

# Signaling and Communication in Plants

## Series Editors

František Baluška

Department of Plant Cell Biology, IZMB, University of Bonn, Kirschallee 1, D-53115  
Bonn, Germany

Jorge Vivanco

Center for Rhizosphere Biology, Colorado State University, 217 Shepardson Building,  
Fort Collins, CO 80523-1173, USA

František Baluška  
Editor

# Plant-Environment Interactions

From Sensory Plant Biology  
to Active Plant Behavior

 Springer

*Editor*  
František Baluška  
Department of Plant Cell Biology  
IZMB  
University of Bonn  
Kirschallee 1  
D-53115 Bonn  
Germany  
email: baluska@uni-bonn.de

ISSN 1867-9048  
ISBN 978-3-540-89229-8 e-ISBN 978-3-540-89230-4  
DOI: 10.1007/978-3-540-89230-4

Library of Congress Control Number: 2008938968

© 2009 Springer-Verlag Berlin Heidelberg

This work is subject to copyright. All rights are reserved, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other way, and storage in data banks. Duplication of this publication or parts thereof is permitted only under the provisions of the German Copyright Law of September 9, 1965, in its current version, and permission for use must always be obtained from Springer-Verlag. Violations are liable for prosecution under the German Copyright Law.

The use of general descriptive names, registered names, trademarks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

*Cover design:* WMXDesign GmbH, Heidelberg, Germany

Printed on acid-free paper

9 8 7 6 5 4 3 2 1

springer.com

*František Baluška dedicates this book to  
Prof. Dieter Volkmann for introducing him  
to sensory plant biology and in recognition  
of his great support and friendship.*

# Preface

Plants are generally considered to be passive and insensitive organisms. One can trace this strong belief back to Aristoteles, who positioned immobile plants outside of the sensitive life domain. The millennia that have elapsed between time of Aristoteles and the present day highlight the fact that it will very difficult to change this almost dogmatic view. For instance, one of the first serious attempts to rehabilitate plants was performed by no less than Charles Darwin, in 1880. At the end of the book *The Power of Movement in Plants*, which he wrote together with his son Francis, they proposed that the root apex represents the brain-like anterior pole of the plant body.

This volume, in fact the whole series, documents a paradigm shift that is currently underway in the plant sciences. In the last two or three decades, plants have been unmasked as being very sensitive organisms that monitor and integrate large numbers of abiotic and biotic parameters from their environment. That plants react to electric stimuli in the same manner as animals was shown by Alexander von Humboldt a few years after Luigi Galvani discovered the electrical stimulation of animal muscles in frogs' legs. Later, when animal action potentials were discovered in animals, similar action potentials were soon recorded in plants too. Initially only "sensitive plants" were tested, but some 30 years ago it was found that all plants use action potentials to respond to environmental stimuli. This rather dramatic breakthrough went almost unnoticed in the mainstream plant sciences. Only recently, the emergence of plant neurobiology has highlighted this neglected aspect of biology. The obvious conservation that occurs throughout evolution means that action potentials provide both plants and animals with evolutionary advantages that are crucial to their adaptive behavior and survival. As plants evolved action potentials independently of animals, this phenomenon also holds the key to illuminating the mystery of convergent evolution, a phenomenon that does not conform to the classical Darwinian principles of biological evolution.

Recent advances in chemical and sensory ecology have revealed that plants communicate via volatile and allelochemical chemical messengers with other plants and insects. By using a wide variety of volatiles, plants are able to attract or repel diverse insects and animals, enabling them to shape actively their biotic niche. The number of volatile compounds released and received by plants for communication

is immense, requiring complex signal-release machinery, as well as “neuronal” decoding apparatus to correctly interpret the received signals. These aspects of plant activity have not been studied yet. Plants integrate and memorize numerous sensory “experiences” in order to adapt effectively to an ever-changing environment.

Plants also show active behavior, including kin and self/nonself recognition, cognition, and a plant-specific form of intelligence. In order to find their prey, parasitic plants use sophisticated sensory detection systems, and after colonizing the prey tissues they conform to an animal-like heterotrophic lifestyle. Plants often apply deception as an effective strategy to manipulate other organisms, including insects, other animals, and perhaps even us humans. They use colors, forms and odors, as well as taste-stimulating, nutritional and neuroactive substances to manipulate insects, animals and humans in order to aid their spread around the globe. Crop plants like wheat, maize, barley and rice are the most successful species in this respect. New concepts are needed and new questions must be asked in order to advance our rather rudimentary understanding of the communicative nature of sensory plants.

One of the goals of current plant science is to improve the agricultural properties and stress adaptabilities of plants. However, we will not achieve this goal until we unravel the communicative, sensory, and cognitive aspects of these organisms. Moreover, our civilization still is—and will continue to be in the future—fully dependent on plants, since they (together with unicellular photosynthetic organisms) are the only primary source of oxygen and organic matter on this planet. Recently, humans have begun to use plants extensively to produce biofuels. Due to the continuing problems with hunger in underdeveloped countries, this presents our civilization with a dilemma: what proportion of plants should be grown for food and what proportion for energy? Our future depends on us gaining a complete understanding of plants in their full complexity.

Bonn, October 2008

František Baluška

## Further Reading

- Baluška F, Volkmann D, Mancuso S (2006) Communication in plants: neuronal aspects of plant life. Springer, Berlin
- Baluška F, Mancuso S (2009) Signaling in plants. Springer, Berlin
- Barlow PW (2008) Reflections on plant neurobiology. *Biosystems* 92:132–147
- Brenner E, Stahlberg R, Mancuso S, Vivanco J, Baluška F, Van Volkenburgh E (2006) Plant neurobiology: an integrated view of plant signaling. *Trends Plant Sci* 11:413–419
- Conway Morris S (2003) Life’s solution: inevitable humans in a lonely universe. Cambridge University Press, Cambridge
- Darwin CR (assisted by Darwin F) (1880) The power of movement in plants. Murray, London
- Karban R (2008) Plant behaviour and communication. *Ecol Lett* 11:727–739
- Mancuso S, Shabala S (2006) Rhythms in plants. Springer, Berlin
- Pollan M (2002) The botany of desire: a plant’s-eye view of the world. Random House, New York
- Volkov AG (2006) Plant electrophysiology. Springer, Berlin
- Scott P (2008) Physiology and behaviour of plants. Wiley, New York

# Contents

<b>Mechanical Integration of Plant Cells</b> . . . . .	1
Anna Kasprowicz, Daniel Kierzkowski, Michalina Maruniewicz, Marta Derba-Maceluch, Ewelina Rodakowska, Paweł Zawadzki, Agnieszka Szuba, and Przemysław Wojtaszek	
<b>Root Behavior in Response to Aluminum Toxicity</b> . . . . .	21
Charlotte Poschenrieder, Montse Amenós, Isabel Corrales, Snezhana Doncheva, and Juan Barceló	
<b>Communication and Signaling in the Plant–Fungus Symbiosis: The Mycorrhiza</b> . . . . .	45
Pascale Seddas, Vivienne Gianinazzi-Pearson, Benoit Schoefs, Helge Küster, and Daniel Wipf	
<b>Role of <math>\gamma</math>-Aminobutyrate and <math>\gamma</math>-Hydroxybutyrate in Plant Communication</b> . . . . .	73
Barry J. Shelp, Wendy L. Allan, and Denis Faure	
<b>Hemiparasitic Plants: Exploiting Their Host’s Inherent Nature to Talk</b> . . . . .	85
John I. Yoder, Pradeepa C. Gunathilake, and Denneal Jamison-McClung	
<b>Host Location and Selection by Holoparasitic Plants</b> . . . . .	101
Mark C. Mescher, Jordan Smith, and Consuelo M. De Moraes	
<b>Plant Innate Immunity</b> . . . . .	119
Jacqueline Monaghan, Tabea Weihmann, and Xin Li	
<b>Airborne Induction and Priming of Defenses</b> . . . . .	137
Martin Heil	
<b>Chemical Signaling During Induced Leaf Movements</b> . . . . .	153
Minoru Ueda and Yoko Nakamura	

<b>Aposematic (Warning) Coloration in Plants</b> . . . . .	167
Simcha Lev-Yadun	
<b>Deceptive Behavior in Plants. I. Pollination by Sexual Deception in Orchids: A Host–Parasite Perspective</b> . . . . .	203
Nicolas J. Vereecken	
<b>Deceptive Behavior in Plants. II. Food Deception by Plants: From Generalized Systems to Specialized Floral Mimicry</b> . . . . .	223
Jana Jersáková, Steven D. Johnson, and Andreas Jürgens	
<b>Cognition in Plants</b> . . . . .	247
Paco Calvo and Fred Keijzer	
<b>Memorization of Abiotic Stimuli in Plants: A Complex Role for Calcium</b> . . . . .	267
Camille Ripoll, Lois Le Sceller, Marie-Claire Verdus, Vic Norris, Marc Tafforeau, and Michel Thellier	
<b>Plants and Animals: Convergent Evolution in Action?</b> . . . . .	285
František Baluška and Stefano Mancuso	
<b>Index</b> . . . . .	303



# Mechanical Integration of Plant Cells

Anna Kasprowicz, Daniel Kierzkowski, Michalina Maruniewicz,  
Marta Derba-Maceluch, Ewelina Rodakowska, Paweł Zawadzki,  
Agnieszka Szuba, and Przemysław Wojtaszek

## 1 Introduction

In order to function in changing environmental conditions, all living organisms need to be equipped with two sets of seemingly contradictory mechanisms; these enable them to (1) function as an integrated entity independent of the environment, and (2) sense and communicate with their immediate surrounding. During the course of evolution, several factors—both physical and chemical—have emerged as organismal integrators. Among these, gravity provides a major directional stimulus, while chemical compounds are usually used as internal integratory molecules (Bhalerao and Bennett 2003).

