

On the Cover: Chloroplast movement is mediated by the actin cytoskeleton. The chloroplast-actin (cp-actin) filaments that are specifically localized on the chloroplast envelope are rapidly reorganized according to the intensity and position of incident blue light. Suetsugu et al. (pp. 1155–1167) showed that PLASTID MOVEMENT IMPAIRED1 (PMI1) mediates chloroplast photorelocation movement via the regulation of cp-actin filaments and is essential for nuclear photorelocation movement in *Arabidopsis* (*Arabidopsis thaliana*) mesophyll cells. PMI1 and the homolog PLASTID MOVEMENT IMPAIRED1-RELATED1 are required for photorelocation movements of both plastids and nuclei in *Arabidopsis* pavement cells. The cover shows the cp-actin filament distribution at the rim of the chloroplasts during avoidance response in reaction to strong blue light focused on the central part of the cell. Cover image credits: Sam-Geun Kong, Kyushu University, Japan.

ON THE INSIDE

Peter V. Minorsky 905

EDITORIAL

Vigilante Science. Michael R. Blatt 907

COMMENTARIES

Visualizing the Photosynthetic Membrane Proteins in Situ: Atomic Force Microscopy. Alexander V. Ruban 910

Nutrient Signaling by Nitrate and Calcium. Nigel Crawford 911

From Leaf to Kernel: Trehalose-6-Phosphate Signaling Moves Carbon in the Field. Sjef Smeekens 912

TOPICAL REVIEW

Living to Die and Dying to Live: The Survival Strategy behind Leaf Senescence. Jos H.M. Schippers, Romy Schmidt, Carol Wagstaff, and Hai-Chun Jing

Leaf senescence is a highly dynamic process that has a major impact on crop production and quality. 914

BREAKTHROUGH TECHNOLOGIES

[OPEN] Targeted Mutagenesis, Precise Gene Editing, and Site-Specific Gene Insertion in Maize Using Cas9 and Guide RNA. Sergei Svitashov, Joshua K. Young, Christine Schwartz, Huirong Gao, S. Carl Falco, and A. Mark Cigan

Genome editing and gene insertion in maize is advanced with Cas9-guide RNA technology. 931

Application of Optical Topometry to Analysis of the Plant Epidermis. Miranda J. Haus, Ryan D. Kelsch, and Thomas W. Jacobs

Optical topometry is a powerful, nondestructive method for rapid, quantitative, high resolution imaging of the plant epidermis, requiring no sample preparation. 946

[OPEN] Cas9-Guide RNA Directed Genome Editing in Soybean. Zhongsen Li, Zhan-Bin Liu, Aiqiu Xing, Bryan P. Moon, Jessica P. Koellhoffer, Lingxia Huang, R. Timothy Ward, Elizabeth Clifton, S. Carl Falco, and A. Mark Cigan

High-frequency and heritable targeted mutagenesis, transgene integration, and endogenous gene editing in soybean is realized using CRISPR Cas9-gRNA. 960

Continued on next page

^[OPEN]A CRISPR/Cas9 Toolbox for Multiplexed Plant Genome Editing and Transcriptional Regulation. *Levi G. Lowder, Dengwei Zhang, Nicholas J. Baltes, Joseph W. Paul III, Xu Tang, Xuelian Zheng, Daniel F. Voytas, Tzung-Fu Hsieh, Yong Zhang, and Yiping Qi*

A CRISPR/Cas9 toolbox enables multiplex genome editing and transcriptional regulation of genes in plants. 971

RESEARCH REPORTS

Direct Recording of Trans-Plasma Membrane Electron Currents Mediated by a Member of the Cytochrome *b561* Family of Soybean. *Cristiana Picco, Joachim Scholz-Starke, Margherita Festa, Alex Costa, Francesca Sparla, Paolo Trost, and Armando Carpaneto*

Electron currents mediated by a soybean cytochrome b561 protein are detected and functionally characterized using a classical electrophysiological approach. 986

SCIENTIFIC CORRESPONDENCE

On the Extent of Tyrosine Phosphorylation in Chloroplasts. *Qintao Lu, Stefan Helm, Anja Rödiger, and Sacha Baginsky*

Reanalysis of published mass spectrometry data on Tyr-phosphorylated chloroplast proteins indicates that the majority of peptide spectrum matches reporting Tyr phosphorylation are ambiguous. 996

