

Functional Plant Biology

Contents

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Special Issue: Plant Signalling: From Molecules to Behaviour

Review: Unravelling the plant signalling machinery: an update on the cellular and genetic basis of plant signal transduction

**Vadim Demidchik, Frans Maathuis
and Olga Voitsekhovskaja**

1–8

Signalling is a central phenomenon in biology. It is crucial to all aspects of plant physiology including growth, development and interactions with the environment. Here, novel hypotheses and experimental data regarding signalling hubs, second messengers, programmed cell death and autophagy are presented from the Fourth Plant Signalling and Behaviour Symposium in Saint Petersburg, Russia, June 2016).

Review: Mechanisms of cytosolic calcium elevation in plants: the role of ion channels, calcium extrusion systems and NADPH oxidase-mediated ‘ROS-Ca²⁺ Hub’

Vadim Demidchik and Sergey Shabala

9–27

Transient elevation of cytosolic Ca²⁺, also referred to as a Ca²⁺ signal, is a central phenomenon of plant signalling. Plants evolved sophisticated systems to initiate, amplify and terminate Ca²⁺ signals. Structure and properties of these systems, including Ca²⁺-permeable ion channels, Ca²⁺-ATPases, Ca²⁺/H⁺ exchangers and ‘ROS-Ca²⁺ hub’ are discussed here. They provide a fine-tuned mechanism for encoding diverse external and internal stimuli.

Review: The role of ion disequilibrium in induction of root cell death and autophagy by environmental stresses

**Vadim Demidchik, Elena V. Tyutereva
and Olga V. Voitsekhovskaja**

28–46

Environmental stresses are main causes for low agricultural productivity. At the cellular level, stresses induce generation of reactive oxygen species (ROS), ion disequilibrium, autophagy and programmed cell death (PCD). Here we propose that these processes interact and that ROS and ion disequilibrium are triggers of autophagy and PCD. Overall, presented data contribute to understanding plant stress physiology.

Review: Cell differentiation in nitrogen-fixing nodules hosting symbiosomes

**Anna V. Tsyganova, Anna B. Kitaeva
and Viktor E. Tsyganov**

47–57

Rhizobium bacteria, which live within the root nodules of legumes, allow plants to capture nitrogen gas from the atmosphere and use it for their own growth. Central to this symbiosis is an intracellular structure, called the symbiosome, in which nitrogen-fixing bacterial cells exchange components with the host cells that harbor them. Recent research on the differentiation of symbiosomes and of the infected cells that accommodate them has helped to decipher some general molecular mechanisms of cell differentiation.

Cover illustration: Panorama of Peter and Paul Fortress, City of St. Petersburg, Russia. This Special Issue contains selected peer reviewed papers from the Fourth International Symposium on Plant Signalling and Behavior, Komarov Botanical Institute RAS/Russian Science Foundation, Saint Petersburg, Russia, 19–23 June 2016. Image by Gregory A. Pozhvanov, <https://pozhvanov.com>.

Review: Melatonin in plant signalling and behaviour
**Lauren A. E. Erland, Praveen K. Saxena
and Susan J. Murch**

58–69

Melatonin is an important hormone and signalling molecule in all forms of life including humans, plants and bacteria. Recent plant physiology and genomic experiments have described the redirection of plant growth and metabolism, and demonstrated a diversity of genes involved in response to melatonin, however, the exact metabolic cascades that translate melatonin signals into physiological responses is not fully understood. This review provides an overview of melatonin mediated signalling manifested as behaviours and its roles in basic and industrial research.

Review: Molecular mechanisms accompanying nitric oxide signalling through tyrosine nitration and S-nitrosylation of proteins in plants
Prachi Jain and Satish C. Bhatla

70–82

Understanding the molecular mechanisms of plant development constitutes an important field of investigations in the current era of plant biology research. Nitric oxide signalling regulates a variety of biochemical processes in plants. This review provides an in-depth analysis of our current understanding on the subject, particularly with reference to plant growth under stress conditions.

