

On the Cover: The genus *Hieracium* subgenus *Pilosella* contains species that form seed asexually by apomixis. Apomixis involves mitotic formation of the female gametophyte in the absence of prior meiosis (apospory) in the ovule and subsequent formation of seeds without fertilization. In this issue, Juranić et al. identify markers for the somatic cell initiating apomixis which forms near cells undergoing sexual female gametogenesis. Juranić et al. show that the cell initiating apomixis makes direct contact with a meiotically derived cell that is fated for the mitotic events of sexual female gametogenesis, proceeding to the mitotic events of apospory. Contact also results in degeneration of the sexual cell and cessation of the sexual pathway. The cover image shows a capitulum of apomictic *H. praealtum* containing mature fruits termed achenes. Each achene contains a single seed and has a hairy pappus that functions as a parachute for wind dispersal. Photo by Martina Juranić and Ivan Bušić.

ON THE INSIDE

Peter V. Minorsky 863

COMMENTARIES

Releasing the Cytokinin Brakes on Root Growth. Magdalena Julkowska 865

Managing Competing Interests: Partitioning S between Glutathione and Protein Synthesis. Amna Mhamdi 867

Subcellular Spice Trade Routes: Crocin Biosynthesis in the Saffron Crocus (*Crocus sativus*). Trevor H. Yeats and Raimund Nagel 869

Save Time and Fish for the Clock. Charlotte M. M. Gommers 871

Cellulose Synthase Stoichiometry Varies among Species and Tissues. Yunqing Yu 873

UPDATE

^[OPEN]Plant Endomembrane Dynamics: Studies of K⁺/H⁺ Antiporters Provide Insights on the Effects of pH and Ion Homeostasis. Heven Sze and Salil Chanroj

Cation/H⁺ antiporters affect signaling, reproduction, and stress tolerance, indicating critical roles of pH and cation balance on trafficking in the endomembrane system. 875

BREAKTHROUGH TECHNOLOGIES

^[OPEN]A New Phenotyping Pipeline Reveals Three Types of Lateral Roots and a Random Branching Pattern in Two Cereals. Sixtine Passot, Beatriz Moreno-Ortega, Daniel Moukouanga, Crispulo Balsera, Soazig Guyomarc'h, Mikael Lucas, Guillaume Lobet, Laurent Laplaze, Bertrand Muller, and Yann Guédon

Lateral roots in both pearl millet and maize can be categorized into three types based on growth rate profiles. 896

RESEARCH REPORTS

^[OPEN]Mesophyll Cells Are the Main Site of Abscisic Acid Biosynthesis in Water-Stressed Leaves.

Scott A. M. McAdam and Timothy J. Brodribb

Analysis of leaves from one angiosperm and four conifers where the mesophyll and vasculature can be mechanically separated revealed that the mesophyll produces substantial amounts of abscisic acid. 911

Continued on next page

Green Algal Hydrogenase Activity Is Outcompeted by Carbon Fixation before Inactivation by Oxygen Takes Place. *Yuval Milrad, Shira Schweitzer, Yael Feldman, and Iftach Yacoby*

In the transition from dark anaerobiosis to light, oxygen deactivates the hydrogenase pool, but only after carbon fixation outcompetes hydrogen production for electrons.

918

RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

^[OPEN]Sulfur Partitioning between Glutathione and Protein Synthesis Determines Plant Growth.

Anna Speiser, Marleen Silbermann, Yihan Dong, Stefan Haberland, Veli Vural Uslu, Shanshan Wang, Sajid A.K. Bangash, Michael Reichelt, Andreas J. Meyer, Markus Wirtz, and Ruediger Hell

Glutamate cysteine ligase activity determines flux of sulfur into protein synthesis via the Target of Rapamycin sensor kinase in Arabidopsis.

927

^[OPEN]GLUCOSAMINE INOSITOLPHOSPHORYLCERAMIDE TRANSFERASE1 (GINT1) Is a

GlcNAc-Containing Glycosylinositol Phosphorylceramide Glycosyltransferase. *Toshiki Ishikawa, Lin Fang, Emilie A. Rennie, Julien Sechet, Jingwei Yan, Beibei Jing, William Moore, Edgar B. Cahoon, Henrik V. Scheller, Maki Kawai-Yamada, and Jenny C. Mortimer*

GINT1 is shown to be an indispensable glycosyltransferase that facilitates the glycosylation of GlcNAccontaining glycosylinositol phosphorylceramides in rice, with a minor role in Arabidopsis.