Tryptophan-Independent Indole-3-Acetic Acid Synthesis: Critical Evaluation of the Evidence. *Heather M. Nonhebel*

Evidence for Trp-independent IAA synthesis is critically reevaluated in the light of tryptophan synthase proteome data, local IAA synthesis and Trp, indole-3-pyruvate, and IAA turnover. 1001

UPDATES

Analysis of Small Ubiquitin-Like Modifier (SUMO) Targets Reflects the Essential Nature of Protein SUMOylation and Provides Insight to Elucidate the Role of SUMO in Plant Development. *Nabil Elrouby*

Analysis of the mechanisms, regulation, and consequences of protein SUMOylation in plants and other eukaryotes highlights the conservation and importance of this process across taxa. 1006

Cellular Signaling Pathways and Posttranslational Modifications Mediated by Nematode Effector Proteins. *Tarek Hewezi*

Plant-parasitic nematodes produce a diverse arsenal of effector proteins that interfere with defined cellular processes in host plants to promote successful parasitism. 1018

RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

Salt-Related MYB1 Coordinates Abscisic Acid Biosynthesis and Signaling during Salt Stress in Arabidopsis. *Ting Wang, Takayuki Tohge, Alexander Ivakov, Bernd Mueller-Roeber, Alisdair R. Fernie, Marek Mutwil, Jos H.M. Schippers, and Staffan Persson*

A salt-related transcription factor regulates abscisic acid synthesis and signaling genes in germinating Arabidopsis seeds under saline conditions. 1027

GLYCOLATE OXIDASE3, a Glycolate Oxidase Homolog of Yeast L-Lactate Cytochrome *c* Oxidoreductase, Supports L-Lactate Oxidation in Roots of Arabidopsis. *Martin K.M. Engqvist, Jessica Schmitz, Anke Gertzmann, Alexandra Florian, Nils Jaspert, Muhammad Arif, Salma Balazadeh, Bernd Mueller-Roeber, Alisdair R. Fernie, and Veronica G. Maurino*

A glycolate oxidase metabolizes L-lactate to pyruvate in vivo and may ensure the maintenance of low levels of L-lactate after its formation under normoxia. 1042

Continued on next page

- [OPEN] Regulation of Nicotine Biosynthesis by an Endogenous Target Mimicry of MicroRNA in Tobacco. Fangfang Li, Weidi Wang, Nan Zhao, Bingguang Xiao, Peijian Cao, Xingfu Wu, Chuyu Ye, Enhui Shen, Jie Qiu, Qian-Hao Zhu, Jiahua Xie, Xueping Zhou, and Longjiang Fan
Endogenous target mimicry of an miRNA affects nicotine biosynthesis. 1062
- [OPEN] Differential Role for Trehalose Metabolism in Salt-Stressed Maize. Clémence Henry, Samuel W. Bledsoe, Cara A. Griffiths, Alec Kollman, Matthew J. Paul, Soulayman Sakr, and L. Mark Lagrimini
Salt treatment of maize increased the sugar sensing metabolite trehalose-6-phosphate, as well as sucrose and hexose sugars, leading to reductions in spikelet growth, silk growth and kernel set. 1072
- [OPEN] The Identification of Maize and Arabidopsis Type I FLAVONE SYNTHASEs Links Flavones with Hormones and Biotic Interactions. María Lorena Falcone Ferreyra, Julia Emiliani, Eduardo José Rodríguez, Valeria Alina Campos-Bermudez, Erich Grotewold, and Paula Casati
Two novel flavone synthase enzymes from maize and Arabidopsis integrate flavone metabolism with hormone and biotic stress responses. 1090
- [OPEN] Overexpression of Arabidopsis Ceramide Synthases Differentially Affects Growth, Sphingolipid Metabolism, Programmed Cell Death, and Mycotoxin Resistance. Kyle D. Lutgeharm, Ming Chen, Amit Mehra, Rebecca E. Cahoon, Jonathan E. Markham, and Edgar B. Cahoon
Overexpression of ceramide synthases has strongly divergent physiological and metabolic effects with implications for improved plant performance. 1108
- [OPEN] Methylated Cytokinins from the Phytopathogen *Rhodococcus fascians* Mimic Plant Hormone Activity. Venkatesan Radhika, Nanae Ueda, Yuuri Tsuboi, Mikiko Kojima, Jun Kikuchi, Takuji Kudo, and Hitoshi Sakakibara
Methylated cytokinins contribute to pathogenesis as hormone-mimics. 1118
- Isolation and Characterization of O-methyltransferases Involved in the Biosynthesis of Glaucine in *Glaucium flavum*. Limei Chang, Jillian M. Hagel, and Peter J. Facchini
A subset of multifunctional O-methyltransferases is involved in the formation of the tetra-O-methylated benzylisoquinoline alkaloid glaucine. 1127
- CELL BIOLOGY**
- [OPEN] Ligand-Mediated cis-Inhibition of Receptor Signaling in the Self-Incompatibility Response of the Brassicaceae. Titima Tantikanjana and June B. Nasrallah
Coexpression of the receptor and ligand that function in crucifer self-incompatibility inhibits receptor signaling and abrogates the ability of stigma epidermal cells to arrest self pollen. 1141
- [OPEN] PLASTID MOVEMENT IMPAIRED1 and PLASTID MOVEMENT IMPAIRED1-RELATED1 Mediate Photorelocation Movements of Both Chloroplasts and Nuclei. Noriyuki Suetsugu, Takeshi Higa, Sam-Geun Kong, and Masamitsu Wada
Two C2 domain proteins regulate light-mediated movements of plastids and nuclei in both mesophyll and pavement cells. 1155

