue of the *Journal of Plant Growth Regulation* explores the effects of gravity on plant growth and development from several perspectives. Most of the review papers consider plants and gravity from the viewpoint of ground-based laboratory research, and several papers consider gravitropism, the directed growth in response to gravity, in some detail. However, another approach to study the effects of gravity on plants is to effectively remove the force due to gravity. A very dramatic way to accomplish this goal is through the free-fall conditions achieved by spacecraft in low Earth orbit, so some of the authors have reviewed recent advances in spaceflight research with plant systems.

Traditionally, plant biologists have studied the effects of one factor or stimulus on plant development. However, as the first two articles show, scientists are increasingly interested in how plants integrate multiple stimuli in generating a growth response. In the first paper of this issue, Fasano, Masa, and Gilroy specifically consider ionic signaling in response to gravity and touch. The approach of Fasano and coworkers is to use recent techniques involving non-invasive imaging of ions in living plant cells (for example, GFP, recombinant aequorin) to study the role of calcium and pH in sensing mechanisms. They suggest that ionic signals are some of the earliest transduction events of mechanoperception and that calcium is emerging as a significant element in both touch and gravity signaling. This supports the hypothesis that gravity sensing is derived from an ancestral touch perception apparatus. To continue on the theme of integration of environmental stimuli, Correll and Kiss discuss the interactions between gravitropism and phototropism in plants. There are both unique and common elements in the transduction processes in these tropisms, and they consider methods to separate the influences of light and gravity in plants.

The next two papers in this issue deal with aspects of gravitropism, particularly gravisensing in plants. Wolverton, Ishikawa, and Evans discuss novel methods to study the kinetics of root gravitropism and the insights provided by these studies. This paper reports that there may be at least two sites of gravity sensing, one within the root cap (that is, columella cells) and another outside of the cap, and these authors propose a revised model of root gravitropism that includes dual sensors and dual motors. In contrast to the columella cells in roots, in shoots, endodermal cells are sites of gravity perception. Kato, Morita, and Tasaka have studied gravitropism in shoots and present a novel model for gravitropic sensing in stem-like organs of plants. They use a molecular genetics approach and propose that the vacuole in endodermal cells plays a key role in graviperception by influencing amyloplast sedimentation.

The cytoskeleton has been implicated in the cellular mechanisms of gravitropism, and the next three articles in this special issue discuss the role of

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the cytoskeleton in gravitropism. In the first paper in this series, Blancaflor focuses on higher plants, and, in particular, on the involvement of the actin cytoskeleton in gravity perception, transduction, and response. He discusses many of the advances in cell biological techniques (that is, GFP, ion imaging in real time) cited by Fasano and coworkers and how they should provide new insights into this field which has had many controversial results in recent years.

The next two papers in this cytosekeletal group deal with model lower plant systems that have been used to study gravitropism. Braun, Buchen, and Sievers review the literature on studies of the rhizoids of the alga *Chara* and focus on actomyosin-mediated statolith (that is, dense cellular structures involved in graviperception) positioning. They consider both ground-based and spaceflight experiments and suggest that there may be a complex interaction between actin and a number of motor proteins that is important in mechanisms of gravitopism in lower and higher plants. Schwuchow and coworkers consider another single-celled system, namely moss protonemata. In contrast to other types of plant cells, protonemata of mosses appear to have microtubules involved in the gravitropism pathway. These authors conclude that conservation of complex patterns of amyloplast sedimentation in different mosses suggests that these patterns are specializations for gravity sensing.

Spaceflight experiments have been valuable in studies of gravitropism and gravity effects in plants, and the last three articles focus specifically on experiments that have been performed in microgravity. Perbal and Driss-Ecole, who have been involved in many spaceflight studies, report that experiments in microgravity have resulted in a reexamination of methods to estimate sensitivity to gravity and lead to the conclusion that the perception and transduction phases of gravitropism can occur within seconds.

Paul and Ferl consider the molecular aspects of the stress faced by plants during spaceflight. They have used reporter genes and transgenic plants to evaluate the effects of spaceflight on stress metabolism. In the long term, such studies may lead to the genetic engineering of plants that are well-adapted for long duration spaceflight missions (for example, Mars exploration). In the final paper of this issue, Porterfield continues some of these themes by discussing the biophysical limitations on physiological and biochemical processes within plants. Understanding these biophysical limitations and overcoming them will also be important for plants during future spaceflight missions, and such studies will also provide insight into the basic physiological mechanisms in plants.

All of the articles in this special issue of the *Journal of Plant Growth Regulation* review important subject areas in plant biology and suggest exciting future directions for research. The authors have provided a valuable perspective on the issues closest to them. Thanks are due to these scientists as well as to the reviewers who provided their peers with valuable input. I have enjoyed working with them to bring their articles and this issue to fruition.

John Z. Kiss
Guest Editor