

**On the Cover:** Self-incompatibility (SI) is an important genetically controlled mechanism to prevent inbreeding in higher plants. SI involves highly specific interactions during pollination, resulting in the rejection of incompatible (self) pollen. The article by Wilkins et al. (pp. 766–779) describes the pivotal role of SI-induced acidification in mediating programmed cell death (PCD) in the SI response. After an incompatible interaction between the female stigmatic *S*-determinant, field poppy (*Papaver rhoeas*) stigma *S*, and the pollen *S*-determinant, field poppy pollen *S*, a signaling cascade is initiated which results in rapid, dramatic acidification of the pollen tube cytosol (green/blue, pH 5.5). Significant acidification occurs within 10 min of SI induction and continues for approximately 60 min. This acidification is essential for the formation of punctate actin foci and PCD in incompatible pollen. The cover shows pseudocolored confocal microscopy images of field poppy pollen tubes labeled with the pH-dependent ratiometric dye, 2,7-bis-(2-carboxyethyl)-5-(and-6)-carboxyfluorescein acetoxymethyl ester. Healthy unchallenged pollen tubes (top two images) have a neutral cytosolic pH (red/orange/yellow; pH 7.15); after SI challenge, the pollen tube cytosol becomes increasingly more acidic as time progresses (yellow/green/pale blue; middle images), reaching pH 5.5 after 60 min (pale blue/dark blue; bottom image). Cover image credits: Katie A. Wilkins (School of Biosciences, University of Birmingham, UK).

## ON THE INSIDE

Peter V. Minorsky

601

## BREAKTHROUGH TECHNOLOGIES

[OPEN] Imaging of Lipids in Microalgae with Coherent Anti-Stokes Raman Scattering Microscopy. *Lillie Cavonius, Helen Fink, Juris Kiskis, Eva Albers, Ingrid Undeland, and Annika Enejder*

*Lipids are accumulated as giant droplets alongside coalescing emerging droplets under excessive lipid storage, in contrast to the multiple micron-sized droplets formed at normal conditions.*

603

[OPEN] Root System Markup Language: Toward a Unified Root Architecture Description Language. *Guillaume Lobet, Michael P. Pound, Julien Diener, Christophe Pradal, Xavier Draye, Christophe Godin, Mathieu Javaux, Daniel Leitner, Féliçien Meunier, Philippe Nacry, Tony P. Pridmore, and Andrea Schnepf*

*Portability of root architecture data with the Root System Markup Language paves the way for central root phenotype repositories.*

617

[OPEN] Live Imaging of Inorganic Phosphate in Plants with Cellular and Subcellular Resolution. *Pallavi Mukherjee, Swayoma Banerjee, Amanda Wheeler, Lyndsay A. Ratliff, Sonia Irigoyen, L. Rene Garcia, Steve W. Lockless, and Wayne K. Versaw*

*Genetically encoded sensors enable dynamic monitoring of phosphate concentrations in cells and cell compartments of live plants.*

628

[OPEN] Direct Detection of Transcription Factors in Cotyledons during Seedling Development Using Sensitive Silicon-Substrate Photonic Crystal Protein Arrays. *Sarah I. Jones, Yafang Tan, Md Shamimuzzaman, Sherine George, Brian T. Cunningham, and Lila Vodkin*

*Transcription factors in seedling cotyledons are quantified using novel silicon photonic crystal protein arrays and their levels are correlated with transcript abundances.*

639

Continued on next page

## RESEARCH ARTICLES

### BIOCHEMISTRY AND METABOLISM

[OPEN] A Heteromeric Membrane-Bound Prenyltransferase Complex from Hop Catalyzes Three Sequential Aromatic Prenylations in the Bitter Acid Pathway. *Haoxun Li, Zhaonan Ban, Hao Qin, Liya Ma, Andrew J. King, and Guodong Wang*

*A membrane-bound prenyltransferase complex is responsible for all prenylations in the bitter acid pathway of hop glandular trichomes.* 650