[OPEN] Distinct Cellular Locations of Carbonic Anhydrases Mediate Carbon Dioxide Control of Stomatal Movements. *Honghong Hu, Wouter-Jan Rappel, Rossana Occhipinti, Amber Ries, Maik Böhmer, Lei You, Chuanlei Xiao, Cawas B. Engineer, Walter F. Boron, and Julian I. Schroeder*

Intracellular targeting of guard cell carbonic anhydrases is characterized and modeled in relation to their roles in CO₂ control of stomatal movements.

1168

Rice *TUTOU1* Encodes a Suppressor of cAMP Receptor-Like Protein That Is Important for Actin Organization and Panicle Development. *Jiaoteng Bai, Xudong Zhu, Qing Wang, Jian Zhang, Hongqi Chen, Guojun Dong, Lei Zhu, Huakun Zheng, Qingjun Xie, Jinqiang Nian, Fan Chen, Ying Fu, Qian Qian, and Jianru Zuo*

An actin nucleation protein affects rice panicle development as well as root growth.

1179

ECOPHYSIOLOGY AND SUSTAINABILITY

[OPEN] High-Resolution Three-Dimensional Structural Data Quantify the Impact of Photoinhibition on Long-Term Carbon Gain in Wheat Canopies in the Field. *Alexandra J. Burgess, Renata Retkute, Michael P. Pound, John Foulkes, Simon P. Preston, Oliver E. Jensen, Tony P. Pridmore, and Erik H. Murchie*

A digital reconstruction method models the effect of photoinhibition on daily canopy photosynthesis in three contrasting wheat canopies.

1192

[OPEN] Stomatal Blue Light Response Is Present in Early Vascular Plants. *Michio Doi, Yuki Kitagawa, and Ken-ichiro Shimazaki*

Blue light responses of stomata occur in a wide lineage of plants except the fern species of Polypodiopsida.

1205

GENES, DEVELOPMENT, AND EVOLUTION

[OPEN] SHORT VEGETATIVE PHASE Up-Regulates *TEMPRANILLO2* Floral Repressor at Low Ambient Temperatures. *Esther Marín-González, Luis Matías-Hernández, Andrea E. Aguilar-Jaramillo, Jeong Hwan Lee, Ji Hoon Ahn, Paula Suárez-López, and Soraya Pelaz*

The functional characterization of two Arabidopsis floral repressors unravels their role and regulation at low ambient temperatures.

1214

[OPEN] *EARLY SENESCENCE1* Encodes a SCAR-LIKE PROTEIN2 That Affects Water Loss in Rice. *Yuchun Rao, Yaolong Yang, Jie Xu, Xiaojing Li, Yujia Leng, Liping Dai, Lichao Huang, Guosheng Shao, Deyong Ren, Jiang Hu, Longbiao Guo, Jianwei Pan, and Dali Zeng*

An actin nucleation protein affects water loss by regulating stomatal density.