Review: Two-pore cation (TPC) channel: not a shorthand one
Igor Pottosin and Oxana Dobrovinskaya

83–92

Large conductance SV/TPC1 channels are ubiquitously and abundantly expressed in the vacuolar membranes of higher plants. They are unique established Ca^{2+} -permeable channels in vacuoles, but their activity is strongly negatively controlled, so that they were believed to be inactive or to act only locally. Recent evidence suggests the key role of SV/TPC1 channels in the long-distance Ca^{2+} signalling.

Review: cGMP signalling in plants: from enigma to main stream
Jean-Charles Isner and Frans J. M. Maathuis

93–101

Cyclic GMP (cGMP) signalling in plants is crucial for many physiological processes. Recent analytical and genomic developments now allow detailed studies into the biochemistry and physiological role of cGMP in plants, and the latest findings are reviewed in this article.

Review: Formation mechanisms of superoxide radical and hydrogen peroxide in chloroplasts, and factors determining the signalling by hydrogen peroxide
**Boris N. Ivanov, Maria M. Borisova-Mubarakshina
and Marina A. Kozuleva**

102–110

Photosynthetic electron transport chain is not the only source of ATP and NADPH for photosynthesis; it is a sensor, informing adaptation systems of plant about environmental changes. An important transmitter of this information is hydrogen peroxide whose mechanisms of formation are presented, laying special emphasis on the formation outside and within thylakoid membrane. It is discussed, that the formation place can ensure definite signal about the specific environmental change.

Review: Plant ion channels and transporters in herbivory-induced signalling
**Shuitian Luo, Xiao Zhang, Jinfei Wang,
Chunyang Jiao, Yingying Chen and Yingbai Shen**

111–131

Clarifying herbivory-induced plant cellular signalling is a critical step to push the research of plant-herbivore interaction forward. We review the role of ion channels/transporters in modulating herbivory-induced early signalling events and rapid systemic signal transmission in plants. This work provides a comprehensive source of information about plant defensive strategies upon attack.

Viewpoint: Electrical signalling in *Nitellopsis obtusa*: potential biomarkers of biologically active compounds
**Vilma Kisnieriene, Indre Lapeikaite
and Vilmantas Pupkis**

132–142

The electrophysiological response pattern of *Nitellopsis obtusa* cell can be assessed to evaluate the effect of many biologically active compounds. We illustrate a variety of electrophysiological approaches for the investigations of electrical signaling after chemical treatment *in vivo*. The insights about the Characean model system are likely to hold for plants in general and even deepen the understanding of the plant evolution.

