

**On the Cover:** Representative root system of hydroponically grown harsh hakea (*Hakea prostrata*), a member of the Proteaceae family that is native to southwestern Australia, after supplementation with suboptimal (1  $\mu\text{m}$ ) inorganic phosphate for 12 weeks. Dense clusters of determinate branch roots known as proteoid roots arise *en masse* from a localized region of the parent root axis. These morphological adaptations are synchronized to activation of the important allosteric enzyme phosphoenolpyruvate carboxylase by a novel pattern of posttranslational modifications. The combined effect of *in vivo* deubiquitination and increased phosphorylation is hypothesized to facilitate phosphoenolpyruvate carboxylase's rapid anaplerotic carboxylation of phosphoenolpyruvate in support of the massive synthesis and excretion of organic acid anions that dominates the carbon metabolism of the mature proteoid roots. This enhances the bioavailability of mineral-bound inorganic phosphate by solubilizing  $\text{Al}^{3+}$ ,  $\text{Fe}^{3+}$ , and  $\text{Ca}^{2+}$  phosphates in the rhizosphere. See the related article by Bartley et al. (pp. 1615–1633). Photo credit: Michael W. Shane.

## ON THE INSIDE

Peter V. Minorsky

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## EDITOR'S CHOICE

Editor's Choice: Evaluating the Potential for Adverse Interactions within Genetically Engineered Breeding Stacks.

Henry-York Steiner, Claire Halpin, Joseph M. Jez, John Kough, Wayne Parrott, Lynne Underhill, Natalie Weber, and L. Curtis Hannah

*When genetically engineered stacks (also known as stacked or combined events) are produced by combining two or more single transgenic events by conventional breeding, the potential for interactions between the products of the events that impact food and feed safety can be evaluated and the need for further safety assessment can be determined on a case-by-case basis.*

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## BREAKTHROUGH TECHNOLOGIES

Correlative Imaging of Fluorescent Proteins in Resin-Embedded Plant Material. Karen Bell, Steve Mitchell, Danae Paultre, Markus Posch, and Karl Oparka

*A simple technique permits fluorescent proteins to be imaged in resin-embedded plant material.*

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<sup>[C][W][OA]</sup>Production of a High-Efficiency TILLING Population through Polyploidization. Helen Tsai, Victor Missirian, Kathie J. Ngo, Robert K. Tran, Simon R. Chan, Venkatesan Sundaresan, and Luca Comai

*Conversion of diploid Arabidopsis to autotetraploidy enables denser mutagenesis, resulting in a highly efficient population for reverse genetics.*

1604

## RESEARCH ARTICLES

### BIOCHEMISTRY AND METABOLISM

<sup>[C][W][OA]</sup>Overexpression of a BAHD Acyltransferase, *OsAt10*, Alters Rice Cell Wall Hydroxycinnamic Acid Content and Saccharification. Laura E. Bartley, Matthew L. Peck, Sung-Ryul Kim, Berit Ebert, Chithra Manisseri, Dawn M. Chiniquy, Robert Sykes, Lingfang Gao, Carsten Rautengarten, Miguel E. Vega-Sánchez, Peter I. Benke, Patrick E. Canlas, Peijian Cao, Susan Brewer, Fan Lin, Whitney L. Smith, Xiaohan Zhang, Jay D. Keasling, Rolf E. Jentoff, Steven B. Foster, Jizhong Zhou, Angela Ziebell, Gynheung An, Henrik V. Scheller, and Pamela C. Ronald

*An acyltransferase reduces cross linking in grass cell walls, yielding grass leaves and stems that can be more easily broken down to make biofuels.*

1615

<sup>[W][OA]</sup>Reciprocal Control of Anaplerotic Phosphoenolpyruvate Carboxylase by *in Vivo* Monoubiquitination and Phosphorylation in Developing Proteoid Roots of Phosphate-Deficient Harsh Hakea. Michael W. Shane, Eric T. Fedosejevs, and William C. Plaxton