Although the same cellular toolkit of their common ancestor gave rise to present-day eukaryotes through evolution, it should be remembered that plant and animal lineages diverged about 1 billion years before they became multicellular organisms. As a consequence, plants and animals differ in their lifestyles, responses to stimuli, and adaptations to the environment. This distinction results from the adoption of two different strategies of coping with the regulation of intracellular water content, and is reflected in the properties and behavior of “naked” animal cells vs. “walled”

---

A. Kasprowicz, D. Kierzkowski, M. Maruniewicz, M. Derba-Maceluch,  
E. Rodakowska, and P. Zawadzki  
Department of Molecular and Cellular Biology, Faculty of Biology, Adam Mickiewicz  
University, Umultowska 89, 61-614 Poznań, Poland

A. Szuba  
Institute of Bioorganic Chemistry, Polish Academy of Sciences, Noskowskiego 12/14,  
61-704 Poznań, Poland

P. Wojtaszek (✉)  
Department of Molecular and Cellular Biology, Faculty of Biology, Adam Mickiewicz  
University, Umultowska 89, 61-614 Poznań, Poland and  
Institute of Bioorganic Chemistry, Polish Academy of Sciences, Noskowskiego 12/14,  
61-704 Poznań, Poland  
e-mail: przemow@amu.edu.pl

plant cells (Peters et al. 2000). Thus, while animals are able to move away when conditions are unfavorable, plants—since they are sessile organisms—must react and/or adapt to changes. As a result, much greater plasticity of plants and their cells is observed (Valladares et al. 2000).

All organisms have the ability to sense and respond to a variety of physical stimuli, such as radiation, temperature, and gravity (Volkman and Baluška 2006). Although physical forces act in the same manner on different organisms, the effects of their actions depend on the organism's habitat. For example, the effect of gravitational force on an organism depends greatly on whether it lives in water or on land. On the other hand, the forces exerted on terrestrial plants by the movement of air are much lower than those exerted on aquatic ones by the movement of water (Niklas et al. 2000). Thus, although the overall construction of any particular plant or plant cell is generally similar to that of any other, the details of their biochemical and mechanical designs can vary considerably, as these are also shaped by the changing conditions in the cell's or organism's immediate surroundings.

## 2 Mechanical Organization of Plant Cells

From a mechanical point of view, the end product of the evolutionary transition to present-day plant cells could be considered a *tensegral hydrostat*. In normal plant cells, compression-resistant turgid protoplast is surrounded by and presses against tension-resistant and mechanically stable cell walls (Wojtaszek 2000; Zonia and Munnik 2007). This design principle has several important implications for the functioning of plant cells and plants: (1) functional cell walls become indispensable elements of plant cells; (2) the vast majority of plant cells do not move in relation to their neighbors; (3) both the cell walls and the steep gradient of hydrostatic pressure across the plasma membrane (which exceeds 2 MPa) can be used to mechanically stabilize plant bodies; (4) the interplay between the cell walls and turgor is the major determinant of cellular shape and organismal morphogenesis; (5) the presence of a hermetic matrix around protoplasts limits the ability to acquire energy and nutrients (Peters et al. 2000; Wojtaszek 2001). However, phragmoplast-based incomplete cytokinesis, which leads to the formation of the cell plate and enables a new type of intercellular communication through plasmodesmata (Lucas et al. 1993; Heinlein and Epel 2004), and the inclusion of newly synthesized cell walls into the supracellular structure of the apoplast (Wojtaszek 2000), have allowed plants to overcome at least some of the constraints of this mechanical design.

The major structural and functional organizer of plant cells is the continuum formed by cell walls, plasma membrane and cytoskeleton (WMC continuum; Wyatt and Carpita 1993; Kohorn 2000; Wojtaszek 2000; Baluška et al. 2003). Plant protoplasts are able to rapidly and reversibly retract from the cell wall in plasmolytic

response to changing osmotic conditions (Lang-Pauluzzi and Gunning 2000) while maintaining localized membrane-wall attachments (Lang et al. 2004). The functioning of the cytoskeleton, which is anchored via plasma membrane to the walls, provides mechanisms for (1) the regulation of cellular volumes (Komis et al. 2003); (2) the directional transport and spatial distribution of cellular components (Sato et al. 2003; Chuong et al. 2006), and; (3) the rearrangement of cellular architecture in response to internal and external stimuli (e.g. Wojtaszek et al. 2005; Schmidt and Panstruga 2007). However, the wall-anchored cytoskeleton seems to function as not only a detector of physical forces but also a transmitter of mechanical signals as well as a transducer of those signals into biochemical messages (Forgacs 1995; Ingber 2003a, b). These processes are rather poorly recognized in plants, and important linker molecules within the WMC continuum are still not characterized (for review see Kohorn 2000; Baluška et al. 2003). However, from studies in animal systems, it is now becoming clear that proper ECM–cytoskeleton contacts are crucial to the determination of cellular shapes and thus cell fate (e.g., Nelson et al. 2005; Engler et al. 2006; Vogel and Sheetz 2006; Assoian and Klein 2008). This reinforces the idea that information stored in molecular and cellular structures is used during the generation of form, giving rise to new, emergent properties that are not directly deducible from the properties of the initial components (Harold 1995).

Our questions about the influence of physical forces on the functioning of cells and organisms are not yet fully answered. However, some general rules of mechanosensing and mechanotransduction are becoming apparent. According to the tensegral model of cellular architecture, microfilaments are tension-responsive elements, whereas microtubules serve as contraction-resisting structures, and the cell and tissue shape depends on a balance between the physical states of those prestressed filamentous networks (Ingber 2003a, b). Upon arrival at the cell surface, mechanical stimuli are recognized by specialized receptors. Those receptors—which are connected to both the ECM and the internal cytoskeleton spanning the whole cytoplasm—will be able to transmit these mechanical signals into cells, while other membrane receptors will fail (Ingber 2003a). At least two possible and nonexclusive ways of mechanotransduction can be envisioned. One of them involves the direct transduction of the mechanical stress imposed on the receptor into a chemical signal which can be propagated into the cell. The other one makes use of local conformational changes of proteins, at least within a portion of the signaling pathway (Kung 2005; Valle et al. 2007). The first path offers the versatility of secondary chemical messengers and the possibility of cross-talk with other signaling pathways, enabling the fine tuning of cellular reactions (Orr et al. 2006). The second provides the speed and fidelity of signal transmission, which is a unique feature of mechanotransduction (Na et al. 2008). Interestingly, if we assume that the same forces act on all elements of the tensegral structure (ignoring the size), the same rules of tensegrity will apply at not only the cellular level but also the tissue and organismal ones (Ingber 2003a).

There are many examples (in plants too) of cellular processes in which the transmission of mechanical force has been documented or is commonly assumed, starting with changes in the activities of enzymes or protein complexes (Aon et al. 2000), through organized movement of molecules, particles and organelles (van der

Honing et al. 2007), and ending with the reorganization of whole cells in response to external cues, such as osmotic stress (e.g., Wojtaszek et al. 2005, 2007) or pathogenic infection (Schmidt and Panstruga 2007; Hardham et al. 2008). Over ten years ago, a direct mechanical connection between the cell surface and the nucleus via the cytoskeleton was demonstrated in animal cells (Maniotis et al. 1997); this profoundly affects the organization of chromatin (Maniotis et al. 2005). Interestingly, it seems that the nucleolus is to some extent mechanically independent from the rest of the nucleus (Yang et al. 2008). In plant cells, nuclei are highly dynamic; they are able to undergo polymorphic shape changes and rapid, long-distance movements (Chytilova et al. 2000). Both the positioning and movements of nuclei are mediated by actin (Baluška et al. 2000). Importantly, mechanical stimulus seems to be the primary signal that induces nuclear repositioning (Hardham et al. 2008), and it has been demonstrated that isolated nuclei are also able to sense physical forces (Xiong et al. 2004). As the position of the nucleus is strictly correlated with the cell cycle progression, especially with the determination of the plane of cell division, the sensing and transduction of mechanical stimuli provide the mechanism for the coordinated development of supracellular plant structures (Lintilhac and Vesecky 1984; Qu and Sun 2007; see also below).

## 2.1 *Constructing the Pathway for Mechanotransduction*

In accordance with what was said above, at least two broad classes of mechanosensitive (MS) molecules can be distinguished. The first comprises proteins that sense the tension within the lipid bilayers of biological membranes (Martinac 2004). These can then open rapidly, allowing a large number of ions to enter, thus amplifying the signal. Examples include the bacterial MscS (mechanosensitive channel of small conductance) channels that regulate cellular responses to osmotic stress. In the *Arabidopsis* genome there are ten genes coding for MscS-like (MSL) proteins. Among them, MSL2 and MSL3 are involved in the control of plastid size and morphology (Haswell and Meyerowitz 2006), while MSL9 and MSL10, and possibly three other MSL proteins, are required for MS channel activities in root cells (Haswell et al. 2008). The regulation of cellular volumes has been ascribed to some MS anion channels (reviewed by Roberts 2006), while the gating of  $\text{Ca}^{2+}$  influx is thought to be a major function of the MS ion channels in lily pollen tubes (Dutta and Robinson 2004) and Mca1 protein from *Arabidopsis* roots (Nakagawa et al. 2007).

Proteins belonging to the second group are characterized by their ability to sense mechanical distortions in either cytoskeleton or extracellular matrices (ECM), such as cell walls in plants. Their ectodomains are usually embedded in ECM or they strongly interact with the ECM components. These domains are connected with transmembrane domains, and—if present—with cytoplasmic domains of various lengths and different activities. On the intracellular side, they interact with cytoskeleton either directly or via cytoskeleton-binding proteins. Further signal transmission can occur in several different and nonexclusive ways, depending on the design of the

given protein. First, the distortion can be propagated as conformational changes within a chain of interacting proteins. Second, the stimulus can be transduced into an electrical signal via the activity of ion channels. Third, the mechanical signal can be transformed into a chemical message, e.g., through the phosphorylation of target proteins by the intracellular domain of a sensor with kinase activity or a specialized kinase interacting with a sensor (Ingber 2003b; Orr et al. 2006). Typical examples taken from animal systems include integrins, which are able to detect and transmit mechanical perturbations in both directions: inside–outside and from the ECM to the cytoskeleton, reacting to changes in the cellular neighborhood and stabilizing cell–ECM interactions. The extent and the quality of the interactions with the integrins are then recognized and transformed into various biochemical messages regulating metabolism and cellular behavior (Arnaout et al. 2007; Assoian and Klein 2008). In plants, the most diverse group of proteins are the protein kinases with specialized extracellular domains. These include receptor-like kinases (RLKs), such as wall-associated kinases (WAKs; Kohorn 2001) and proline-rich extensin-like receptor kinases (PERK), and other kinases with, say, carbohydrate-binding motifs (reviewed by Shiu and Bleecker 2001). Although WAKs (for example) have been shown to be embedded in the pectin matrix of the walls (Decreux and Messiaen 2005), the involvement of RLKs in mechanotransduction has rarely been demonstrated (Gouget et al. 2006). An interesting example is the specialized potassium channel KAT1, located in plasma membrane and probably associated with the surrounding cell walls of *Vicia faba* guard cells, although whether it transmits mechanical distortion into the cell is yet to be elucidated (Homann et al. 2007).