938

Dynamic Changes between Two LHCX-Related Energy Quenching Sites Control Diatom Photoacclimation. *Lucilla Taddei, Volha U. Chukhutsina, Bernard Lepetit, Giulio Rocco Stella, Roberto Bassi, Herbert van Amerongen, Jean-Pierre Bouly, Marianne Jaubert, Giovanni Finazzi, and Angela Falciatore*

Multiple LHCX-related quenching sites control short- and long-term high-light acclimation in the marine diatom Phaeodactylum tricornutum.

953

^[OPEN]The Extra-Pathway Interactome of the TCA Cycle: Expected and Unexpected Metabolic

Interactions. *Youjun Zhang, Corné Swart, Saleh Alseekh, Federico Scossa, Liang Jiang, Toshihiro Obata, Alexander Graf, and Alisdair R. Fernie*

The extra-pathway interaction network of the Arabidopsis TCA cycle was generated by affinity purification proteomics and partly confirmed by bimolecular fluorescence complementation, yeast two-hybrid, and mutant analysis.

966

Carbonic Anhydrase Mutants in *Zea mays* Have Altered Stomatal Responses to Environmental Signals. *Allison R. Kolbe, Thomas P. Brutnell, Asaph B. Cousins, and Anthony J. Studer*

Analysis of carbonic anhydrase mutants in Zea mays revealed slowed stomatal closure to high CO₂ and dark transition as well as a role for carbonic anhydrase in water-use efficiency.

980

^[OPEN]Candidate Enzymes for Saffron Crocin Biosynthesis Are Localized in Multiple Cellular

Compartments. *Olivia Costantina Demurtas, Sarah Frusciante, Paola Ferrante, Gianfranco Diretto, Noraddin Hosseinpour Azad, Marco Pietrella, Giuseppe Aprea, Anna Rita Taddei, Elena Romano, Jianing Mi, Salim Al-Babili, Lorenzo Frigerio, and Giovanni Giuliano*

Carotenoid cleavage dioxygenase 2 and candidate aldehyde dehydrogenase and UDP-glycosyltransferase enzymes involved in saffron crocin biosynthesis are localized in the chromoplast, the endoplasmic reticulum, and the cytoplasm.

990

CELL BIOLOGY

[OPEN] Selective Elimination of Membrane-Damaged Chloroplasts via Microautophagy. *Sakuya Nakamura, Jun Hidema, Wataru Sakamoto, Hiroyuki Ishida, and Masanori Izumi*

Chlorophagy is a selective autophagy process that removes swollen chloroplasts caused by high light-induced membrane damage via tonoplast-mediated transport in Arabidopsis thaliana.

1007

[OPEN] Asexual Female Gametogenesis Involves Contact with a Sexually-Fated Megaspore in Apomictic Hieracium. *Martina Juranić, Matthew R. Tucker, Carolyn J. Schultz, Neil J. Shirley, Jennifer M. Taylor, Andrew Spriggs, Susan D. Johnson, Vincent Bulone, and Anna M. Koltunow*

Cells initiating asexual female gametogenesis in Hieracium are marked with arabinogalactan protein epitopes and must make contact with a sexually fated functional megaspore to undergo mitosis.

1027

ECOPHYSIOLOGY AND SUSTAINABILITY

[OPEN] The Ancient Phosphatidylinositol 3-Kinase Signaling System Is a Master Regulator of Energy and Carbon Metabolism in Algae. *Rishiram Ramanan, Quynh-Giao Tran, Dae-Hyun Cho, Jae-Eun Jung, Byung-Hyuk Kim, Sang-Yoon Shin, Sae-Hae Choi, Kwang-Hyeon Liu, Dae-Soo Kim, Seon-Jin Lee, José L. Crespo, Hee-Gu Lee, Hee-Mock Oh, and Hee-Sik Kim*

Phosphatidylinositol 3-kinase signaling influences biofuel yields in algae by regulating membrane lipid hydrolysis, lipogenesis, tricarboxylic acid cycle, and mitochondrial ATP synthesis.

1050

[OPEN] Low Vulnerability to Xylem Embolism in Leaves and Stems of North American Oaks.

Robert Paul Skelton, Todd E. Dawson, Sally E. Thompson, Yuzheng Shen, Andrew P. Weitz, and David Ackerly

North American oaks are more resistant to xylem embolism than previously thought, suggesting that avoiding stem embolism is a critical component of drought tolerance in woody trees.

1066

[OPEN] Root Engineering in Barley: Increasing Cytokinin Degradation Produces a Larger Root System, Mineral Enrichment in the Shoot and Improved Drought Tolerance. *Eswarayya Ramireddy, Seyed A. Hosseini, Kai Eggert, Sabine Gillandt, Heike Gnad, Nicolaus von Wirén, and Thomas Schmölling*

Root-specific expression of a cytokinin-degrading CKX gene in barley roots causes formation of a larger root system leading to higher element content in shoot organs and improved drought tolerance.