*A novel pattern of *in vivo* posttranslational modifications activates phosphoenolpyruvate carboxylase in maturing proteoid roots of harsh hakea.*

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<sup>[W]</sup><sup>[OA]</sup>The Regulatory Properties of Rubisco Activase Differ among Species and Affect Photosynthetic Induction during Light Transitions. *A. Elizabete Carmo-Silva and Michael E. Salvucci*

*The regulatory properties of Rubisco activase from different species suggest a new strategy for enhancing photosynthetic performance by increasing the rate of photosynthetic induction.* 1645

<sup>[W]</sup>Reprogramming the Phenylpropanoid Metabolism in Seeds of Oilseed Rape by Suppressing the Orthologs of REDUCED EPIDERMAL FLUORESCENCE1. *Juliane Mittasch, Christoph Böttcher, Andrej Frolov, Dieter Strack, and Carsten Milkowski*

*Metabolic redirection in seeds of oilseed rape defines the role of an aldehyde dehydrogenase as a branch-point enzyme in the plant phenylpropanoid pathway.* 1656

<sup>[W]</sup>Understanding the Role of Defective Invertases in Plants: Tobacco Nin88 Fails to Degrade Sucrose. *Katrien Le Roy, Rudy Vergauwen, Tom Struyf, Shuguang Yuan, Willem Lammens, Janka Mátrai, Marc De Maeyer, and Wim Van den Ende*

*An inactive invertase may indirectly stimulate the activity of active cell wall invertases.* 1670

<sup>[W]</sup><sup>[OA]</sup>Autophagy Contributes to Nighttime Energy Availability for Growth in Arabidopsis. *Masanori Izumi, Jun Hidema, Amane Makino, and Hiroyuki Ishida*

*Autophagic recycling of proteins supplies nighttime energy sources such as amino acids under conditions of limited sugar availability.* 1682

<sup>[C]</sup><sup>[W]</sup><sup>[OA]</sup>Chromoplast-Specific Carotenoid-Associated Protein Appears to Be Important for Enhanced Accumulation of Carotenoids in *hp1* Tomato Fruits. *Himabindu Vasuki Kilambi, Rakesh Kumar, Rameshwar Sharma, and Yellamaraju Sreelakshmi*

*A chromoplast protein may assist in the sequestration and stabilization of carotenoids.* 2085

## CELL BIOLOGY

<sup>[C]</sup><sup>[W]</sup>Multiple Functions of Kip-Related Protein5 Connect Endoreduplication and Cell Elongation. *Teddy Jégu, David Latrasse, Marianne Delarue, Christelle Mazubert, Mickaël Bourge, Elodie Hudik, Sophie Blanchet, Marie-Noëlle Soler, Céline Charon, Lieven De Veylder, Cécile Raynaud, Catherine Bergounioux, and Moussa Benhamed*

*The cell cycle inhibitor KRP5 binds chromatin to coordinately control endoreduplication and chromatin structure and to allow the expression of genes required for cell elongation.* 1694

<sup>[W]</sup>Distribution of Transglutaminase in Pear Pollen Tubes in Relation to Cytoskeleton and Membrane Dynamics. *Stefano Del Duca, Claudia Faleri, Rosa Anna Iorio, Mauro Cresti, Donatella Serafini-Fracassini, and Giampiero Cai*

*Distribution of a cell wall enzyme in pollen depends both on actin filaments and membrane trafficking.* 1706

<sup>[W]</sup>The Rab GTPase RabG3b Positively Regulates Autophagy and Immunity-Associated Hypersensitive Cell Death in Arabidopsis. *Soon Il Kwon, Hong Joo Cho, Sung Ryul Kim, and Ohkmae K. Park*

*A Rab GTPase protein connects autophagy with plant immunity-triggered hypersensitive response and programmed cell death.* 1722

<sup>[W]</sup><sup>[OA]</sup>Time-Resolved Fluorescence Imaging Reveals Differential Interactions of N-Glycan Processing Enzymes across the Golgi Stack in *Planta*. *Jennifer Schoberer, Eva Liebming, Stanley W. Botchway, Richard Strasser, and Chris Hawes*