[OPEN] Reexamination of Chlorophyllase Function Implies Its Involvement in Defense against Chewing Herbivores. *Xueyun Hu, Satoru Makita, Silvia Schelbert, Shinsuke Sano, Masanori Ochiai, Tohru Tsuchiya, Shigeaki F. Hasegawa, Stefan Hörtensteiner, Ayumi Tanaka, and Ryouichi Tanaka*

*A jasmonate-inducible chlorophyllase catabolizes chlorophyll upon tissue disruption to generate compounds that are toxic to insect herbivores.* 660

Phosphoenolpyruvate Carboxylase in Arabidopsis Leaves Plays a Crucial Role in Carbon and Nitrogen Metabolism. *Jianghua Shi, Keke Yi, Yu Liu, Li Xie, Zhongjing Zhou, Yue Chen, Zhanghua Hu, Tao Zheng, Renhu Liu, Yunlong Chen, and Jinqing Chen*

*Phosphoenolpyruvate carboxylase in Arabidopsis leaves balances carbon and nitrogen metabolism.* 671

[OPEN] ECERIFERUM2-LIKE Proteins Have Unique Biochemical and Physiological Functions in Very-Long-Chain Fatty Acid Elongation. *Tegan M. Haslam, Richard Haslam, Didier Thoraval, Stéphanie Pascal, Camille Delude, Frédéric Domergue, Aurora Mañas Fernández, Frédéric Beaudoin, Johnathan A. Napier, Ljerka Kunst, and Jérôme Joubès*

*An Arabidopsis protein that lacks enzymatic activity in long-chain fatty-acid condensation nonetheless affects chain length specificity of very-long-chain fatty acid elongation, which is important for cuticle and pollen coat function.* 682

[OPEN] The MYB182 Protein Down-Regulates Proanthocyanidin and Anthocyanin Biosynthesis in Poplar by Repressing Both Structural and Regulatory Flavonoid Genes. *Kazuko Yoshida, Dawei Ma, and C. Peter Constabel*

*A poplar repressor protein negatively regulates flavonoid and proanthocyanidin pathway genes by interacting with other transcription factors.* 693

### CELL BIOLOGY

[OPEN] COBRA-LIKE2, a Member of the Glycosylphosphatidylinositol-Anchored COBRA-LIKE Family, Plays a Role in Cellulose Deposition in Arabidopsis Seed Coat Mucilage Secretory Cells. *Daniela Ben-Tov, Yael Abraham, Shira Stav, Kevin Thompson, Ann Loraine, Rivka Elbaum Amancio de Souza, Markus Pauly, Joseph J. Kieber, and Smadar Harpaz-Saad*

*A previously uncharacterized protein plays a role in cellulose deposition during the course of seed coat epidermal cell differentiation.* 711

[OPEN] HIGHLY METHYL ESTERIFIED SEEDS Is a Pectin Methyl Esterase Involved in Embryo Development. *Gabriel Levesque-Tremblay, Kerstin Müller, Shawn D. Mansfield, and George W. Haughn*

*An Arabidopsis gene is required for normal levels of pectin methylesterase activity and embryo cell expansion during the accumulation of storage reserves.* 725

Continued on next page

[OPEN] Importin- $\alpha$ -Mediated Nucleolar Localization of Potato Mop-Top Virus TRIPLE GENE BLOCK1 (TGB1) Protein Facilitates Virus Systemic Movement, Whereas TGB1 Self-Interaction Is Required for Cell-to-Cell Movement in *Nicotiana benthamiana*. Nina I. Lukhovitskaya, Graham H. Cowan, Ramesh R. Vetukuri, Jens Tilsner, Lesley Torrance, and Eugene I. Savenkov

*Interaction of the potato mop-top virus movement protein with importin- $\alpha$  facilitates nucleolar passage and virus systemic movement.*

738

[OPEN] SUMOylation by a Stress-Specific Small Ubiquitin-Like Modifier E2 Conjugase Is Essential for Survival of *Chlamydomonas reinhardtii* under Stress Conditions. Amy R. Knobbe, Kempton M. Horken, Thomas M. Plucinak, Eniko Balassa, Heriberto Cerutti, and Donald P. Weeks