In animal cells, integrin activity can be directly modulated by peptides containing RGD (Arg–Gly–Asp) motifs that are characteristic of many of the extracellular proteins interacting with integrins. Although genes coding for integrins or integrin-interacting proteins have not been identified in the *Arabidopsis* genome (Hussey et al. 2002), the existence of proteins similar to integrins (e.g., those recognized by heterologous antibodies) has been demonstrated in many plant species. Moreover, the treatment of plant cells with RGD-containing peptides affects their functioning in processes such as gravisensing (Wayne et al. 1992), the plasmolytic cycle (Canut et al. 1998), the plant defense response to fungal infection (Mellersh and Heath 2001), as well as growth and differentiation (Schindler et al. 1989; Barthou et al. 1998). The application of RGD peptides also leads to the modulation of cytoplasmic streaming (Hayashi and Takagi 2003) and the formation of Hechtian strands (Canut et al. 1998; Mellersh and Heath 2001). As Hechtian strands contain both actin filaments and microtubules, these observations provide direct evidence of active linkages between plasma membrane proteins and the cytoskeleton, which play an important role in cell-to-cell communication and signal transduction from the cell wall into the protoplast.

Several other molecules have been proposed to function as linkers within the WMC continuum; myosin VIII and formins are thought to be the most probable adhesive molecules (reviewed by Kohorn 2000; Baluška et al. 2003). Their localization at the cross-walls of cells in the axial organs may be crucial to their functioning (Deeks et al. 2002; Baluška and Hlavačka 2005). Intriguingly, some of the proposed

WMC linkers, such as WAKs and arabinogalactan proteins (AGPs), were found to associate with plasma membrane-located MS calcium-selective channels in tobacco BY-2 cells, supporting the view that the WMC continuum is the sensor and transducer of mechanical signals (Gens et al. 2000). Interestingly, such an association enables the discrimination of various signals, as stretch-activated  $\text{Ca}^{2+}$  channels are involved in the sensing of both hypotonic and hypertonic conditions, whereas the WMC continuum is only involved in sensing a hypertonic environment (Hayashi et al. 2006).

### 3 Control of Cell Morphogenesis and Fate Determination

Cell organization and functioning takes place in four dimensions (Wojtaszek 2000). To understand these processes, we must, in the words of Frank Harold (1995), “ask how organisms produce successive shapes as they traverse their life cycles. This query focuses attention on structures, forces and flows that modulate form, rather than on molecules and genes.” Research on various systems, but especially animal cells, has provided evidence that cellular shapes and the sensing of geometry and mechanical environment are tightly intertwined with cellular functions. For example, cell–ECM interactions are crucial in deciding the cellular fate (Engler et al. 2006) and the frequency of cell division within an organ (Nelson et al. 2005). The presence of turgor and the “walled” organization of plant cells (Peters et al. 2000) provide other mechanisms of shape determination. As turgor is a scalar quantity, its effects are isodiametric, and wall-less protoplasts are invariably spherical. The continuous interplay between turgor and the differentiated mechanics of wall domains surrounding individual cells provide the means to achieve the great diversity of cellular shapes (Panteris and Galatis 2005; Mathur 2006). Even more importantly, although the organized cytoskeleton carries out cytokinesis, it is the presence of the walls as well as the resulting shape of the cell that provide spatial cues that are indispensable when organizing the cytoskeleton and determining the plane of cell division (Meyer and Abel 1975; Niklas 1992; Green 1999; Cleary 2001). In growing plants, the characteristic mechanical environment of the cells in a given organ results in an ordered pattern of cell divisions. This is lost in regenerating tissues such as callus, but can be restored with the external application of directional forces (Lintilhac and Vesecky 1984), which are sensed by protoplasts (Lynch and Lintilhac 1997). Moreover, the mechanical environment of the maternal tissues has a crucial influence on the plane of first asymmetric division in fertilized zygotes (Kaplan and Cooke 1997). Mechanical patterns are also important in suspension-cultured cells, in which mechanical stimuli dictate the proper organization of cellular metabolic networks (Yahraus et al. 1995; Aon et al. 2000).

At the cellular level, the turgor is used to identify mechanically weaker domains of the cellular boundary in order to enable growth in that direction (Mathur 2006). As the cellulose–hemicellulose network constitutes the major tension-resistant element of the walls, it is commonly assumed that the orientation of newly deposited cellulose microfibrils restricts the possible growth directions of expanding cells. However, the question of what

determines the orientation of cellulose microfibrils is still a matter of debate. The classical point of view is that the deposition of cellulose microfibrils is affected by the alignment of cortical microtubules (Wymer and Lloyd 1996). Experiments with tobacco suspension-cultured cells have demonstrated that spatial cues for the organization of microtubules might come from biophysical forces, and that microtubules themselves can respond to vectorial changes in such forces (Wymer et al. 1996). According to the geometrical model, new microfibrils are oriented by the cell geometry together with existing wall components, while the orientation of microtubules is a simple reflection of the directed delivery of cellulose synthase complexes to the plasma membrane (reviewed by Emons and Mulder 2000). However, recent biochemical and genetic data suggest the existence of a bidirectional flow of information between cortical microtubules and cellulose microfibrils, with the latter providing spatial cues for the internal organization of microtubules, most probably through the cellulose synthesis machinery (Fisher and Cyr 1998; Paredez et al. 2006, 2008). Microtubules aside, filamentous actin is also essential for cell elongation during plant development (Baluška et al. 2001) and for the directed delivery of cellulose synthase complexes to the sites of wall synthesis (Wightman and Turner 2008).

In many cases, tissue geometry has a crucial influence on cell fate. In axial plant organs, the pressure exerted by external epidermal cell walls allows inner cells of the root to perceive the mechanical environment nearby and adjust properly to it (Kutschera 2008). Externally applied pressure can lead to an ordering of the cell division planes in callus (Lintilhac and Vesecky 1984), and to an altered developmental pattern, combined with changes in organ identity (Hernández and Green 1993). The laser removal of cells from *Arabidopsis* root meristem reorients the emerging division planes in remaining cells to fill in the empty space. Moreover, daughter cells are able to change their directions of development and differentiate according to their new positions in the root (van den Berg et al. 1995, 1997). These changes can be coupled with the remodeling of the structure and composition of the cell wall in order to reinforce and stabilize the mechanical message. This was first demonstrated in fucoid algae, where zygote differentiation into thallus and rhizoid cells depends on asymmetric division and the formation of cell-specific cell walls (Berger et al. 1994). Similarly, during zygotic embryogenesis in tobacco, the original zygotic cell wall is crucial for the maintenance of apical–basal polarity and for determining the fates of daughter cells (He et al. 2007).

## 4 Responses of Plants and Plant Cells to Mechanical Stimuli

In the classical view, for an organism to be able to respond to a given stimulus, it should be equipped with a complete signaling pathway that ends with the modulation of the activities of regulatory elements that affect the expression of stimulation-dependent genes. The activities of the gene products would eventually lead to changes at the cell level and at the organismal level. As mentioned above, sensing and transduction of mechanical stimuli are among the oldest evolutionary mechanisms

that enable plant cells to respond to external cues. It should be noted, however, that although reactions to osmoticum, touch, and gravity are all responses to physical signals, they can be and are differentiated according to their “directionality.” Touch stimuli arrive from the outside of the cell and are signaled into the cell. In contrast, the reaction to a gravitational stimulus is initiated through its sensing inside the cell. Finally, the reaction to osmotic changes is most probably bidirectional, as it involves sensing the stimulus at both the plasma membrane and the tonoplast.

#### **4.1 Osmoregulation in Plant Cells**

Water availability is crucial to the proper functioning of the plant cell, as a hypotonic environment causes an influx of water into the protoplast, causing it to swell, whereas hypertonic conditions draw the water out of the cell, decreasing turgor and inducing a plasmolytic response. Stresses such as drought and high salinity result in effects similar to those evoked by a hyperosmotic environment, leading to a loss of mechanical strength and a wilting of soft, nonlignified plant tissues (Boudsocq and Laurière 2005). Osmotic conditions are carefully sensed by all cells, and their changes induce active responses, mainly mechanisms regulating the cell volume (Zonia and Munnik 2007). In walled cells such as yeast, osmotic stress sensing depends on cell wall integrity (Hohmann 2002), and this is also postulated for plant cells (Marshall and Dumbroff 1999; Nakagawa and Sakurai 2001).