1078

GENES, DEVELOPMENT, AND EVOLUTION

Cellulose Synthase Stoichiometry in Aspen Differs from Arabidopsis and Norway Spruce.

Xueyang Zhang, Pia Guadalupe Dominguez, Manoj Kumar, Joakim Bygdell, Sergey Miroshnichenko, Björn Sundberg, Gunnar Wingsle, and Totte Niittylä

Changes in secondary cell wall cellulose synthase stoichiometry coincide with changes in cellulose microfibril diameter in aspen.

1096

Identification of Genes Related to Cold Tolerance and a Functional Allele That Confers Cold Tolerance. *Ning Xiao, Yong Gao, Huangjun Qian, Qiang Gao, Yunyu Wu, Dongping Zhang, Xiaoxiang Zhang, Ling Yu, Yuhong Li, Cunhong Pan, Guangqing Liu, Changhai Zhou, Min Jiang, Niansheng Huang, Zhengyuan Dai, Chengzhi Liang, Zhou Chen, Jianmin Chen, and Aihong Li*

A genome-wide association study identified genes and single-nucleotide polymorphisms related to cold tolerance in rice.

1108

- [OPEN] Revised Phylogeny of the Cellulose Synthase Gene Superfamily: Insights into Cell Wall Evolution. Alan Little, Julian G. Schwerdt, Neil J. Shirley, Shi F. Khor, Kylie Neumann, Lisa A. O'Donovan, Jelle Lahnstein, Helen M. Collins, Marilyn Henderson, Geoffrey B. Fincher, and Rachel A. Burton
Sequenced genomes of land plants enabled a renewal of cellulose synthase gene superfamily phylogeny, which revealed a previously unknown eudicot lineage, CslM, and showed that (1,3;1,4)- β -glucan synthesis is not restricted to the Poaceae. 1124
- DAWDLE Interacts with DICER-LIKE Proteins to Mediate Small RNA Biogenesis. Shuxin Zhang, Yongchao Dou, Shengjun Li, Guodong Ren, David Chevalier, Chi Zhang, and Bin Yu
DAWDLE modulates small RNA processing through its interaction with DCL proteins. 1142
- [OPEN] NLR Mutations Suppressing Immune Hybrid Incompatibility and Their Effects on Disease Resistance. Kostadin E. Atanasov, Changxin Liu, Alexander Erban, Joachim Kopka, Jane E. Parker, and Rubén Alcázar
*A suppressor screen for immune-related hybrid incompatibilities identifies multiple TNL intragenic mutations improving fitness, with no costs on disease resistance to a local *H. arabidopsidis* isolate.* 1152
- [OPEN] Decoys Untangle Complicated Redundancy and Reveal Targets of Circadian Clock F-Box Proteins. Chin-Mei Lee, Ann Feke, Man-Wah Li, Christopher Adamchek, Kristofor Webb, José Pruneda-Paz, Eric J. Bennett, Steve A. Kay, and Joshua M. Gendron
Decoy circadian clock proteins, which bind interacting proteins but prevent their degradation, reveal new functions and interactions of redundant E3 ubiquitin ligases. 1170
- DDM1 Represses Noncoding RNA Expression and RNA-Directed DNA Methylation in Heterochromatin. Feng Tan, Yue Lu, Wei Jiang, Tian Wu, Ruoyu Zhang, Yu Zhao, and Dao-Xiu Zhou
*The rice (*Oryza sativa*) chromatin remodeling factor DDM1 represses the expression of noncoding RNA and RNA-directed DNA methylation in heterochromatin.* 1187
- [OPEN] Reproductive Long Intergenic Noncoding RNAs Exhibit Male Gamete Specificity and Polycomb Repressive Complex 2-Mediated Repression. Cameron Johnson, Liza J. Conrad, Ravi Patel, Sarah Anderson, Chenxin Li, Andy Pereira, and Venkatesan Sundaresan
*Long noncoding RNAs in rice with major reproductive and Polycomb complex 2-regulated subclasses have conserved members detected in *Brachypodium* and maize.* 1198
- [OPEN] A Maternally Deposited Endosperm Cuticle Contributes to the Physiological Defects of transparent testa Seeds. Sylvain Loubéry, Julien De Giorgi, Anne Utz-Pugin, Lara Demonsais, and Luis Lopez-Molina
A maternal cuticle is deposited in the outer surface of the endosperm during seed development where it contributes to the physiological defects of transparent testa mutant seeds. 1218
- The Major Origin of Seedless Grapes Is Associated with a Missense Mutation in the MADS-Box Gene *VviAGL11*. Carolina Royo, Rafael Torres-Pérez, Nuria Mauri, Nieves Diestro, José Antonio Cabezas, Cécile Marchal, Thierry Lacombe, Javier Ibáñez, Manuel Tornel, Juan Carreño, José Miguel Martínez-Zapater, and Pablo Carbonell-Bejerano
*Integrative genetics and genomics approaches revealed a missense substitution in the MADS-box gene *VviAGL11* as the mutation leading to seed abortion in most seedless table grape varieties.* 1234