*The green algae Chlamydomonas reinhardtii possesses at least two SUMO conjugates, one involved in housekeeping and the other in response to stress.*

753

[OPEN] Self-Incompatibility-Induced Programmed Cell Death in Field Poppy Pollen Involves Dramatic Acidification of the Incompatible Pollen Tube Cytosol. Katie A. Wilkins, Maurice Bosch, Tamanna Haque, Nianjun Teng, Natalie S. Poulter, and Veronica E. Franklin-Tong

*Self-incompatibility triggers rapid cytosolic acidification that is necessary and sufficient for programmed cell death and pivotal in reorganizing F-actin and associated proteins within punctate foci.*

766

[OPEN] The Fragile Fiber1 Kinesin Contributes to Cortical Microtubule-Mediated Trafficking of Cell Wall Components. Chuanmei Zhu, Anindya Ganguly, Tobias I. Baskin, Daniel D. McClosky, Charles T. Anderson, Cliff Foster, Kristoffer A. Meunier, Ruth Okamoto, Howard Berg, and Ram Dixit

*A microtubule-associated kinesin moves processively along cortical microtubules and contributes to the production of both primary and secondary walls by mediating membrane trafficking.*

780

## ECOPHYSIOLOGY AND SUSTAINABILITY

Does Low Stomatal Conductance or Photosynthetic Capacity Enhance Growth at Elevated CO<sub>2</sub> in Arabidopsis? Hsien Ming Easlon, Eli Carlisle, John K. McKay, and Arnold J. Bloom

*Low stomatal conductance and photosynthetic capacity increases Arabidopsis CO<sub>2</sub> growth enhancement under N-limited but not N-sufficient conditions.*

793

[OPEN] Leaf Responses to Mild Drought Stress in Natural Variants of Arabidopsis. Pieter Clauw, Frederik Coppens, Kristof De Beuf, Stijn Dhondt, Twiggy Van Daele, Katrien Maleux, Veronique Storme, Lieven Clement, Nathalie Gonzalez, and Dirk Inzé

*Arabidopsis accessions show different phenotypes in response to mild drought, yet a robust transcriptome response is conserved between the accessions.*

800

[OPEN] GROWTH REGULATING FACTOR5 Stimulates Arabidopsis Chloroplast Division, Photosynthesis, and Leaf Longevity. Liesbeth Vercauysen, Vanesa B. Tognetti, Nathalie Gonzalez, Judith Van Dingenen, Liesbeth De Milde, Agnieszka Bielach, Riet De Rycke, Frank Van Breusegem, and Dirk Inzé

*A transcription factor increases plant productivity by delaying leaf senescence and stimulating leaf cell division, chloroplast division, photosynthesis, and tolerance to nitrogen deprivation.*

817

Continued on next page

[OPEN]The Evolution of Mechanisms Driving the Stomatal Response to Vapor Pressure Deficit. Scott A.M. McAdam and Timothy J. Brodribb

*The mechanism for a stomatal response to vapor pressure deficit evolved from a passive regulation in basal vascular plants to mediation by ABA in the earliest angiosperms.* 833

## GENES, DEVELOPMENT, AND EVOLUTION

[OPEN]A KNOTTED1-LIKE HOMEBOX Protein Regulates Abscission in Tomato by Modulating the Auxin Pathway. Chao Ma, Shimon Meir, Langtao Xiao, Jianhua Tong, Qing Liu, Michael S. Reid, and Cai-Zhong Jiang

*A KNOTTED1-LIKE HOMEBOX protein regulates abscission through modulating auxin concentration and transport.* 844

[OPEN]Network of GRAS Transcription Factors Involved in the Control of Arbuscule Development in *Lotus japonicus*. Li Xue, Haitao Cui, Benjamin Buer, Vinod Vijayakumar, Pierre-Marc Delaux, Stefanie Junkermann, and Marcel Bucher