Sensing and signaling systems for osmotic conditions occur in all groups of organisms. Relatively little is known about osmosensors in plants (Grefen and Harter 2004). Plasma membrane protein AHK1 has been identified in *Arabidopsis* and was shown to be a homolog of yeast osmosensory two-component histidine kinase SLN1 (Urao et al. 1999). Its involvement in water stress responses in plants has been demonstrated (Wohlbach et al. 2008). There are eight genes coding for two-component histidine kinases in total in the *Arabidopsis* genome, some of which are also potential receptors for cytokinins and ethylene (Grefen and Harter 2004). Interestingly, one of the cytokinin receptors—CRE1—is also regulated by changes in turgor pressure (Reiser et al. 2003). A close homolog of another cytokinin receptor (AHK3 from *Medicago sativa*) has been shown to be transcriptionally activated in response to high salinity, which suggests that MSHK1 can also function as an osmosensor (Coba de la Peña et al. 2008). On the other hand, the overexpression of the transmembrane protein NtC7, which is most similar to RLKs, provides tobacco with a tolerance to the osmotic stress evoked by 500 mM mannitol. Interestingly, this tolerance appears to be stress-specific, as seeds were not able to germinate on media containing high salt concentrations (Tamura et al. 2003). Such stress-specific response phenomena have also been demonstrated in other osmotic signaling steps (Zonia and Munnik 2004). During the drought, the detection of the cell's turgor state forms part of a hydraulic signaling pathway that allows for a rapid stomatal response in cooperation with the abscisic acid signaling pathway that is activated in roots (Comstock 2002). The tight control over stomatal aperture size



depends on osmotically induced rapid shrinking–swelling cycles of guard cells (Blatt 2000). These plasmolytic cycles also involve continuous membrane turnover (Shope et al. 2003; Meckel et al. 2005).

Changes in hydrostatic pressure across the plasma membrane generate stretch and compression forces that induce rapid responses in plant cells. The hydrodynamic condition of the plant cell and oscillations between different osmotic states have recently been postulated to affect cell shape, structure and growth as well as vesicle trafficking (Proseus et al. 2000; Shope et al. 2003; Meckel et al. 2005; Mathur 2006; Proseus and Boyer 2006a, b; Zonia et al. 2006). The cell walls and cytosol are highly anisotropic. Inside the cell, organelles and cytoskeleton are organized and distributed nonrandomly (e.g., Wojtaszek et al. 2005; Chuong et al. 2006). These features allow for a local response to the vector of mechanical force. The anisotropic tip growth of pollen tubes and root hairs is strictly controlled by the local weakening of cell walls and cortical cytoskeleton arrays (Mathur 2006). Following the appearance of the bulge, tip growth is still maintained due to the weaker cortical arrays at the tip than in the distal regions. Modulation of culture medium osmolality causes changes in apical volume, cell wall composition and expansion, and this affects pollen tube growth rates (Zonia et al. 2002, 2006; Zonia and Munnik 2004). The mechanical properties of cell walls can thus be tuned precisely, using either enzymatic or nonenzymatic mechanisms, to withstand dynamic changes in extra- and intracellular pressure.

## 4.2 Reactions to Touch

All plants sense and respond to mechanical perturbations in their environment, such as wind, rain, snow and sound waves, as well as to contact with other organisms or elements of the physical environment, like soil. These reactions are collectively termed touch responses, and are usually divided into thigmotropic or thigmonastic reactions, depending on the influence of the stimulus vector on the direction of movement. The former usually occur in the direction determined by the arriving stimulus, while nastic movements are largely independent of the direction of the stimulus. Touch responses can be extremely quick, as in carnivorous plants or *Mimosa pudica*, or very slow, eventually resulting in changes to the morphology of the plant in a process called thigmomorphogenesis (Braam 2005; Esmon et al. 2005; Telewski 2006). An interesting example is the growth of roots in the soil, as it combines responses to both touch and gravity (Fasano et al. 2002; see also below). Under normal conditions, plant roots grow along the gravitational vector. However, when a root approaches an obstacle, it seems that gravitropic behavior is compromised and touch responses take place (Okada and Shimura 1990; Massa and Gilroy 2003).

Although responses of plants to mechanical stimuli are usually observed at an organismal level, there are changes at the cellular and subcellular levels that are crucial to the selection and modulation of those responses. It has been demonstrated

in yeast that cell walls exhibit local temperature-dependent nanomechanical motion with an amplitude of ca. 3 nm (Pelling et al. 2004). If the situation is similar in plant cells, this may suggest that touching such an oscillator will immediately induce not only a slight perturbation of the surface of the wall but also changes in either the frequency or amplitude of the wall's oscillations. Thus, even a very small stimulus could be recognized and transduced into a cellular response. This response can be further amplified by the activities of cellular machinery and maintained over time, giving rise to all kinds of responses. At the cellular level, touching the cell surface induces very rapid changes in both cellular metabolism and intracellular organization, like chloroplast movement (Sato et al. 2003) or nuclear and cytoplasmic migration towards the contact site (Hardham et al. 2008). The cell returns to its previous state as soon as stimulus is removed. Examples include the reactions of plant cells to physical forces exerted by fungal or oomycete pathogens infecting plant epidermal cells. In many cases, fungi use mechanical force to break through the physical barriers of plant cell walls, and these attempts can be detected in a mechanosensitive way (Gus-Mayer et al. 1998). Such reactions can also be induced experimentally, by applying gentle pressure to the epidermal cell surface using a microneedle. Interestingly, the changed cell morphology tracks the needle tip as it moves along the plant cell surface (Hardham et al. 2008).

Several genes that are upregulated in response to touch stimulation (*TCH*) have been identified and characterized (Braam and Davis 1990). Interestingly, the expression of *TCH* genes is also regulated in response to other environmental stimuli (reviewed by Braam et al. 1997), and at least some of them also seem to be under the phytohormonal control of, e.g., auxin and brassinosteroids (Antosiewicz et al. 1995; Xu et al. 1995). Touch stimulation leads to the rapid and transient elevation of  $[Ca^{2+}]_{\text{cyt}}$  in plants (Knight et al. 1991), while the exogenous addition of  $Ca^{2+}$  to suspension-cultured cells upregulates the expression of *TCH* genes (Braam 1992). These findings strongly support the idea that  $Ca^{2+}$  acts as a second messenger in touch responses (Braam et al. 1997), and probably also as a stimulus-specific signal that allows touch and gravitational stimulation to be discriminated (Legué et al. 1997). Thus, it is not a surprise to discover that three out of four of the initially identified *TCH* genes are in fact calcium-binding proteins. *TCH1* is a plant calmodulin, while *TCH2* and *TCH3* belong to a family of calmodulin-like proteins that are also able to bind  $Ca^{2+}$ , but their exact role is unknown (Braam et al. 1997; McCormack and Braam 2003). An interesting suggestion derives from the finding that *TCH3* interacts with PINOID—a serine/threonine kinase involved in auxin signaling—to regulate its activity in response to changes in calcium levels (Benjamins et al. 2003). Finally, the product of *TCH4* is xyloglucan endotransglycosylase/hydrolase (XTH), one of the major wall-modifying enzymes. The *TCH4* expression pattern is also touch- and  $Ca^{2+}$ -dependent, and changes in localization are also observed (Xu et al. 1995; Antosiewicz et al. 1997).

In the years following the description of the *TCH* genes, many other genes were found to be induced by touch. Genome-wide analysis of expression patterns in touch-stimulated *Arabidopsis* plants revealed that expression of 589 genes was upregulated within 30 min

of touch stimulation, while 171 genes were downregulated (Lee et al. 2005). As expected, a relatively high proportion of the upregulated genes coded for proteins involved in cellular calcium binding as well as cell wall synthesis and modification. Interestingly, among seven genes coding for calmodulins, only *TCH1* was upregulated by touch stimulus. Importantly, genes implicated in disease resistance formed the third biggest functional group of upregulated genes (Lee et al. 2005).

### 4.3 Responses to Gravity

As mentioned above, gravity is a major relatively constant physical force on Earth and is thus considered to be one of the major driving forces in evolution (Volkman and Baluška 2006). At the organismal level, gravity is the most important integratory physical factor, and it is also a source of mechanical stress that must be accommodated (Kern et al. 2005). Gravity affects plant body architecture via two mechanisms: gravitropism and gravity resistance. Gravitropism is the orientation of the growth of plant organs along (e.g., roots) or against (e.g., shoots) the gravitational vector (Blancaflor and Masson 2003). On the other hand, gravity resistance comprises there are also a set of mechanisms that allow plants to support their own weight, e.g., by strengthening their cell walls (Ko et al. 2004; Hoson et al. 2005). Gravitropism is the first step in a series of events leading to various graviresponses. Its major element is a translation of an internal mechanical stimulus, usually caused by the displacement of some mass, into biophysical and biochemical signals (Perbal and Driss-Ecole 2003). Although graviperception in plants is now understood in quite some detail, the precise mechanisms involved are still a matter of debate. It seems also that mechanisms of graviperception utilized in gravitropism and in resistance to gravity are at least partially different (Hoson et al. 2005).

Different cells are specialized in order to detect the gravitational vector in gravitropism. In roots, these cells are statocytes, which are located in the root-cap columella; in hypocotyls, these are dedicated cells within the endodermal cell layer; in shoots, they are cells within the bundle sheath parenchyma (Blancaflor et al. 1998; Fukaki et al. 1998). Some data indicate, however, that the orientation of the gravitational vector can also be perceived outside of those regions (Wolverton et al. 2002). Following transduction, the perceived gravitational signal is transferred from the statocytes to the responding tissues (Perbal and Driss-Ecole 2003; Perrin et al. 2005). Statocytes are polarized cells containing starch-filled amyloplasts (statoliths; Driss-Ecole et al. 2003). Because they are quite different in density from the cytoplasm, statocytes are able to sediment. This notion gave rise to the commonly accepted explanation of gravity sensing: the starch–statolith hypothesis, according to which the sedimentation of statoliths provides the vectorial information required to orient the direction of organ growth (reviewed by, e.g., Sack 1997; Blancaflor and Masson 2003). Observations of the gravitropic responses of starch-deficient mutants and starch-overproducing mutants as well as experiments utilizing high-gradient magnetic fields generally support this model (Kuznetsov and Hasenstein

1997; Kiss et al. 1997; Vitha et al. 2007). However, some data indicate that starch-deficient mutants still exhibit some degree of gravitropic response (Caspar and Pickard 1989).