1225

[OPEN] Meta-Analysis of Arabidopsis *KANADI1* Direct Target Genes Identifies a Basic Growth-Promoting Module Acting Upstream of Hormonal Signaling Pathways. *Yakun Xie, Daniel Straub, Tenai Eguen, Ronny Brandt, Mark Stahl, Jaime F. Martínez-García, and Stephan Wenkel*

The comparative study of the gene targets of the KANADI1 transcription factor indicates that it is part of a basic growth-promoting module.

1240

Convergent Evolution of Endosymbiont Differentiation in Dalbergioid and Inverted Repeat-Lacking Clade Legumes Mediated by Nodule-Specific Cysteine-Rich Peptides. *Pierre Czernic, Djamel Gully, Fabienne Cartieaux, Lionel Moulin, Ibtissem Guefrachi, Delphine Patrel, Olivier Pierre, Joël Fardoux, Clémence Chaintreuil, Phuong Nguyen, Frédéric Gressent, Corinne Da Silva, Julie Poulain, Patrick Wincker, Valérie Rofidal, Sonia Hem, Quentin Barrière, Jean-François Arrighi, Peter Mergaert, and Eric Giraud*

Several species from an ancient legume lineage independently evolved a novel class of cysteine-rich peptides to impose a differentiation process on their endosymbionts.

1254

Continued on next page

[OPEN] Second-Site Mutagenesis of a Hypomorphic *argonaute1* Allele Identifies *SUPERKILLER3* as an Endogenous Suppressor of Transgene Posttranscriptional Gene Silencing. *Agnès Yu, Baptiste Saudemont, Nathalie Bouteiller, Emilie Elvira-Matelot, Gersende Lepère, Jean-Sébastien Parent, Jean-Benoit Morel, Jun Cao, Taline Elmayan, and Hervé Vaucheret*

Addressing RNAs to the 3'-to-5' exoribonuclease of the cytoplasmic exosome counteracts posttranscriptional transgene silencing. 1266

[OPEN] SENESCENCE-SUPPRESSED PROTEIN PHOSPHATASE Directly Interacts with the Cytoplasmic Domain of SENESCENCE-ASSOCIATED RECEPTOR-LIKE KINASE and Negatively Regulates Leaf Senescence in Arabidopsis. *Dong Xiao, Yanjiao Cui, Fan Xu, Xinxin Xu, Guanxiao Gao, Yaxin Wang, Zhaoxia Guo, Dan Wang, and Ning Ning Wang*

A protein phosphatase negatively regulates Arabidopsis leaf senescence through dephosphorylating a senescence-promoting receptor-like kinase. 1275

MEMBRANES, TRANSPORT, AND BIOENERGETICS

[OPEN] Genetic and Physical Interaction Studies Reveal Functional Similarities between ALBINO3 and ALBINO4 in Arabidopsis. *Raphael Trösch, Mats Töpel, Úrsula Flores-Pérez, and Paul Jarvis*

A thylakoid membrane protein shares functional similarity and physical interactions with the homologous protein insertase, despite sequence-level divergence in a critical C-terminal domain. 1292

Lack of Phosphatidylglycerol Inhibits Chlorophyll Biosynthesis at Multiple Sites and Limits Chlorophyllide Reutilization in *Synechocystis* sp. Strain PCC 6803. *Jana Kopečná, Jan Pilný, Vendula Krynická, Aleš Tomčala, Mihály Kis, Zoltan Gombos, Josef Komenda, and Roman Sobotka*

The lack of lipid phosphatidylglycerol inhibits chlorophyll biosynthesis and induces accumulation of an aberrant protein complex containing monomeric PSI and CP43 antenna of PSII. 1307

[OPEN] The Use of Contact Mode Atomic Force Microscopy in Aqueous Medium for Structural Analysis of Spinach Photosynthetic Complexes. *Witchukorn Phuthong, Zubin Huang, Tyler M. Wittkopp, Kinga Sznee, Mark L. Heinzel, Jan P. Dekker, Raoul N. Frese, Fritz B. Prinz, and Arthur R. Grossman*

Characterization of spinach grana membranes by contact mode atomic force microscopy in aqueous medium distinguishes molecular features and the distribution of the lumen-exposed domains of PSII. 1318

[OPEN] Overexpression of BAX INHIBITOR-1 Links Plasma Membrane Microdomain Proteins to Stress. *Toshiki Ishikawa, Toshihiko Aki, Shuichi Yanagisawa, Hirofumi Uchimiyu, and Maki Kawai-Yamada*