*A network of transcription factors regulates arbuscular mycorrhizal symbiosis in Lotus.* 854

Insights into the Origin and Evolution of the Plant Hormone Signaling Machinery. Chunyang Wang, Yang Liu, Si-Shen Li, and Guan-Zhu Han

*Nine major plant hormone signaling pathways originated at different times, with horizontal gene transfer possibly contributing to their origin and evolution.* 872

[OPEN]Genome-Wide Analysis of PHOSPHOLIPID:DIACYLGLYCEROL ACYLTRANSFERASE (PDAT) Genes in Plants Reveals the Eudicot-Wide PDAT Gene Expansion and Altered Selective Pressures Acting on the Core Eudicot PDAT Paralogs. Xue Pan, Fred Y. Peng, and Randall J. Weselake

*Ancient gene duplication may have led to the diversification of a key acyltransferase of plant triacylglycerol synthesis in the core eudicots.* 887

[OPEN]Methyl-CpG-Binding Domain Protein MBD7 Is Required for Active DNA Demethylation in Arabidopsis. Chunlei Wang, Xiaomei Dong, Dan Jin, Yusheng Zhao, Shaojun Xie, Xiaojie Li, Xinjian He, Zhaobo Lang, Jinsheng Lai, Jian-Kang Zhu, and Zhizhong Gong

*A methyl-CpG-binding domain protein participates in active DNA demethylation and appears to act as an anti-silencing agent in Arabidopsis.* 905

[OPEN]SUCROSE NONFERMENTING1-RELATED PROTEIN KINASE2.6, an Ortholog of OPEN STOMATA1, Is a Negative Regulator of Strawberry Fruit Development and Ripening. Yu Han, Ruihong Dang, Jinxi Li, Jinzhu Jiang, Ning Zhang, Meiru Jia, Lingzhi Wei, Ziqiang Li, Bingbing Li, and Wensuo Jia

*A negative regulator of strawberry fruit development and ripening in strawberry fruit ripening is a homolog of a well-characterized protein kinase.* 915

The Zinc Finger Transcription Factor SIZFP2 Negatively Regulates Abscisic Acid Biosynthesis and Fruit Ripening in Tomato. Lin Weng, Fangfang Zhao, Rong Li, Changjie Xu, Kunsong Chen, and Han Xiao

*A transcription factor represses abscisic acid biosynthesis and fruit ripening.* 931

Continued on next page

## MEMBRANES, TRANSPORT, AND BIOENERGETICS

[<sup>OPEN</sup>]Crystal Structure and Functional Characterization of Photosystem II-Associated Carbonic Anhydrase CAH3 in *Chlamydomonas reinhardtii*. Reyes Benlloch, Dmitriy Shevela, Tobias Hainzl, Christin Grundström, Tatyana Shutova, Johannes Messinger, Göran Samuelsson, and A. Elisabeth Sauer-Eriksson

*Luminal carbonic anhydrase is required for efficient turnover of the water-oxidizing complex of PSII.* 950

[<sup>OPEN</sup>]Phloem as Capacitor: Radial Transfer of Water into Xylem of Tree Stems Occurs via Symplastic Transport in Ray Parenchyma. Sebastian Pfautsch, Justine Renard, Mark G. Tjoelker, and Anya Salih

*Visual evidence for the radial transfer of water from phloem into xylem supports theoretical predictions that phloem acts as a water storage capacitor in tree stems.* 963

Characterization of Chloroplast Protein Import without Tic56, a Component of the 1-Megadalton Translocon at the Inner Envelope Membrane of Chloroplasts. Daniel Köhler, Cyril Montandon, Gerd Hause, Petra Majovsky, Felix Kessler, Sacha Baginsky, and Birgit Agne

*Plastids import a significant number of proteins in the absence of the chloroplast inner envelope membrane translocon subunit.* 972