The question how the displacement of starch-filled amyloplasts is sensed in statocytes is still debatable. One possibility is that statoliths act as ligands that activate receptors located in the cellular membrane system (Braun 2002; Limbach et al. 2005). However, not all of the experimental data fit into such a model (Wendt et al. 1987). The sensing of statolith movement by MS ion channels is another possibility (Yoder et al. 2001; Pickard 2007). Over the last two decades, various MS ion channel activities have been identified in plant membranes (see above). It has been shown that gravitational stimulation of roots is correlated with the rapid alkalization of the cytosol and the transient influx of  $\text{Ca}^{2+}$  into protoplasts (Fasano et al. 2001; Plieth and Trewavas 2002). The question of how statolith movement activates the MS channels remains, however. At the moment it appears that the tensegral concept of cellular organization provides the answer, and that the mechanical signal is sensed within the WMC continuum (Blancaflor 2002; Baluška et al. 2003). The statoliths' trajectories indicated that they usually move along cellular channels located at the interface between the ER-less central region and the ER-dense cortical region of columella cells. These regions are pervaded by the prestressed actin network, which is denser in the ER-less region. Statolith movement can then disturb the mechanical balance of the cytoskeleton, and this (through the connection to the plasma membrane) can activate the MS ion channels (Yoder et al. 2001). In accordance with this, pharmacological disruption of the microfilaments affects the distribution and sedimentation of amyloplasts (Baluška and Hasenstein 1997; Palmieri and Kiss 2005). At the same time, such disruption does not usually abolish gravitropic response (Staves et al. 1997; Yamamoto and Kiss 2002; Hou et al. 2004). This may indicate that other cytoskeletal components are also important, and a role for microtubules has indeed already been suggested (Himmelspach et al. 1999). It is also important to note that the sedimentation of statoliths is probably not a free, passive precipitation, as their positions are precisely controlled by the actomyosin system (Braun et al. 2002; Wojtaszek et al. 2005). Finally, the precise spatial organization of the actin filaments and the way that they are anchored to the walls via polysaccharides and proteins are also important for gravisensing (Wayne et al. 1992; Wojtaszek et al. 2005, 2007).

Another hypothesis for gravisensing has been proposed by Staves (1997). The hydrostatic pressure model postulates that what is sensed is not the disturbance in the balance of forces within intracellular structures, but rather the difference in the tension/compression forces exerted by the entire protoplast between the apical and basal sites of attachment to the walls in axial organs (Staves et al. 1992). The tension exerted by an entire protoplast could also locally activate MS ion channels (Pickard 2007), triggering the transduction of the gravitational signal. It has also been proposed that such differences can result in a shift in the positions of symplastic domains that secrete auxin, resulting in the accumulation of auxin at the bottoms of the cells (Friml et al. 2002). Such a shift could result from

differential membrane trafficking in domains subjected to variable tensile forces (Morris and Homann 2001). Finally, the possibility that several gravisensing mechanisms operate together cannot be excluded (Barlow 1995; LaMotte and Pickard 2004).

In contrast to gravitropism, gravity resistance can occur in virtually all cells, so there is probably no signal transmission between perceiving and responding cells (Hoson et al. 2005). In this case, gravity produces tensile and compressive forces in some regions of the plant body. The gravisensing that occurs in resistance to gravity is independent of statolith sedimentation, since mutants that have abolished gravitropism and lack sedimentable amyloplasts still exhibit full gravity resistance reactions (Tasaka et al. 2001). Also, the removal of the root cap does not influence gravity resistance (Soga et al. 2005a). On the other hand, MS ion channels have been shown to be a crucial element here (Soga et al. 2002, 2005b), as has the composition of the cellular membranes, with sterols being particularly important (Koizumi et al. 2007). Moreover, upregulation of tubulin gene expression is involved in gravity-induced modification of microtubule dynamics, which may play an important role in the resistance of plant organs to gravity (Soga et al. 2006; Matsumoto et al. 2007). However, further elaboration of the molecular mechanisms of gravity resistance is strongly needed.

## References

- Antosiewicz D, Polisensky D, Braam J (1995) Cellular localization of the Ca<sup>2+</sup> binding CH3 protein of *Arabidopsis*. *Plant J* 8:623–636
- Antosiewicz D, Purugganan M, Polisensky D, Braam J (1997) Cellular localization of *Arabidopsis* xyloglucan endotransglycosylase-related proteins during development and after wind stimulation. *Plant Physiol* 115:1319–1328
- Aon MA, Cortassa S, Gomez Casati DF, Iglesias AA (2000) Effects of stress on cellular infrastructure and metabolic organization in plant cells. *Int Rev Cytol* 194:239–273
- Arnaout MA, Goodman SL, Xiong J-P (2007) Structure and mechanics of integrin-based cell adhesion. *Curr Opin Cell Biol* 19:495–507
- Assoian RK, Klein EA (2008) Growth control by intracellular tension and extracellular stiffness. *Trends Cell Biol* 18:347–352
- Baluška F, Hasenstein KH (1997) Root cytoskeleton: its role in perception of and response to gravity. *Planta* 203:S69–S78
- Baluška F, Hlavačka A (2005) Plant formins come of age: something special about cross-walls. *New Phytol* 168:499–503
- Baluška F, Salaj J, Mathur J, Braun M, Jasper F, Šamaj J, Chua N-H, Barlow PW, Volkmann D (2000) Root hair formation: F-actin-dependent tip growth is initiated by local assembly of profilin-supported F-actin meshworks accumulated within expansin-enriched bulges. *Dev Biol* 227:618–632
- Baluška F, Jasik J, Edelmann HG, Salajova T, Volkmann D (2001) Latrunculin B-induced plant dwarfism: plant cell elongation is F-actin-dependent. *Dev Biol* 231:113–124
- Baluška F, Šamaj J, Wojtaszek P, Volkmann D, Menzel D (2003) Cytoskeleton–plasma membrane–cell wall continuum in plants. Emerging links revisited. *Plant Physiol* 133:482–491
- Barlow P (1995) Gravity perception in plants—a multiplicity of systems derived by evolution. *Plant Cell Environ* 18:951–962

- Barthou H, Petitprez M, Brière C, Souvré A, Alibert G (1998) RGD-mediated membrane-matrix adhesion triggers agarose-induced embryoid formation in sunflower protoplasts. *Protoplasma* 206:143–151
- Benjamins R, Ampudia C, Hooykaas P, Offringa R (2003) PINOID-mediated signaling involves calcium-binding proteins. *Plant Physiol* 132:1623–1630
- Berger F, Taylor A, Brownlee C (1994) Cell fate determination by the cell wall in early *Fucus* development. *Science* 263:1421–1423
- Bhalerao RP, Bennett MJ (2003) The case for morphogens in plants. *Nat Cell Biol* 5:939–943
- Blancaflor EB (2002) The cytoskeleton and gravitropism in higher plants. *J Plant Growth Regul* 21:120–136
- Blancaflor EB, Masson PH (2003) Plant gravitropism. Unraveling the up and downs of a complex process. *Plant Physiol* 133:1677–1690
- Blancaflor EB, Fasano JM, Gilroy S (1998) Mapping the functional roles of cap cells in the response of *Arabidopsis* primary roots to gravity. *Plant Physiol* 116:213–222
- Blatt MR (2000) Cellular signaling and volume control in stomatal movements in plants. *Annu Rev Cell Dev Biol* 16:221–241
- Boudsocq M, Laurière C (2005) Osmotic signalling in plants. Multiple pathways mediated by emerging kinase families. *Plant Physiol* 138:1185–1194
- Braam J (1992) Regulated expression of the calmodulin-related TCH genes in cultured *Arabidopsis* cells: Induction by calcium and heat shock. *Proc Natl Acad Sci USA* 89:3213–3216
- Braam J (2005) In touch: plant responses to mechanical stimuli. *New Phytol* 165:373–389
- Braam J, Davis R (1990) Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in *Arabidopsis*. *Cell* 60:357–364
- Braam J, Sistrunk M, Polisensky D, Xu W, Purugganan M, Antosiewicz D, Campbell P, Johnson K (1997) Plant responses to environmental stress: regulation and functions of the *Arabidopsis* TCH genes. *Planta* 203:S35–S41
- Braun M (2002) Gravity perception requires statoliths settles on specific plasma membrane areas in characean rhizoids and protonemata. *Protoplasma* 219:150–159
- Braun M, Buchen B, Sievers A (2002) Actomyosin-mediated statolith positioning in gravisensing plant cells studied in microgravity. *J Plant Growth Regul* 21:137–145
- Canut H, Carrasco A, Galaud JP, Cassan C, Bouyssou H, Vita N, Ferrara P, Pont-Lezica R (1998) High affinity RGD-binding sites at the plasma membrane of *Arabidopsis thaliana* links the cell wall. *Plant J* 16:63–71
- Caspar T, Pickard BG (1989) Gravitropism in starchless mutant of *Arabidopsis*—implication for the starch-statolith theory of gravity sensing. *Planta* 177:185–197
- Chuong SDX, Franceschi VR, Edwards GE (2006) The cytoskeleton maintains organelle partitioning required for single-cell  $C_4$  photosynthesis in Chenopodiaceae species. *Plant Cell* 18:2207–2223
- Chytilova E, Macas J, Śliwinska E, Rafelski SM, Lambert GM, Galbraith DW (2000) Nuclear dynamics in *Arabidopsis thaliana*. *Mol Biol Cell* 11:2733–2741
- Cleary AL (2001) Plasma membrane-cell wall connections: roles in mitosis and cytokinesis revealed by plasmolysis of *Tradescantia virginiana* leaf epidermal cells. *Protoplasma* 215:21–34
- Coba de la Peña T, Cárcamo CB, Almonacid L, Zaballos A, Lucas MM, Balomenos D, Pueyo JJ (2008) A salt stress-responsive cytokinin receptor homologue isolated from *Medicago sativa* nodules. *Planta* 227:769–779
- Comstock JP (2002) Hydraulic and chemical signalling in the control of stomatal conductance and transpiration. *J Exp Bot* 53:195–200
- Decreux A, Messiaen J (2005) Wall-associated kinase WAK1 interacts with cell wall pectins in a calcium-induced conformation. *Plant Cell Physiol* 46:268–278
- Deeks MJ, Hussey PJ, Davies B (2002) Formins: intermediates in signal-transduction cascades that affect cytoskeletal reorganization. *Trends Plant Sci* 7:492–498
- Driss-Ecole D, Lefranc A, Perbal G (2003) A polarized cell: root statocyte. *Physiol Plant* 118:305–312
- Dutta R, Robinson KR (2004) Identification and characterization of stretch-activated ion channels in pollen protoplasts. *Plant Physiol* 135:1398–1406