*The biophysical technique of in planta FRET-FLIM provides evidence for the existence of homo- and heteromeric N-glycan processing enzyme complexes, which are predominantly formed between cis- and medial-Golgi enzymes.* 1737

<sup>[C]</sup><sup>[W]</sup>AtMMS21, an SMC5/6 Complex Subunit, Is Involved in Stem Cell Niche Maintenance and DNA Damage Responses in Arabidopsis Roots. *Panglian Xu, Dongke Yuan, Ming Liu, Chunxin Li, Yiyang Liu, Shengchun Zhang, Nan Yao, and Chengwei Yang*

*AtMMS21 acts in double-strand break amelioration and stem cell niche maintenance during Arabidopsis root development.* 1755

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[W]Traffic of Human  $\alpha$ -Mannosidase in Plant Cells Suggests the Presence of a New Endoplasmic Reticulum-to-Vacuole Pathway without Involving the Golgi Complex. *Francesca De Marchis, Michele Bellucci, and Andrea Pompa*

*Noncanonical protein traffic from the endoplasmic reticulum to the vacuole may bypass the Golgi complex altogether.* 1769

[C][OA]Chloroplast DNA Replication Is Regulated by the Redox State Independently of Chloroplast Division in *Chlamydomonas reinhardtii*. *Yukihiro Kabeya and Shin-ya Miyagishima*

*Chloroplast DNA replication is regulated by the redox state in the cell, which is sensed by the chloroplast nucleoids in Chlamydomonas reinhardtii.* 2102

## ECOPHYSIOLOGY AND SUSTAINABILITY

[W][OA]Transcriptome Responses to Combinations of Stresses in Arabidopsis. *Simon Rasmussen, Pankaj Barah, Maria Cristina Suarez-Rodriguez, Simon Bressendorff, Pia Friis, Paolo Costantino, Atle M. Bones, Henrik Bjørn Nielsen, and John Mundy*

*In Arabidopsis, the response of the majority of the genes cannot be predicted from single stress experiments and only a small fraction of the genes have potential antagonistic responses, indicating that plants have evolved to cope with combinations of stresses and therefore may be bred to endure them.* 1783

[W]LESION SIMULATING DISEASE1, ENHANCED DISEASE SUSCEPTIBILITY1, and PHYTOALEXIN DEFICIENT4 Conditionally Regulate Cellular Signaling Homeostasis, Photosynthesis, Water Use Efficiency, and Seed Yield in Arabidopsis. *Weronika Wituszyńska, Ireneusz Ślesak, Sandy Vanderauwera, Magdalena Szechyńska-Hebda, Andrzej Kornaś, Katrien Van Der Kelen, Per Mühlenbock, Barbara Karpińska, Sebastian Maćkowski, Frank Van Breusegem, and Stanisław Karpiński*

*Gene functions should be studied not only under stable laboratory conditions, but also in the environment abounding in multiple stresses.* 1795

[W]Introgression of Novel Traits from a Wild Wheat Relative Improves Drought Adaptation in Wheat. *Dante F. Placido, Malachy T. Campbell, Jing J. Folsom, Xinping Cui, Greg R. Kruger, P. Stephen Baenziger, and Harkamal Walia*

*Agropyron elongatum introgression into bread wheat (Triticum aestivum) improves root traits for drought adaptation.* 1806

[W][OA]In Vivo Visualizations of Drought-Induced Embolism Spread in *Vitis vinifera*. *Craig Robert Brodersen, Andrew Joseph McElrone, Brendan Choat, Eric Franklin Lee, Kenneth Andrew Shackel, and Mark Allen Matthews*

*Time-lapse x-ray tomography uncovers the importance of intervessel connections in the xylem network in drought-induced embolism.* 1820