MEMBRANES, TRANSPORT, AND BIOENERGETICS

[OPEN] Boron Alleviates Aluminum Toxicity by Promoting Root Alkalization in Transition Zone via Polar Auxin Transport. *Xuwen Li, Yalin Li, Jingwen Mai, Lin Tao, Mei Qu, Jiayou Liu, Renfang Shen, Guilian Xu, Yingming Feng, Hongdong Xiao, Lishu Wu, Lei Shi, Shaoxue Guo, Jian Liang, Yiyong Zhu, Yongming He, František Baluška, Sergey Shabala, and Min Yu*

Boron promotes PIN2-based polar auxin transport in the apical transition zone of pea (Pisum sativum) roots, leading to root alkalization and thereby reducing aluminum toxicity.

1254

[OPEN] Vacuolar Iron Stores Gated by NRAMP3 and NRAMP4 Are the Primary Source of Iron in Germinating Seeds. *Emma L. Bastow, Vanesa S. Garcia de la Torre, Andrew E. Maclean, Robert T. Green, Sylvain Merlot, Sebastien Thomine, and Janneke Balk*

Failure to mobilize vacuolar iron stores in germinating seeds triggers iron deficiency responses, and strongly affects plastids but not mitochondria.

1267

Glycolate Induces Redox Tuning Of Photosystem II in Vivo: Study of a Photorespiration Mutant. *Marine Messant, Stefan Timm, Andrea Fantuzzi, Wolfram Weckwerth, Hermann Bauwe, A. William Rutherford, and Anja Krieger-Liszkay*

Glycolate accumulated in a photorespiration mutant replaces the bicarbonate on the acceptor-side iron of PSII, lowering the yield of singlet oxygen by redox tuning the primary quinone.

1277

SIGNALING AND RESPONSE

[OPEN] The NAC Transcription Factor SINAP2 Regulates Leaf Senescence and Fruit Yield in Tomato. *Xuemin Ma, Youjun Zhang, Veronika Turečková, Gang-Ping Xue, Alisdair R. Fernie, Bernd Mueller-Roeber, and Salma Balazadeh*

The abscisic acid-activated NAC transcription factor SINAP2 controls leaf senescence and fruit yield in tomato.

1286

DIACYLGLYCEROL ACYLTRANSFERASE and DIACYLGLYCEROL KINASE Modulate Triacylglycerol and Phosphatidic Acid Production in the Plant Response to Freezing Stress. *Wei-Juan Tan, Yi-Cong Yang, Ying Zhou, Li-Ping Huang, Le Xu, Qin-Fang Chen, Lu-Jun Yu, and Shi Xiao*

DGAT1 and DGK2/3/5 modulate the conversion of DAG to TAG and PA, respectively, and determine cold stress tolerance in Arabidopsis.

1303

SYSTEMS AND SYNTHETIC BIOLOGY

[OPEN] Molecular Mechanisms Preventing Senescence in Response to Prolonged Darkness in a Desiccation-Tolerant Plant. *Meriem Durgud, Saurabh Gupta, Ivan Ivanov, M. Amin Omidbakhshfard, Maria Benina, Saleh Alseekh, Nikola Staykov, Mareike Hauenstein, Paul P. Dijkwel, Stefan Hörtensteiner, Valentina Toneva, Yariv Brotman, Alisdair R. Fernie, Bernd Mueller-Roeber, and Tsanko S. Gechev*

During long-term darkness, specific transcriptional reprogramming and metabolome reconfigurations enable Haberlea rhodopensis to preserve most of their chlorophyll and counteract starvation by using proteins and polar lipids as alternative nitrogen and energy sources.

1319

CORRECTIONS

The ROXY1 C-Terminal L**LL Motif Is Essential for the Interaction with TGA Transcription Factors. *Li S., Gutsche N., and Zachgo S.*

1339

Continued from preceding page

Arabidopsis Basic Leucine-Zipper Transcription Factors TGA9 and TGA10 Interact with Floral Glutaredoxins ROXY1 and ROXY2 and Are Redundantly Required for Anther Development.
Murmu J., Bush M.J., DeLong C., Li S., Xu M., Khan M., Malcolmson C., Fobert P.R., Zachgo S., and Hepworth S.R.

1342

[OPEN] Articles can be viewed without a subscription.