- Emons AMC, Mulder BM (2000) How the deposition of cellulose microfibrils builds cell wall architecture. *Trends Plant Sci* 5:35–40
- Engler AJ, Sen S, Sweeney HL, Discher DE (2006) Matrix elasticity directs stem cell lineage specification. *Cell* 126:677–689
- Esmon C, Pedmale U, Liscum E (2005) Plant tropisms: providing the power of movement to a sessile organism. *Int J Dev Biol* 49:665–674
- Fasano JM, Swanson SJ, Blancaflor EB, Dowd PE, Kao TH, Gilroy S (2001) Changes in root cap pH are required for gravity response of the *Arabidopsis* root. *Plant Cell* 13:907–921
- Fasano JM, Massa GD, Gilroy S (2002) Ionic signaling in plant responses to gravity and touch. *J Plant Growth Regul* 21:71–88
- Fisher DD, Cyr RJ (1998) Extending the microtubule/microfibril paradigm. Cellulose synthesis is required for normal cortical microtubule alignment in elongating cells. *Plant Physiol* 116:1043–1051
- Forgacs G (1995) On the possible role of cytoskeletal filamentous networks in intracellular signaling: an approach based on percolation. *J Cell Sci* 108:2131–2143
- Friml J, Wisniewska J, Benkova G, Mendgen K, Palme K (2002) Lateral relocation of auxin efflux regulator PIN3 mediates tropism in *Arabidopsis*. *Nature* 415:806–809
- Fukaki H, Wysocka-Diller J, Kato T, Fujisawa H, Benfey PN, Tasaka M (1998) Genetic evidence that the endodermis is essential for shoot gravitropism in *Arabidopsis thaliana*. *Plant J* 14:425–430
- Gens JS, Fujiki M, Pickard BG (2000) Arabinogalactan protein and wall-associated kinase in a plasmalemmal reticulum with specialized vertices. *Protoplasma* 212:115–134
- Gouget A, Senchou V, Govers F, Sanson A, Barre A, Rouge P, Pont-Lezica R, Canut H (2006) Lectin receptor kinases participate in protein–protein interactions to mediate plasma membrane–cell wall adhesions in *Arabidopsis*. *Plant Physiol* 140:81–90
- Green PB (1999) Expression of pattern in plants: combining molecular and calculus-based biophysical paradigms. *Am J Bot* 86:1059–1076
- Grefen C, Harter K (2004) Plant two-component systems: principles, functions, complexity and cross talk. *Planta* 219:733–742
- Gus-Mayer S, Naton B, Hahlbrock K, Schmelzer E (1998) Local mechanical stimulation induces components of the pathogen defense response in parsley. *Proc Natl Acad Sci USA* 95:8398–8403
- Hardham AR, Takemoto D, White RG (2008) Rapid and dynamic subcellular reorganization following mechanical stimulation of *Arabidopsis* epidermal cells mimics responses to fungal and oomycete attack. *BMC Plant Biol* 8:63
- Harold FM (1995) From morphogenes to morphogenesis. *Microbiology* 141:2765–2778.
- Haswell ES, Meyerowitz E (2006) MscS-like proteins control plastid size and shape in *Arabidopsis thaliana*. *Curr Biol* 16:1–11
- Haswell ES, Peyronnet R, Barbier-Brygoo H, Meyerowitz E, Frachisse J-M (2008) Two MscS homologs provide mechanosensitive channel activities in the *Arabidopsis* root. *Curr Biol* 18:730–734
- Hayashi T, Takagi S (2003) Ca<sup>2+</sup>-dependent cessation of cytoplasmic streaming induced by hypertonic treatment in *Vallisneria* mesophyll cells: possible role of cell wall–plasma membrane adhesion. *Plant Cell Physiol* 44:1027–1036
- Hayashi T, Harada A, Sakai T, Takagi S (2006) Ca<sup>2+</sup> transient induced by extracellular changes in osmotic pressure in *Arabidopsis* leaves: differential involvement of cell wall–plasma membrane adhesion. *Plant Cell Environ* 29:661–672
- He YC, He YQ, Qu LH, Sun MX, Yang HY (2007) Tobacco zygotic embryogenesis in vitro: the original cell wall of the zygote is essential for maintenance of cell polarity, the apical–basal axis and typical suspensor formation. *Plant J* 49:515–527
- Heinlein M, Epel BL (2004) Macromolecular transport and signaling through plasmodesmata. *Int Rev Cytol* 235:93–164
- Hernández LF, Green PB (1993) Transductions for the expression of structural pattern: analysis in sunflower. *Plant Cell* 5:1725–1738
- Himmelspach R, Wymer CL, Lloyd CW, Nick P (1999) Gravity-induced reorientation of cortical microtubules observed in vivo. *Plant J* 18:449–453

- Hohmann S (2002) Osmotic stress signaling and osmoadaptation in yeasts. *Microbiol Mol Biol Rev* 66:300–372
- Homann U, Meckell T, Hewing J, Hütt M-T, Hurst AC (2007) Distinct fluorescent pattern of KAT1::GFP in the plasma membrane of *Vicia faba* guard cells. *Eur J Cell Biol* 86:489–500
- Hoson T, Saito Y, Soga K, Wakabayashi K (2005) Signal perception, transduction, and response in gravity resistance. Another graviresponse in plants. *Adv Space Res* 36:1196–1202
- Hou G, Kramer VL, Wang YS, Chen R, Perbal G, Gilroy S, Blancaflor EB (2004) The promotion of gravitropism in *Arabidopsis* roots upon disruption is coupled with the extended alkalization of the columella cytoplasm and a persistent lateral auxin gradient. *Plant J* 39:113–125
- Hussey P, Allwood E, Smertenko A (2002) Actin-binding proteins in the *Arabidopsis* genome database: properties of functionally distinct plant actin-depolymerizing factors/cofilins. *Philos Trans R Soc Lond B Biol Sci* 357:791–798
- Ingber DE (2003a) Tensegrity I. Cell structure and hierarchical systems biology. *J Cell Sci* 116:1157–1173
- Ingber DE (2003b) Tensegrity II. How structural network influence cellular information processing network. *J Cell Sci* 116:1397–1408
- Kaplan DR, Cooke TJ (1997) Fundamental concepts in the embryogenesis of dicotyledons: a morphological interpretation of embryo mutants. *Plant Cell* 9:1903–1919
- Kern VD, Schwuchow JM, Reed DW, Nadeau JA, Lucas J, Skripnikov A, Sack FD (2005) Gravitropic moss cells default to spiral growth on the clinostat and in microgravity during spaceflight. *Planta* 221:149–157
- Kiss JZ, Guisinger M, Miller A, Stackhouse K (1997) Reduced gravitropism in hypocotyls of starch-deficient mutants of *Arabidopsis*. *Plant Cell Physiol* 38:518–525
- Knight M, Campbell A, Smith S, Trewavas A (1991) Transgenic plant aequorin reports the effects of touch and cold-shock and elicitors on cytoplasmic calcium. *Nature* 352:524–526
- Ko JH, Han KH, Park S, Yang J (2004) Plant body weight-induced secondary growth in *Arabidopsis* and its transcription phenotype revealed by whole-transcriptome profiling. *Plant Physiol* 135:1069–1083
- Kohorn BD (2000) Plasma membrane–cell wall contacts. *Plant Physiol* 124:31–38
- Kohorn BD (2001) WAKs: cell wall associated kinases. *Curr Opin Cell Biol* 13:529–533
- Koizumi T, Sakaki T, Usui S, Soga K, Wakabayashi K, Hoson T (2007) Changes in a membrane lipid composition in adzuki bean epicotyls under hypergravity conditions: possible role of membrane sterols in gravity resistance. *Adv Space Res* 39:1198–1203
- Komis G, Apostolakos P, Galatis B (2003) Actomyosin is involved in the plasmolytic cycle: gliding movement of the deplasmolyzing protoplast. *Protoplasma* 221:245–256
- Kung C (2005) A possible unifying principle of mechanosensation. *Nature* 436:647–654
- Kutschera U (2008) The growing outer epidermal wall: design and physiological role of a composite structure. *Ann Bot* 101:615–621
- Kuznetsov OA, Hasenstein KH (1997) Magnetophoretic induction of curvature in coleoptiles and hypocotyls. *J Exp Bot* 48:1951–1957
- LaMotte CE, Pickard BG (2004) Control of gravitropic orientation. II. Dual receptor model for gravitropism. *Funct Plant Biol* 31:109–120
- Lang I, Barton DA, Overall RL (2004) Membrane-wall attachments in plasmolysed plant cells. *Protoplasma* 224:231–243
- Lang-Pauluzzi I, Gunning BES (2000) A plasmolytic cycle: the fate of cytoskeletal elements. *Protoplasma* 212:174–185
- Lee D, Polisensky D, Braam J (2005) Genome-wide identification of touch- and darkness- regulated *Arabidopsis* gene: a focus on calmodulin-like and XTH genes. *New Phytol* 165:429–444
- Legué V, Blancaflor E, Wymer C, Perbal G, Fantin D, Gilroy S (1997) Cytoplasmic free Ca<sup>2+</sup> in *Arabidopsis* roots changes in response to touch but not gravity. *Plant Physiol* 114:789–800
- Limbach C, Hauslage J, Schöfer C, Braun M (2005) How to activate a plant gravireceptor. Early mechanisms of gravity sensing studied in Characean rhizoids during parabolic flights. *Plant Physiol* 139:1030–1040