[<sup>OPEN</sup>]SENSITIVE TO PROTON RHIZOTOXICITY1, CALMODULIN BINDING TRANSCRIPTION ACTIVATOR2, and Other Transcription Factors Are Involved in ALUMINUM-ACTIVATED MALATE TRANSPORTER1 Expression. Mutsutomo Tokizawa, Yuriko Kobayashi, Tatsunori Saito, Masatomo Kobayashi, Satoshi Iuchi, Mika Nomoto, Yasuomi Tada, Yoshiharu Y. Yamamoto, and Hiroyuki Koyama

*A set of unexpected transcription factors affects complex regulatory control of AtALMT1 expression in response to Al stress.* 991

## SIGNALING AND RESPONSE

[<sup>OPEN</sup>]Membrane-Localized Extra-Large G Proteins and G $\beta\gamma$  of the Heterotrimeric G Proteins Form Functional Complexes Engaged in Plant Immunity in Arabidopsis. Natsumi Maruta, Yuri Trusov, Eric Brenya, Urvi Parekh, and José Ramón Botella

*Arabidopsis immunity against multiple pathogens depends on unconventional G protein complexes.* 1004

[<sup>OPEN</sup>]ARACINs, Brassicaceae-Specific Peptides Exhibiting Antifungal Activities against Necrotrophic Pathogens in Arabidopsis. Jenny Neukermans, Annelies Inzé, Janick Mathys, Barbara De Coninck, Brigitte van de Cotte, Bruno P.A. Cammue, and Frank Van Breusegem

*Two new antimicrobial peptides exhibit antifungal activities against necrotrophic pathogens.* 1017

[<sup>OPEN</sup>]Small Heat Shock Proteins Can Release Light Dependence of Tobacco Seed during Germination. Hyun Jo Koo, Soo Min Park, Keun Pill Kim, Mi Chung Suh, Mi Ok Lee, Seong-Kon Lee, Xia Xinli, and Choo Bong Hong

*Ectopically expressed and heat shock-induced proteins trigger light-independent seed germination in tobacco.* 1030

Continued on next page

Two Distinct Families of Protein Kinases Are Required for Plant Growth under High External  $Mg^{2+}$  Concentrations in Arabidopsis. Junro Mogami, Yasunari Fujita, Takuya Yoshida, Yoshifumi Tsukiori, Hirofumi Nakagami, Yuko Nomura, Toru Fujiwara, Sho Nishida, Shuichi Yanagisawa, Tetsuya Ishida, Fuminori Takahashi, Kyoko Morimoto, Satoshi Kidokoro, Junya Mizoi, Kazuo Shinozaki, and Kazuko Yamaguchi-Shinozaki

*Two sets of ABA-activated protein kinases and their interacting partners are required for plant growth under high external  $Mg^{2+}$  concentrations in Arabidopsis.*

1039

TYPE-ONE PROTEIN PHOSPHATASE4 Regulates Pavement Cell Interdigitation by Modulating PIN-FORMED1 Polarity and Trafficking in Arabidopsis. Xiaola Guo, Qianqian Qin, Jia Yan, Yali Niu, Bingyao Huang, Liping Guan, Yuan Li, Dongtao Ren, Jia Li, and Suiwen Hou

*Interaction with a protein phosphatase and dephosphorylation affects the polar localization and endocytic trafficking of an auxin-related membrane protein and its impact on cell pattern formation.*

1058

The Arabidopsis Transcription Factor BRASSINOSTEROID INSENSITIVE1-ETHYL METHANESULFONATE-SUPPRESSOR1 Is a Direct Substrate of MITOGEN-ACTIVATED PROTEIN KINASE6 and Regulates Immunity. Sining Kang, Fan Yang, Lin Li, Huamin Chen, She Chen, and Jie Zhang

*MAP kinase-mediated phosphorylation of a transcription factor regulates plant immunity.*

1076

<sup>[OPEN]</sup>The WRKY45-2 WRKY13 WRKY42 Transcriptional Regulatory Cascade Is Required for Rice Resistance to Fungal Pathogen. Hongtao Cheng, Hongbo Liu, Yong Deng, Jinghua Xiao, Xianghua Li, and Shiping Wang