Overexpression of a cell death suppressor modulates sphingolipid and protein composition of plasma membrane microdomains, leading to enhanced tolerance to stress. 1333

[OPEN] Phosphorylation and Dephosphorylation of the Presequence of Precursor MULTIPLE ORGANELLAR RNA EDITING FACTOR3 during Import into Mitochondria from Arabidopsis. *Yee-Song Law, Renshan Zhang, Xiaoqian Guan, Shifeng Cheng, Feng Sun, Owen Duncan, Monika W. Murcha, James Whelan, and Boon Leong Lim*

Phosphorylation of the presequence of an RNA editing factor by cytosolic kinases and its dephosphorylation by an outer mitochondrial membrane phosphatase contribute to mitochondrial import of the factor protein. 1344

SIGNALING AND RESPONSE

[OPEN] Changes in the Common Bean Transcriptome in Response to Secreted and Surface Signal Molecules of *Rhizobium etli*. *Virginia Dalla Via, Candela Narduzzi, Orlando Mario Aguilar, María Eugenia Zanetti, and Flavio Antonio Blanco*

Transcriptional profiling of common bean roots exposed to rhizobial molecules uncovers unique aspects of root nodule symbiosis, including early modulation of genes encoding circadian clock components. 1356

Continued on next page

- [OPEN] Overaccumulation of γ -Glutamylcysteine in a Jasmonate-Hypersensitive Arabidopsis Mutant Causes Jasmonate-Dependent Growth Inhibition. *Hsin-Ho Wei, Martha Rowe, Jean-Jack M. Riethoven, Ryan Grove, Jiri Adamec, Yusuke Jikumaru, and Paul Staswick*
- The glutathione precursor γ -glutamylcysteine modulates plant growth inhibition by the jasmonate hormone.* 1371
- [OPEN] Drought Induces Distinct Growth Response, Protection, and Recovery Mechanisms in the Maize Leaf Growth Zone. *Viktoriya Avramova, Hamada AbdElgawad, Zhengfeng Zhang, Bartosz Fotschki, Romina Casadevall, Lucia Vergauwen, Dries Knapen, Edith Taleisnik, Yves Guisez, Han Asard, and Gerrit T.S. Beemster*
- Drought inhibits cell division and expansion in the maize leaf growth zone by reducing antioxidant levels and increases photosynthetic capacity to allow for enhanced growth upon recovery.* 1382
- The Calcium Ion Is a Second Messenger in the Nitrate Signaling Pathway of Arabidopsis. *Eleodoro Riveras, José M. Alvarez, Elena A. Vidal, Carolina Oses, Andrea Vega, and Rodrigo A. Gutiérrez*
- Nitrate sensed by the NRT1.1/NPF6.3 nitrate transceptor activates a PLC activity which causes an increase in the concentration of cytoplasmic Ca^{2+} and stimulates expression of nitrate responsive genes.* 1397
- [OPEN] The RING E3 Ligase KEEP ON GOING Modulates JASMONATE ZIM-DOMAIN12 Stability. *Laurens Pauwels, Andrés Ritter, Jonas Goossens, Astrid Nagels Durand, Hongxia Liu, Yangnan Gu, Jan Geerinck, Marta Boter, Robin Vanden Bossche, Rebecca De Clercq, Jelle Van Leene, Kris Gevaert, Geert De Jaeger, Roberto Solano, Sophia Stone, Roger W. Innes, Judy Callis, and Alain Goossens*
- An E3 ubiquitin ligase involved in abscisic acid signaling modulates the stability of a central jasmonate signaling component.* 1405
- CORRECTIONS**
- Water Transport Properties of the Grape Pedicel during Fruit Development: Insights into Xylem Anatomy and Function Using Microtomography. *Knipfer T., Fei J., Gambetta G.A., McElrone A.J., Shackel K.A., and Matthews M.A.* 1418
- RBF1, A Plant Homolog of the Bacterial Ribosome-Binding Factor RbfA, Acts in Processing of the Chloroplast 16S Ribosomal RNA. *Fristedt R., Scharff L.B., Clarke C.A., Wang Q., Lin C., Merchant S.S., and Bock R.* 1419
- [OPEN] Articles can be viewed without a subscription.