

The electronic form of this issue, available as of November 6, 2014, at [www.plantphysiol.org](http://www.plantphysiol.org), is considered the journal of record.

**On the Cover:** Weedy or red rice (*Oryza sativa*) infests cultivated rice fields worldwide, reducing yields and causing great economic losses. In recent years, use of herbicide resistant (HR) rice cultivars known as Clearfield rice has increased greatly in the United States, providing an option to control weedy rice using imidazolinone herbicides. However, the impact of HR cultivated rice on the evolutionary dynamics of U.S. weedy rice has not been explored. In this issue, Burgos et al. (pp. 1208–1220) characterize the morphology and population structure of weedy rice that has acquired the herbicide resistance trait, sampled from cultivated fields with a history of Clearfield use. Great morphological variation is seen in HR weedy rice, with some plants exhibiting reduced weediness in terms of reduced seed dormancy, later flowering, and reduced seed shattering. A significant portion of the local rice crop genome is introgressed into HR weedy rice, though crop-weed introgression occurred very rarely prior to Clearfield use. Whereas the majority of weedy rice in the United States prior to Clearfield use had straw-colored hulls, black-colored hulls predominate among contemporary HR weedy rice. Genotyping-by-sequencing data confirm that the evolution of HR weedy rice is a consequence of preferential hybridization between cultivated rice and historical black-hull weedy populations. The cover shows a cultivated rice field in Arkansas with at least two seasons of Clearfield use, which is being sampled for escaped weedy rice plants. The inset is a straw-hull weedy rice plant sampled from the field. Cover image credits: David Gealy, Nilda Burgos (photography) and Ana Caicedo (design).

## FOCUS ON WEED CONTROL

### EDITORIAL

Focus on Weed Control. *Robert Edwards and Matthew Hannah* 1087

### UPDATES

Natural Compounds as Next-Generation Herbicides. *Franck E. Dayan and Stephen O. Duke*

*Natural products are an important resource in the discovery of herbicides.* 1090

Metabolism-Based Herbicide Resistance and Cross-Resistance in Crop Weeds: A Threat to Herbicide Sustainability and Global Crop Production. *Qin Yu and Stephen Powles*

*An important, but often unrecognized issue is the metabolic capacity of crop weeds to resist herbicides which poses a threat to herbicide sustainability and world crop production.* 1106

Herbicides as Weed Control Agents: State of the Art: I. Weed Control Research and Safener Technology: The Path to Modern Agriculture. *Hansjoerg Kraehmer, Bernd Laber, Chris Rosinger, and Arno Schulz*

*The development of weed control and safeners and of screening tools to find them has evolved substantially over the past 100 years.* 1119

<sup>[C]</sup>Herbicides as Weed Control Agents: State of the Art: II. Recent Achievements. *Hansjoerg Kraehmer, Andreas van Almsick, Roland Beffa, Hansjoerg Dietrich, Peter Eckes, Erwin Hacker, Ruediger Hain, Harry John Streck, Hermann Stuebler, and Lothar Willms*

*Herbicide discovery has faced significant challenges over the past few decades, and weed control innovations are urgently required.* 1132

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Use of Multicopy Transposons Bearing Unfitness Genes in Weed Control: Four Example Scenarios.

Jonathan Gressel and Avraham A. Levy

*Multicopy transposons could disseminate potentially lethal/unfit genes in weed populations, especially when coupled with positive selection to facilitate rapid dissemination.*

1221

RESEARCH ARTICLES

[W][OPEN]Dual Function of the Cytochrome P450 CYP76 Family from *Arabidopsis thaliana* in the Metabolism of Monoterpenols and Phenylurea Herbicides. René Höfer, Benoît Boachon, Hugues Renault, Carole Gavira, Laurence Miesch, Juliana Iglesias, Jean-François Ginglinger, Lionel Allouche, Michel Miesch, Sebastien Grec, Romain Larbat, and Danièle Werck-Reichhart

*Fast diversification and versatility of a subfamily of cytochrome P450 enzymes in Brassicaceae has been important in their metabolism of both monoterpenols and herbicides.*

1149

[W][OPEN]Broad 4-Hydroxyphenylpyruvate Dioxygenase Inhibitor Herbicide Tolerance in Soybean with an Optimized Enzyme and Expression Cassette. Daniel L. Siehl, Yumin Tao, Henrik Albert, Yuxia Dong, Matthew Heckert, Alfredo Madrigal, Brishette Lincoln-Cabatu, Jian Lu, Tamara Fenwick, Ericka Bermudez, Marian Sandoval, Caroline Horn, Jerry M. Green, Theresa Hale, Peggy Pagano, Jenna Clark, Ingrid A. Udranszky, Nancy Rizzo, Timothy Bourett, Richard J. Howard, David H. Johnson, Mark Vogt, Goke Akinsola, and Linda A. Castle

*A modified native promoter, dual protein localization, and an evolved desensitized maize protein variant enables field tolerance in soybean to multiple herbicides.*

1162

[C][W][OPEN]Indaziflam Herbicidal Action: A Potent Cellulose Biosynthesis Inhibitor. Chad Brabham, Lei Lei, Ying Gu, Jozsef Stork, Michael Barrett, and Seth DeBolt

*Indaziflam is a cellulose biosynthesis inhibitor that has a different mechanism of action than previously characterized inhibitors and causes an increase in CELLULOSE SYNTHASE A particle density and reduced, but not paused, velocity at the plasma membrane focal plane.*

1177

[C][W][OPEN]De Novo Assembly and Characterization of the Transcriptome of the Parasitic Weed Dodder Identifies Genes Associated with Plant Parasitism. Aashish Ranjan, Yasunori Ichihashi, Moran Farhi, Kristina Zumstein, Brad Townsley, Rakefet David-Schwartz, and Neelima R. Sinha