*Three transcription factors form a sequential transcriptional regulatory cascade which is involved in rice response to the infection of Magnaporthe oryzae.*

1087

Induced Jasmonate Signaling Leads to Contrasting Effects on Root Damage and Herbivore Performance. Jing Lu, Christelle Aurélie Maud Robert, Michael Riemann, Marco Cosme, Laurent Mène-Saffrané, Josep Massana, Michael Joseph Stout, Yonggen Lou, Jonathan Gershenzon, and Matthias Erb

*Jasmonates reduce root damage by belowground herbivores, but enhanced jasmonate biosynthesis improves herbivore growth.*

1100

<sup>[OPEN]</sup>Perturbation of Maize Phenylpropanoid Metabolism by an AvrE Family Type III Effector from *Pantoea stewartii*. Jo Ann E. Asselin, Jinshan Lin, Alvaro L. Perez-Quintero, Irene Gentzel, Doris Majerczak, Stephen O. Opiyo, Wanying Zhao, Seung-Mann Paek, Min Gab Kim, David L. Coplin, Joshua J. Blakeslee, and David Mackey

*The virulence activity of an effector protein belonging to the widely conserved AvrE family is linked to its ability to cause system-wide reprogramming of phenylpropanoid metabolism in susceptible maize seedlings.*

1117

Bean Metal-Responsive Element-Binding Transcription Factor Confers Cadmium Resistance in Tobacco. Na Sun, Meng Liu, Wentao Zhang, Wanning Yang, Xiujuan Bei, Hui Ma, Fan Qiao, and Xiaoting Qi

*A bean transcription factor binds to a metal-responsive element and confers Cd tolerance in tobacco by activation of tryptophan biosynthesis.*

1136

Continued on next page

Inhibition of Auxin Signaling in *Frankia* Species-Infected Cells in *Casuarina glauca* Nodules Leads to Increased Nodulation. *Antony Champion, Mikael Lucas, Alexandre Tromas, Virginie Vaissayre, Amandine Crabos, Issa Diédhiou, Hermann Prodjino, Daniel Moukouanga, Elodie Pirolles, Maïmouna Cissoko, Jocelyne Bonneau, Hassen Gherbi, Claudine Franche, Valérie Hoher, Sergio Svistoonoff, and Laurent Laplaze*

*Inhibition of auxin signaling in plant cells infected by endosymbiotic nitrogen-fixing bacteria increases nodulation.*

1149

## SYSTEMS AND SYNTHETIC BIOLOGY

[OPEN] Transcriptome and Metabolite Profiling of the Infection Cycle of *Zymoseptoria tritici* on Wheat Reveals a Biphasic Interaction with Plant Immunity Involving Differential Pathogen Chromosomal Contributions and a Variation on the Hemibiotrophic Lifestyle Definition. *Jason J. Rudd, Kostya Kanyuka, Keywan Hassani-Pak, Mark Derbyshire, Ambrose Andongabo, Jean Devonshire, Artem Lysenko, Mansoor Saqi, Nalini M. Desai, Stephen J. Powers, Juliet Hooper, Linda Ambroso, Arvind Bharti, Andrew Farmer, Kim E. Hammond-Kosack, Robert A. Dietrich, and Mikael Courbot*

*The temporal dynamics of Zymoseptoria tritici reproduction on Triticum aestivum involves a biphasic manipulation of plant defense responses.*

1158

Revealing Shared and Distinct Gene Network Organization in Arabidopsis Immune Responses by Integrative Analysis. *Xiaobao Dong, Zhenhong Jiang, You-Liang Peng, and Ziding Zhang*

*Multiscale network analysis shows a robust gene network architecture in effector-triggered immunity of Arabidopsis.*

1186

## CORRECTIONS

A Secreted Protein with Plant-Specific Cysteine-Rich Motif Functions as a Mannose-Binding Lectin That Exhibits Antifungal Activity. *Miyakawa T., Hatano K., Miyauchi Y., Suwa Y., Sawano Y., and Tanokura M.*

1204

[OPEN] Articles can be viewed without a subscription.