## GENES, DEVELOPMENT, AND EVOLUTION

[C][W][OA]A Developmental Transcriptional Network for Maize Defines Coexpression Modules. *Gregory S. Downs, Yong-Mei Bi, Joseph Colasanti, Wenqing Wu, Xi Chen, Tong Zhu, Steven J. Rothstein, and Lewis N. Lukens*

*Analyzing transcript abundance between tissues and during development identifies sets of coexpressed genes and related transcriptional controls.* 1830

[W][OA]Prevalent Role of Gene Features in Determining Evolutionary Fates of Whole-Genome Duplication Duplicated Genes in Flowering Plants. *Wen-kai Jiang, Yun-long Liu, En-hua Xia, and Li-zhi Gao*

*Some gene features, including evolution rate and gene structural complexity, are highly correlated to a gene's evolutionary fate after whole-genome duplication.* 1844

[W][OA]Oleosin of Subcellular Lipid Droplets Evolved in Green Algae. *Nan-Lan Huang, Ming-Der Huang, Tung-Ling L. Chen, and Anthony H.C. Huang*

*Oleosin, the surface structural protein on plant seed oil bodies, evolved in green algae in which the oleosin genes have weak but cell/development-specific expression.* 1862

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[W] Widespread Long Noncoding RNAs as Endogenous Target Mimics for MicroRNAs in Plants. *Hua-Jun Wu, Zhi-Min Wang, Meng Wang, and Xiu-Jie Wang*

*A computational method systematically identifies intergenic or noncoding gene-originated target mimics (eTMs) for 20 conserved microRNAs in Arabidopsis and rice and validates the biological functions of some eTMs.*

1875

[C][W][IOA] A Role for MORE AXILLARY GROWTH1 (MAX1) in Evolutionary Diversity in Strigolactone Signaling Upstream of MAX2. *Richard J. Challis, Jo Hepworth, Céline Mouchel, Richard Waites, and Ottoline Leyser*

*Phylogenetic and functional analysis of strigolactone pathway genes across the plant kingdom suggests considerable promiscuity in events upstream allowing for signal diversity and its later refinement.*

1885

[C][W][IOA] Spatiotemporal Seed Development Analysis Provides Insight into Primary Dormancy Induction and Evolution of the *Lepidium* DELAY OF GERMINATION1 Genes. *Kai Graeber, Antje Voegele, Annette Büttner-Mainik, Katja Sperber, Klaus Mummenhoff, and Gerhard Leubner-Metzger*

*Expression of a set of related proteins in Arabidopsis and its relative *Lepidium papillosum* (Brassicaceae) precede the onset of seed dormancy.*

1903

[W][IOA] Potential Functional Replacement of the Plastidic Acetyl-CoA Carboxylase Subunit (*accD*) Gene by Recent Transfers to the Nucleus in Some Angiosperm Lineages. *Mathieu Rousseau-Gueutin, Xun Huang, Emily Higginson, Michael Ayliffe, Anil Day, and Jeremy N. Timmis*

*Functional transfer of a chloroplast gene to the nucleus of Campanulaceae species is a remarkable example of the processes underpinning endosymbiotic evolution.*

1918

[W][IOA] Jasmonate Controls Leaf Growth by Repressing Cell Proliferation and the Onset of Endoreduplication while Maintaining a Potential Stand-By Mode. *Sandra Noir, Moritz Bömer, Naoki Takahashi, Takashi Ishida, Tjir-Li Tsui, Virginia Balbi, Hugh Shanahan, Keiko Sugimoto, and Alessandra Devoto*

*The plant hormone jasmonate inhibits leaf growth by delaying the switch from the mitotic cell cycle to the endoreduplication cycle and maintains the cell in a stand-by mode but ready-to-go after the stress.*

1930

[W][IOA] Early Induction of Apple Fruitlet Abscission Is Characterized by an Increase of Both Isoprene Emission and Abscisic Acid Content. *Giulia Eccher, Alessandro Botton, Mariano Dimauro, Andrea Boschetti, Benedetto Ruperti, and Angelo Ramina*