- Lintilhac PM, Vesecky TB (1984). Stress-induced alignment of division plane in plant tissues grown in vitro. *Nature* 307:363–364
- Lucas WJ, Ding B, van der Schoot C (1993) Plasmodesmata and the supracellular nature of plants. *New Phytol* 125:435–476
- Lynch TM, Lintilhac PM (1997) Mechanical signals in plant development: a new method for single cell studies. *Dev Biol* 181:246–256
- Maniotis AJ, Chen CS, Ingber DE (1997) Demonstration of mechanical connections between integrins, cytoskeletal filaments, and nucleoplasm that stabilize nuclear structure. *Proc Natl Acad Sci USA* 94:849–854
- Maniotis AJ, Valyi-Nagy K, Karavitis J, Moses J, Boddipali V, Wang Y, Nuñez R, Setty S, Arbieva Z, Bissell MJ, Folberg R (2005) Chromatin organization measured by *AluI* restriction enzyme changes with malignancy and is regulated by the extracellular matrix and the cytoskeleton. *Am J Pathol* 166:1187–1203
- Marshall JG, Dumbroff EB (1999) Turgor regulation via cell wall adjustment in white spruce. *Plant Physiol* 119:313–319
- Martinac B (2004) Mechanosensitive ion channels: molecules of mechanotransduction. *J Cell Sci* 117:2449–2460
- Massa GD, Gilroy S (2003) Touch modulates gravity sensing to regulate the growth of primary roots of *Arabidopsis thaliana*. *Plant J* 33:435–445
- Mathur J (2006) Local interactions shape plant cells. *Curr Opin Cell Biol* 18:40–46
- Matsumoto S, Saito Y, Kamasaki S, Soga K, Wakabayashi K, Hoson T (2007) Up-regulation of expression of tubulin genes and roles of microtubules in hypergravity-induced growth modification in *Arabidopsis* hypocotyls. *Adv Space Res* 39:1179–1181
- McCormack E, Braam J (2003) Calmodulins and related potential calcium sensors of *Arabidopsis*. *New Phytol* 159:585–598
- Meckel T, Hurst AC, Thiel G, Homann U (2005) Guard cells undergo constitutive and pressure driven membrane turnover. *Protoplasma* 226:23–29
- Mellersh DG, Heath MC (2001) Plasma membrane–cell wall adhesion is required for expression of plant defense responses during fungal penetration. *Plant Cell* 13:413–424
- Meyer Y, Abel WO (1975) Importance of the wall for cell division and in the activity of the cytoplasm in cultured tobacco protoplasts. *Planta* 123:33–40
- Morris CE, Homann U (2001) Cell surface area regulation and membrane tension. *J Membrane Biol* 179:79–102
- Na S, Collin O, Chowdhury F, Tay B, Ouyang M, Wang Y, Wang N (2008) Rapid signal transduction in living cells is a unique feature of mechanotransduction. *Proc Natl Acad Sci USA* 105:6626–6631
- Nakagawa N, Sakurai N (2001) Cell wall integrity controls expression of endoxyloglucan transferase in tobacco BY2 cells. *Plant Cell Physiol* 42:240–244
- Nakagawa Y, Katagiri T, Shinozaki K, Qi Z, Tatsumi H, Furuichi T, Kishigami A, Sokabe M, Kojima I, Sato S, Kato T, Tabata S, Lida K, Terashima A, Nakano M, Ikeda M, Yamanaka T, Lida H (2007) *Arabidopsis* plasma membrane protein crucial for Ca<sup>2+</sup> influx and touch sensing in roots. *Proc Natl Acad Sci USA* 104:3639–3644
- Nelson CM, Jean RP, Tan JL, Liu WF, Sniadecki NJ, Spector AA, Chen CS (2005) Emergent patterns of growth controlled by multicellular form and mechanics. *Proc Natl Acad Sci USA* 102:11594–11599
- Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. University of Chicago Press, Chicago
- Okada K, Shimura Y (1990) Reversible root-tip rotation in *Arabidopsis* seedlings induced by obstacle-touching stimulus. *Science* 250:274–276
- Orr AW, Helmke BP, Blackman BR, Schwartz MA (2006) Mechanisms of mechanotransduction. *Dev Cell* 10:11–20
- Palmieri M, Kiss JZ (2005) Disruption of F-actin cytoskeleton limits statolith movement in *Arabidopsis* hypocotyls. *J Exp Bot* 56:2539–2550
- Panteris E, Galatis B (2005) The morphogenesis of lobed plant cells in the mesophyll and epidermis: organization and distinct roles of cortical microtubules and actin filaments. *New Phytol* 167:721–732

- Paredes AR, Somerville CR, Ehrhardt DW (2006) Visualization of cellulose synthase demonstrates functional association with microtubules. *Science* 312:1491–1495
- Paredes AR, Persson S, Ehrhardt DW, Somerville CR (2008) Genetic evidence that cellulose synthase activity influences microtubule cortical array organization. *Plant Physiol* 147(4):1723–1734
- Pelling AE, Sehati S, Gralla EB, Valentine JS, Gimzewski JK (2004) Local nanomechanical motion of the cell wall of *Saccharomyces cerevisiae*. *Science* 305:1147–1150
- Perbal G, Driss-Ecole D (2003) Mechanotransduction in gravisensing cells. *Trends Plant Sci* 8:498–504
- Perrin R, Young L, Murthy N, Harrison B, Wang Y, Will A, Masson PH (2005) Gravity signal transduction in primary roots. *Ann Bot* 96:737–743
- Peters WS, Hagemann W, Tomos DA (2000) What makes plants different? Principles of extracellular matrix function in “soft” plant tissues. *Comp Biochem Physiol A* 125:151–167
- Pickard BG (2007) Delivering force and amplifying signals in plant mechanosensing. In: *Mechanosensitive ion channels*, Part A. Elsevier, New York, pp 361–392
- Plieth C, Trewavas AJ (2002) Reorientation of seedlings in the Earth’s gravitational field induces cytosolic calcium transiently. *Plant Physiol* 129:789–796
- Proseus TE, Boyer JS (2006a) Identifying cytoplasmic input to the cell wall of growing *Chara corallina*. *J Exp Bot* 57:3231–3242
- Proseus TE, Boyer JS (2006b) Periplasm turgor pressure controls wall deposition and assembly in growing *Chara corallina* cells. *Ann Bot* 98:93–105
- Proseus TE, Zhu GL, Boyer JS (2000) Turgor, temperature and the growth of plant cells: using *Chara corallina* as a model system. *J Exp Bot* 51:1481–1494
- Qu L-H, Sun M-X (2007) The plant cell nucleus is constantly alert and highly sensitive to repetitive local mechanical stimulation. *Plant Cell Rep* 26:1187–1193
- Reiser V, Raitt DC, Saito H (2003) Yeast osmosensor Sln1 and plant cytokinin receptor Cre1 respond to changes in turgor pressure. *J Cell Biol* 161:1035–1040
- Roberts SK (2006) Plasma membrane anion channels in higher plants and their putative functions in roots. *New Phytol* 169:647–666
- Sack FD (1997) Plastids and gravity sensing. *Planta* 203:S63–S68
- Sato Y, Kadota A, Wada M (2003) Chloroplast movement: dissection of events downstream of photo- and mechano-perception. *J Plant Res* 116:1–5
- Schindler M, Meiners S, Cheresch DA (1989) RGD-dependent linkage between plant cell wall and plasma membrane: Consequences for growth. *J Cell Biol* 108:1955–1965
- Schmidt SM, Panstruga R (2007) Cytoskeleton functions in plant-microbe interactions. *Physiol Mol Plant Pathol* 71:135–148
- Shiu SH, Bleeker AB (2001) Receptor-like kinases from *Arabidopsis* form a monophyletic gene family related to animal receptor kinases. *Proc Natl Acad Sci USA* 98:10763–10768
- Shope JC, DeWald DB, Mott KA (2003) Changes in surface area of intact guard cells are correlated with membrane internalization. *Plant Physiol* 133:1314–1321
- Soga K, Wakabayashi K, Kamisaka S, Hoson T (2002) Perception of gravity stimuli by mechanosensitive ion channels in plant seedlings. *Plant Cell Physiol* 43:182
- Soga K, Wakabayashi K, Kamisaka S, Hoson T (2005a) Mechanoreceptors rather than sedimentable amyloplasts perceive the gravity signal in hypergravity-induced inhibition of root growth in adzuki bean. *Funct Plant Biol* 32:175–179
- Soga K, Wakabayashi K, Kamisaka S, Hoson T (2005b) Hypergravity inhibits elongation growth of adzuki bean epicotyls independently of the direction of stimuli. *Adv Space Res* 36:1269–1279
- Soga K, Wakabayashi K, Kamisaka S, Hoson T (2006) Hypergravity induces reorientation of cortical microtubules and modifies growth anisotropy in adzuki bean epicotyls. *Planta* 224:1485–1494
- Staves MP (1997) Cytoplasmic streaming and gravity sensing in *Chara* internodal cells. *Planta* 203(Suppl 1):S79–S84
- Staves MP, Wayne R, Leopold AC (1992) Hydrostatic pressure mimics gravitational pressure in characean cells. *Protoplasma* 168:141–152