<p>Rapid changes in root HvPIP2;2 aquaporins abundance and ABA concentration are required to enhance root hydraulic conductivity and maintain leaf water potential in response to increased evaporative demand Dmitry S. Veselov, Guzel V. Sharipova, Stanislav Yu. Veselov, Ian C. Dodd, Igor Ivanov and Guzel R. Kudoyarova</p>	143–149	<p>The ABA-deficient barley mutant Az34 and wild type (WT) were exposed to air warming. Although transpiration rate of both genotypes increased, leaf water potential decreased in the mutant but was maintained in WT plants. Only WT plants showed increased root ABA accumulation, which increased root hydraulic conductivity and aquaporin abundance, which seems important in maintaining leaf hydration.</p>
<p>Two native types of phytochrome A, phyA' and phyA'', differ by the state of phosphorylation at the N-terminus as revealed by fluorescence investigations of the Ser/Ala mutant of rice phyA expressed in transgenic <i>Arabidopsis</i> Vitaly A. Sineshchekov, Larissa A. Koppel and Cordelia Bolle</p>	150–159	<p>Plants adapt to environmental light conditions with the use of the sophisticated phytochrome system. In this work, polymorphism of its major component – phytochrome A– was investigated. With the use of transgenic <i>Arabidopsis</i> and fluorescence technique, it was shown that two molecular types of the photoreceptor differ by the state of phosphorylation and their existence accounts for its complex functions.</p>
<p>Parameters of electrical signals and photosynthetic responses induced by them in pea seedlings depend on the nature of stimulus Vladimir Vodeneev, Maxim Mudrilov, Elena Akinchits, Irina Balalaeva and Vladimir Sukhov</p>	160–170	<p>Plants, like animals, produce electrical signals in response to various external influences. In this study we raised a question whether the electrical signals transmit information about the nature of the stimulus, and found out that different stimuli induce signals of varied parameters. The obtained results explain how plants adapt to changing environment.</p>
<p><i>Arabidopsis thaliana</i> phytaspase: identification and peculiar properties Nina V. Chichkova, Raisa A. Galiullina, Larisa V. Mochalova, Svetlana V. Trusova, Zulfazli M. Sobri, Patrick Gallois and Andrey B. Vartapetian</p>	171–179	<p>Although plant proteases of the phytaspase family are important contributors to stress-induced plant cell death, phytaspase of a classical model plant <i>Arabidopsis thaliana</i> has escaped identification thus far. We identified the <i>Arabidopsis</i> phytaspase-encoding gene and characterised the recombinant enzyme. Substrate specificity and properties of the <i>Arabidopsis</i> phytaspase display both important similarities with and distinctions from the already characterised phytaspses.</p>
<p>Spatial distribution of organelles in leaf cells and soybean root nodules revealed by focused ion beam-scanning electron microscopy Brandon C. Reagan, Paul J. -Y. Kim, Preston D. Perry, John R. Dunlap and Tessa M. Burch-Smith</p>	180–191	<p>Focussed ion beam scanning electron microscopy (FIB-SEM) is a technique that can be used to generate 3D renderings of cells and their contents. Although FIB-SEM has been regularly used to investigate animal cells and tissues, it has rarely been deployed to study plant structures. Here we demonstrate that FIB-SEM can easily be used to study plant samples and have discovered previously unknown arrangements of organelles and membranes in those samples.</p>
<p>Studies of cytokinin receptor–phosphotransmitter interaction provide evidences for the initiation of cytokinin signalling in the endoplasmic reticulum Sergey N. Lomin, Yulia A. Myakushina, Dmitry V. Arkhipov, Olga G. Leonova, Vladimir I. Popenko, Thomas Schmülling and Georgy A. Romanov</p>	192–202	<p>Cytokinin is an important plant hormone and its mode of action has been extensively studied; however, to date, the subcellular localisation of cytokinin perception and signal transduction remains a matter of debate. This study describes cytokinin receptor–phosphotransmitter interaction and its subcellular localisation in living plant cells and it provides several experimental evidences for receptor activity at the endoplasmic reticulum (ER) membrane. It is concluded that intracellular cytokinins within the ER lumen may play an important role in cytokinin signalling, at least in some cell types.</p>

Phloem fibres as motors of gravitropic behaviour of flax plants: level of transcriptome

Oleg Gorshkov, Natalia Mokshina, Nadezda Ibragimova, Marina Ageeva, Natalia Gogoleva and Tatyana Gorshkova

203–214

Plant fibres with a tertiary cell wall (G-layer) may function as plant ‘muscles’. Large-scale transcriptome profiling of isolated flax phloem fibres permitted to identify the major players and regulatory elements that operate during graviresponce specifically in the fibres of the pulling stem side. The suggested mechanisms of phloem fibre involvement in tropisms may considerably renew the concept of herbaceous plant behaviour upon gravistimulation.

Cytokinins regulate root growth through its action on meristematic cell proliferation but not on the transition to differentiation

Victor B. Ivanov and Alexey N. Filin

215–221

Root growth is controlled by phytohormones, but what cellular processes are regulated and how it occurs is still an open question. Here it is shown that cytokinin affects root growth mainly through its effect on cell proliferation, and does not initiate the transition of cells to differentiation as previously thought. Cellular analysis performed could be applied for the analysis of how any plant hormone influences developmental processes in plant roots.

Sunpatiens compact hot coral: memristors in flowers

Alexander G. Volkov and Eunice K. Nyasani

222–227

Memristors, or resistors with memory, exist *in vivo* as components of plasma membranes in plants, fruits, roots and seeds. Authors found memristors in an androecium, spur, petals and pedicel in Sunpatiens flowers. The discovery of memristors in Sunpatiens (*Impatiens* spp.) creates a new direction in the modelling and understanding of electrophysiological phenomena and memory elements in flowers.