*Isoprene is an early marker of apple fruitlet abscission induction and its emission is correlated with the levels of bioactive abscisic acid and the activation of the abscission zone.*

1952

[W][IOA] Rice *LHS1/OsMADS1* Controls Floret Meristem Specification by Coordinated Regulation of Transcription Factors and Hormone Signaling Pathways. *Imtiyaz Khanday, Shri Ram Yadav, and Usha Vijayraghavan*

*Integration of transcriptional and signaling pathways promote rice floret meristem specification and organ development.*

1970

[C][W][IOA] AGAMOUS-Like15 Promotes Somatic Embryogenesis in Arabidopsis and Soybean in Part by the Control of Ethylene Biosynthesis and Response. *Qiaolin Zheng, Yumei Zheng, and Sharyn E. Perry*

*The MADS domain transcription factor AGL15 promotes somatic embryogenesis in part through the control of ethylene biosynthesis and response in Arabidopsis and soybean.*

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## MEMBRANES, TRANSPORT, AND BIOENERGETICS

[C][W] A *Nostoc punctiforme* Sugar Transporter Necessary to Establish a Cyanobacterium-Plant Symbiosis. *Martin Ekman, Silvia Picossi, Elsie L. Campbell, John C. Meeks, and Enrique Flores*

*The major facilitator superfamily GlcP glucose permease of the symbiont cyanobacterium *Nostoc punctiforme* is necessary for infection of its plant partner, the hornwort *Anthoceros punctatus*.*

1984

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- [W][OA] A Major Latex-Like Protein Is a Key Factor in Crop Contamination by Persistent Organic Pollutants. Hideyuki Inui, Mami Sawada, Junya Goto, Kiyoshi Yamazaki, Noriko Kodama, Hiroki Tsuruta, and Heesoo Eun  
*A latex-like protein binds and transports polychlorinated biphenyls into the aerial part of plants.* 2128
- SIGNALING AND RESPONSE**
- [C][W][OA] Identification of Genes in *Thuja plicata* Foliar Terpenoid Defenses. Adam J. Foster, Dawn E. Hall, Leanne Mortimer, Shelley Abercromby, Regine Gries, Gerhard Gries, Jörg Bohlmann, John Russell, and Jim Mattsson  
*Transcriptome profiling of foliage with and without resin glands identifies candidate gene products in thujone biosynthesis.* 1993
- [C][W][OA] Disease Resistance Gene-Induced Growth Inhibition Is Enhanced by *rcd1* Independent of Defense Activation in Arabidopsis. Ying Zhu, Baijuan Du, Jun Qian, Baohong Zou, and Jian Hua  
*Growth inhibition induced by a disease resistance gene is uncoupled from plant defense activation.* 2005
- [C][W] The Epiphytic Fungus *Pseudozyma aphidis* Induces Jasmonic Acid- and Salicylic Acid/Nonexpressor of PR1-Independent Local and Systemic Resistance. Kobi Buxdorf, Ido Rahat, Aviva Gafni, and Maggie Levy  
*An epiphytic fungus induces plant resistance against pathogens.* 2014
- [W] The Anticipation of Danger: Microbe-Associated Molecular Pattern Perception Enhances AtPep-Triggered Oxidative Burst. Pascale Flury, Dominik Klauser, Birgit Schulze, Thomas Boller, and Sebastian Bartels  
*Microbial elicitors and the plant defense hormone jasmonic acid differentially modulates the plant's innate immune response.* 2023
- [C][W][OA] Identification of a Dual-Targeted Protein Belonging to the Mitochondrial Carrier Family That Is Required for Early Leaf Development in Rice. Jiming Xu, Jian Yang, Zhongchang Wu, Huili Liu, Fangliang Huang, Yunrong Wu, Chris Carrie, Reena Narsai, Monika Murcha, James Whelan, and Ping Wu  
*A novel mitochondrial carrier protein is required for early leaf development in rice.* 2036
- [C][W][OA] Phosphorylation of HopQ1, a Type III Effector from *Pseudomonas syringae*, Creates a Binding Site for Host 14-3-3 Proteins. Fabian Giska, Małgorzata Lichocka, Marcin Piechocki, Michał Dadlez, Elmon Schmelzer, Jacek Hennig, and Magdalena Krzymowska  
*A pathogen effector protein undergoes specific phosphorylation and associates with host 14-3-3 proteins, which affects its subcellular distribution and stability.* 2049
- [C][W][OA] The *Pseudomonas syringae* Effector HopQ1 Promotes Bacterial Virulence and Interacts with Tomato 14-3-3 Proteins in a Phosphorylation-Dependent Manner. Wei Li, Koste A. Yadeta, James Mitch Elmore, and Gitta Coaker  
*A bacterial effector is delivered into plant cells during infection, is phosphorylated, and binds plant 14-3-3 proteins in a phosphorylation-dependent manner.* 2062
- [W][OA] Interplay between Heat Shock Proteins HSP101 and HSA32 Prolongs Heat Acclimation Memory Posttranscriptionally in Arabidopsis. Ting-ying Wu, Yu-ting Juan, Yang-hsin Hsu, Sze-hsien Wu, Hsiu-ting Liao, Raymond W.M. Fung, and Yee-yung Charng  
*Positive feedback between two heat shock proteins, and the consequent delayed degradation of one, extends tolerance to temperature extremes.* 2075
- [W][OA] Conditional Involvement of CONSTITUTIVE PHOTOMORPHOGENIC1 in the Degradation of Phytochrome A. Dimitry Debrieux, Martine Trevisan, and Christian Fankhauser  
*Light-induced reduction of phyA levels depends on cullin1, while COP1 only regulates this process in specific conditions.* 2136