- Staves MP, Wayne R, Leopold AC (1997) Cytochalasin D does not inhibit gravitropism in roots. *Am J Bot* 84:1530–1535
- Tamura T, Hara K, Yamaguchi Y, Koizumi N, Sano H (2003) Osmotic stress tolerance of transgenic tobacco expressing a gene encoding a membrane-located receptor-like protein from tobacco plants. *Plant Physiol* 131:454–462
- Tasaka M, Kato T, Fukaki H (2001) Genetic regulation of gravitropism in higher plants. *Int Rev Cytol* 206:135–154
- Telewski F (2006) A unified hypothesis of mechanoperception in plants. *Am J Bot* 93:1466–1476
- Urao T, Yakubov B, Satoh R, Yamaguchi-Shinozaki K, Seki M, Hirayama T, Shinozaki K (1999) A transmembrane hybrid-type histidine kinase in *Arabidopsis* functions as an osmosensor. *Plant Cell* 11:1743–1754
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763
- Valle F, Sandal M, Samori B (2007) The interplay between chemistry and mechanics in the transduction of a mechanical signal into a biochemical function. *Physics Life Rev* 4:157–188
- van den Berg C, Willemsen V, Hage W, Weisbeek P, Scheres B (1995) Cell fate in the *Arabidopsis* root meristem determined by directional signalling. *Nature* 378:62–65
- van den Berg C, Willemsen V, Hendriks G, Weisbeek P, Scheres B (1997) Short-range control of cell differentiation in the *Arabidopsis* root meristem. *Nature* 390:287–289
- van der Honing HS, Emons AMC, Ketelaar T (2007) Actin based processes that could determine the cytoplasmic architecture of plant cells. *Biochim Biophys Acta* 1773:604–614
- Vitha S, Yang M, Sack FD, Kiss JZ (2007) Gravitropism in the starch excess mutant of *Arabidopsis thaliana*. *Am J Bot* 94:590–598
- Vogel V, Sheetz M (2006) Local force and geometry sensing regulate cell functions. *Nat Rev Mol Cell Biol* 7:265–275
- Volkmann D, Baluška F (2006) Gravity: one of the driving forces in evolution. *Protoplasma* 229:143–148
- Wayne R, Staves MP, Leopold AC (1992) The contribution of the extracellular matrix to gravisensing in characean cells. *J Cell Sci* 101:611–623
- Wendt M, Kuo-Huang L, Sievers A (1987) Gravitropic bending of cress roots without contact between amyloplasts and complexes of endoplasmic reticulum. *Planta* 172:321–329
- Wightman R, Turner SR (2008) The roles of the cytoskeleton during cellulose deposition at the secondary cell wall. *Plant J* 54:794–805
- Wohlbach DJ, Quirino BF, Sussman MR (2008) Analysis of the *Arabidopsis* histidine kinase ATHK1 reveals a connection between vegetative osmotic stress sensing and seed maturation. *Plant Cell* 20:1101–1117
- Wojtaszek P (2000) Genes and plant cell walls: a difficult relationship. *Biol Rev* 75:437–475
- Wojtaszek P (2001) Organismal view of a plant and a plant cell. *Acta Biochim Polon* 48:443–451
- Wojtaszek P, Anielska-Mazur A, Gabry H, Baluška F, Volkmann D (2005) Rapid relocation of myosin VIII between cell periphery and plastid surfaces are root-specific and provide the evidence for actomyosin involvement in osmosensing. *Funct Plant Biol* 32:721–736
- Wojtaszek P, Baluška F, Kasprówicz A, Łuczak M, Volkmann D (2007) Domain-specific mechanosensory transmission of osmotic and enzymatic cell wall disturbances to the actin cytoskeleton. *Protoplasma* 230:217–230
- Wolverton C, Mullen JL, Ishikawa H, Evens ML (2002) Root gravitropism in response to a signal originating outside of the cap. *Planta* 215:153–157
- Wyatt SE, Carpita NC (1993) The plant cytoskeleton–cell wall continuum. *Trends Cell Biol* 3:413–417
- Wymer C, Lloyd C (1996) Dynamic microtubules: implications for cell wall patterns. *Trends Plant Sci* 1:222–228
- Wymer CL, Wymer SA, Cosgrove DJ, Cyr RJ (1996) Plant cell growth responds to external forces and the response requires intact microtubules. *Plant Physiol* 110:425–430

- Xiong TC, Jauneau A, Ranjeva R, Mazars C (2004) Isolated plant nuclei as mechanical and thermal sensors involved in calcium signalling. *Plant J* 40:12–21
- Xu W, Purugganan M, Polisensky D, Antosiewicz D, Fry S, Braam J (1995) *Arabidopsis* TCH4, regulated by hormones and the environment, encodes a xyloglucan endotransglycosylase. *Plant Cell* 7:1555–1567
- Yahraus T, Chandra S, Legendre L, Low PS (1995) Evidence for a mechanically induced oxidative burst. *Plant Physiol* 109:1259–1266
- Yamamoto K, Kiss JZ (2002) Disruption of the actin cytoskeleton results in the promotion of gravitropism in inflorescence stems and hypocotyls of *Arabidopsis*. *Plant Physiol* 128:669–681
- Yang L, Reece JM, Cho J, Bortner CD, Shears SB (2008) The nucleolus exhibits an osmotically regulated gatekeeping activity that controls the spatial dynamics and functions of nucleolin. *J Biol Chem* 283:11823–11831
- Yoder TL, Zheng HQ, Todd P, Staehelin A (2001) Amyloplast sedimentation dynamics in maize columella cells support a new model for the gravity-sensing apparatus of root. *Plant Physiol* 125:1045–1060
- Zonia L, Munnik T (2004) Osmotically induced cell swelling versus cell shrinking elicits specific changes in phospholipid signals in tobacco pollen tubes. *Plant Physiol* 134: 813–823
- Zonia L, Munnik T (2007) Life under pressure: hydrostatic pressure in cell growth and function. *Trends Plant Sci* 12:90–97
- Zonia L, Cordeiro S, Tupý J, Feijó JA (2002) Oscillatory chloride efflux at the pollen tube apex has a role in growth and cell volume regulation and is targeted by inositol 3,4,5,6-tetrakisphosphate. *Plant Cell* 14:2233–2249
- Zonia L, Müller M, Munnik T (2006) Hydrodynamics and cell volume oscillations in the pollen tube apical region are integral components of the biomechanics of *Nicotiana tabacum* pollen tube growth. *Cell Biochem Biophys* 46:209–232

# Root Behavior in Response to Aluminum Toxicity

Charlotte Poschenrieder, Montse Amenós, Isabel Corrales,  
Snezhana Doncheva, and Juan Barceló

**Abstract** Roots have an extraordinary capacity for adaptive growth which allows them to avoid toxic soil patches or layers and grow into fertile sites. The response of roots to aluminum toxicity, a widespread problem in acid soils, is an excellent model system for investigating the mechanisms that govern this root behavior. In this review, after a short introduction to root growth movement in response to chemical factors in the soil, we explore the basic mechanisms of Al-induced inhibition of root growth. The actinomyosin network and endocytic vesicle trafficking are highlighted as common targets for Al toxicity in cell types with quite different origins: root tip transition zone cells, tip-growing cells like root hairs or pollen tubes, and astrocytes of the animal or human brain. In the roots of sensitive plants, the perception of toxic Al leads to a change in root tip cell patterning. The disturbance of polar auxin transport by Al seems to be a major factor in these developmental changes. In contrast, Al activates organic acid efflux and the binding of Al in a nontoxic form in Al-resistant genotypes.

## 1 Introduction

Individual terrestrial higher plants are sessile, living anchored to the substrate by their roots. Migration to better, more fertile soil conditions is only possible for their genetic information (pollen) or their offspring (seeds), which have different mechanisms of

---

C. Pochenrieder (✉)

Lab. Fisiología Vegetal, Facultad Biociencias, Universidad Autónoma de Barcelona E-08193  
Bellaterra, Spain

e-mail: charlotte.poschenrieder@uab.es

M. Amenós, I. Corrales, and J. Barceló

Plant Physiology, Bioscience Faculty, Autonomous University of Barcelona,  
Universidad Autónoma de Barcelona, E-08193, Bellaterra, Spain

S. Doncheva

Popov Institute of Plant Physiology, Bulgarian Academy of Sciences, Sofia, Bulgaria

dissemination. Slow movement away from the original placement is also possible as clones by vegetative propagation, e.g., through the formation of stolons or rhizomal growth (Hart 1990).

Investigations into plant movements have so far mainly focused on aerial plant parts. Different mechanisms can be distinguished: those based on turgor changes (e.g., nyctinasty and thigmonasty), or those based on differential growth (such as phototropism and epinasty). An exception is gravitropism, another growth-based movement, which has mainly been investigated in roots. However, bending in response to gravitational stimulus is far from being the only movement available to roots (Barlow 1994). Hydrotropism, the directed growth of roots in relation to the gradient of soil water potential, is a well-established growth-based movement of roots in response to an essential chemical soil factor (water) (Ponce et al. 2008). The availability of other essential nutrients can also induce changes in the orientation of root growth in order to improve acquisition. Phosphorus and nitrogen are the best-studied examples (Desnos 2008). The movement of roots into nutrient-rich soil patches implies complex morphogenetic events, such as root hair formation, the induction of new laterals, or—in certain species—proteoid root formation. These trophomorphogenetic responses are controlled directly by the nutrient concentration in the external medium or indirectly by the nutrient status of the plant, or by both (Forde and Lorenzo 2001).

Avoiding toxic soil conditions by altering root growth patterns is a further mechanism that allows plants to move away and try to escape from inadequate growth conditions. Two different scenarios can be envisaged: (1) heterogeneous soil contamination with small hotspots of high toxicant concentrations embedded in less toxic soil, and (2) extended toxic layers in the subsoil.

A heterogeneous distribution of potentially toxic concentrations of metal ions is frequently observed in soils polluted by mining activities. The observation that less Cd was taken up by *Brassica juncea* from soil with a heterogeneous Cd distribution than from uniformly polluted soil supports the view that plants are able to sense the spot contamination and avoid growth into contaminated sites (Manciuela and Ramsey 2006). Contrastingly, *Thlaspi caerulescens*, a metal hyperaccumulating species with unusually high Zn requirements (Tolrà et al. 1996), exhibits zincophilic root foraging patterns, i.e., preferential growth into hot spots with high Zn concentrations (Haines 2002). The efficiencies of both avoidance and foraging responses seem to depend on the root system size of the species. While a negative correlation between species root biomass and precision of placement has been observed in foraging studies on nutrient-rich patches (Wijesinghe et al. 2001), larger root systems seem to be more effective at avoiding toxic spots than small ones (Manciuela and Ramsey 2006). A well-developed tap root system can also be very useful for avoiding the relatively uniform topsoil contamination produced by (for example) smelting activities or after years of applying copper sulfate to vines or hopyards.

In contrast, subsoil acidity is a typical scenario where the extension of roots into the deep soil is hampered by the presence of a layer of soil with high metal availability extending from several decimeters below the soil surface. Crop plants used in tropical and subtropical agriculture and forest stands affected by natural acidification or that due to acid rain are the plants of most concern in this context