Photochemical activity changes accompanying the embryogenesis of pea (*Pisum sativum*) with yellow and green cotyledons

Galina Smolkova, Vladimir Kreslavski, Olga Shiroglazova, Tatiana Bilova, Elena Sharova, Andrej Frolov and Sergei Medvedev

228–235

We studied the dynamics of photochemical activity in seed coats and cotyledons during development of yellow- and green-seeded pea cultivars by using the pulse amplitude modulation fluorometric analysis. The fast transients of the chlorophyll *a* fluorescence revealed higher photochemical activity in the coats of yellow-seeded cultivar at the early- and middle cotyledon stages of seed development in comparison to those observed in the green-seeded ones. Photochemical activity in the cotyledons of both cultivars could not be any more detected at the late cotyledon stage. This process was triggered by dehydration of seed tissues.

Cyclosis-mediated long distance communications of chloroplasts in giant cells of Characeae

Anna V. Komarova, Vladimir S. Sukhov and Alexander A. Bulychev

236–246

Intracellular communications in plant cells of large dimensions rely primarily on cytoplasmic streaming, because diffusion is too slow for the transport on mm-scale distances. Illumination of a small cell spot at various distances from the point of chlorophyll fluorescence measurements revealed the wave-like propagation of the fluorescence response along the cell length. The results show that the photosynthetic function of immobile chloroplasts under constant light can be affected by long-distance transmission of a photosynthetically active metabolite from the remote cell parts.

The levels of peroxisomal catalase protein and activity modulate the onset of cell death in tobacco BY-2 cells via reactive oxygen species levels and autophagy

Elena V. Tyutereva, Ksenia S. Dobryakova, Andreas Schiermeyer, Maria F. Shishova, Katharina Pawlowski, Vadim Demidchik, Sigrun Reumann and Olga V. Voitsekhovskaja

247–258

Peroxisomes balance the cellular levels of reactive oxygen species (ROS) and therefore should modulate ROS-regulated programs like autophagy or cell death. We used tobacco suspension cultures to show that degradation of peroxisomes via autophagy was a prerequisite for cell death and depended on the levels of the major peroxisomal protein, catalase. This suggests a role of plant catalase in the regulation of peroxisome turnover and autophagic cell death.

Myotubularins, PtdIns5P, and ROS in ABA-mediated stomatal movements in dehydrated *Arabidopsis* seedlings

**Akanksha Nagpal, Ammar Hassan,
Ivan Ndamukong, Zoya Avramova
and František Baluška**

259–266

Arabidopsis myotubularins AtMTM1 and AtMTM2 control stomata movements via reactive oxygen species (ROS) homeostasis under drought stress. Acting as a secondary messenger in the ABA-induced ROS production in guard cells, PtdIns5P emerges as an evolutionarily conserved signalling molecule downstream of AtMTMs calibrating cellular ROS levels under stress. AtMTM1 and AtMTM2 activities balance ABA-induced ROS and cellular homeostasis under dehydration stress.

Molecular insights into the functional role of nitric oxide (NO) as a signal for plant responses in chickpea

**Parankusam Santisree, Pooja Bhatnagar-Mathur
and Kiran K. Sharma**

267–283

Although many studies established nitric oxide (NO) as a signaling molecule in plants, the identification of target molecules of NO has remained elusive due to the lack of in depth molecular studies. Our quantitative proteome analysis suggests the differential regulation of 248 proteins and dynamic regulation of metabolic pathways by exogenous NO donor in chickpea. This is the first report in legumes pointing at the potential candidates that attribute the reported functions of NO in plants.

Endoplasmic reticulum stress regulates glutathione metabolism and activities of glutathione related enzymes in *Arabidopsis*

**Baris Uzilday, Rengin Ozgur, A. Hediye Sekmen
and Ismail Turkan**

284–296

Prolonged endoplasmic reticulum (ER) stress oxidises the cellular glutathione pool. To elucidate the role of glutathione during ER stress, biosynthesis and degradation of glutathione and activities of related enzymes were evaluated. Our data demonstrated that glutathione biosynthesis and an apoplasmic but not cytoplasmic catabolic pathway was induced. In addition, the activities of enzymes that use glutathione as a substrate were increased by ER stress.