<sup>[C][W][OA]</sup> Heterotrimeric G Proteins Serve as a Converging Point in Plant Defense Signaling Activated by Multiple Receptor-Like Kinases. Jinman Liu, Pingtao Ding, Tongjun Sun, Yukino Nitta, Oliver Dong, Xingchuan Huang, Wei Yang, Xin Li, José Ramón Botella, and Yuelin Zhang

*Arabidopsis heterotrimeric G proteins function as a converging point of plant defense signaling by mediating responses initiated by multiple receptor-like kinases, which may fulfill equivalent roles to GPCRs in fungi and animals.*

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<sup>[C][W]</sup> Lipoygenase6-Dependent Oxylipin Synthesis in Roots Is Required for Abiotic and Biotic Stress Resistance of Arabidopsis. Wiebke Grebner, Nadja E. Stingl, Ayla Oenel, Martin J. Mueller, and Susanne Berger

*A defect in lipoygenase6 abolishes production of jasmonates in roots and renders plants more susceptible to drought and crustacean feeding.*

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## SYSTEMS AND SYNTHETIC BIOLOGY

<sup>[C][W][OA]</sup> Protein-Coding cis-Natural Antisense Transcripts Have High and Broad Expression in Arabidopsis. Shuhua Zhan and Lewis Lukens

*Protein-coding overlapping genes in Arabidopsis have unexpectedly high levels and breadths of expression.*

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## CORRECTIONS

Characterization of a Viral Synergism in the Monocot *Brachypodium distachyon* Reveals Distinctly Altered Host Molecular Processes Associated with Disease. Madadi K.K. and Scholthof K.-B.G.

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## RETRACTIONS

Crop Improvement through Modification of the Plant's Own Genome. Rommens C.M., Humara J.M., Ye J., Yan H., Richael C., Zhang L., Perry R., and Swords K.

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## ADDENDA

Plant-Derived Transfer DNAs. Rommens C.M., Bougri O., Yan H., Humara J.M., Owen J., Swords K., and Ye J.

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<sup>[C]</sup> Some figures in this article are displayed in color online but in black and white in the print edition.

<sup>[W]</sup> Indicates Web-only data.

<sup>[OA]</sup> Open Access articles can be viewed online without a subscription.