*Transcriptional dynamics during parasitism in the parasitic weed *Cuscuta pentagona* reveals increased expression of genes encoding transporters and stimulus response regulators, and a decrease in the expression of genes encoding photosynthetic proteins.*

1186

[W][OPEN]Tandem Amplification of a Chromosomal Segment Harboring 5-Enolpyruvylshikimate-3-Phosphate Synthase Locus Confers Glyphosate Resistance in *Kochia scoparia*. Mithila Jugulam, Kindsey Niehues, Amar S. Godar, Dal-Hoe Koo, Tatiana Danilova, Bernd Friebe, Sunish Sehgal, Vijay K. Varanasi, Andrew Wiersma, Philip Westra, Phillip W. Stahlman, and Bikram S. Gill

*Genes encoding enolpyruvylshikimate phosphate synthase are tandemly arranged on chromosomes of field-evolved glyphosate-resistant *Kochia scoparia*.*

1200

[W][OPEN]The Impact of Herbicide-Resistant Rice Technology on Phenotypic Diversity and Population Structure of United States Weedy Rice. Nilda Roma Burgos, Vijay Singh, Te Ming Tseng, Howard Black, Nelson D. Young, Zhongyun Huang, Katie E. Hyma, David R. Gealy, and Ana L. Caicedo

*Use of herbicide-resistant rice cultivars in the United States has led to the emergence of herbicide-resistant weedy rice formed predominantly by hybridization of cultivars with historical weeds characterized by black hulls and awns.*

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[C][W][OPEN] A Novel Rice Cytochrome P450 Gene, *CYP72A31*, Confers Tolerance to Acetolactate Synthase-Inhibiting Herbicides in Rice and Arabidopsis. Hiroaki Saika, Junko Horita, Fumio Taguchi-Shiobara, Satoko Nonaka, Ayako Nishizawa-Yokoi, Satoshi Iwakami, Kiyosumi Hori, Takashi Matsumoto, Tsuyoshi Tanaka, Takeshi Itoh, Masahiro Yano, Koichiro Kaku, Tsutomu Shimizu, and Seiichi Toki

*A novel cytochrome P450 monooxygenase is involved in multiple-herbicide detoxification and could be useful in herbicide development and molecular breeding in crops.*

1232

[C][W][OPEN] De Novo Genome Assembly of the Economically Important Weed Horseweed Using Integrated Data from Multiple Sequencing Platforms. Yanhui Peng, Zhao Lai, Thomas Lane, Madhugiri Nageswara-Rao, Miki Okada, Marie Jasieniuk, Henriette O'Geen, Ryan W. Kim, R. Douglas Sammons, Loren H. Rieseberg, and C. Neal Stewart

*De novo genome assembly and genomic resources of horseweed will be useful to understand the genetic and molecular bases of weediness.*

1241

[W] In Vivo <sup>31</sup>P-Nuclear Magnetic Resonance Studies of Glyphosate Uptake, Vacuolar Sequestration, and Tonoplast Pump Activity in Glyphosate-Resistant Horseweed. Xia Ge, D. André d'Avignon, Joseph J.H. Ackerman, and R. Douglas Sammons

*Rapid vacuole sequestration, the glyphosate resistance mechanism observed in glyphosate-resistant horseweed, is associated with plasma membrane and tonoplast ATP-binding cassette transporters.*

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## REGULAR ISSUE

### ON THE INSIDE

On the Inside. Peter V. Minorsky

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### BREAKTHROUGH TECHNOLOGIES

[C][W][OPEN] Pico Gauges for Minimally Invasive Intracellular Hydrostatic Pressure Measurements. Jan Knoblauch, Daniel L. Mullendore, Kaare H. Jensen, and Michael Knoblauch

*Pico gauges allow fast, minimally invasive intracellular pressure measurements in cells of all sizes and over all ranges of pressure.*

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### RESEARCH REPORTS

[C][W] Rapid Identification of a Natural Knockout Allele of *ARMADILLO REPEAT-CONTAINING KINESIN1* That Causes Root Hair Branching by Mapping-By-Sequencing. Louai Rishmawi, Hequan Sun, Korbinian Schneeberger, Martin Hülskamp, and Andrea Schrader

*Mapping-by-sequencing identifies a naturally occurring variant of a kinesin that causes root hairs to branch.*

1280

### SCIENTIFIC CORRESPONDENCE

[W] Targeted Mutagenesis of the Tomato PROCERA Gene Using Transcription Activator-Like Effector Nucleases. Vai S. Lor, Colby G. Starker, Daniel F. Voytas, David Weiss, and Neil E. Olszewski

*Transcription activator-like effector nucleases successfully generate a heritable tomato mutant.*

1288

Efficient Gene Editing in Tomato in the First Generation Using the Clustered Regularly Interspaced Short Palindromic Repeats/CRISPR-Associated9 System. Christopher Brooks, Vladimir Nekrasov, Zachary B. Lippman, and Joyce Van Eck

*The CRISPR/Cas9 system is highly efficient at generating targeted mutations in stable transgenic tomato plants, and homozygous deletions of a desired size can be created in the first generation.*

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## RESEARCH ARTICLES

### BIOCHEMISTRY AND METABOLISM

[C][W][OPEN] Pepper Mitochondrial *FORMATE DEHYDROGENASE1* Regulates Cell Death and Defense Responses against Bacterial Pathogens. *Du Seok Choi, Nak Hyun Kim, and Byung Kook Hwang*

*Formate dehydrogenase contributes to defense-related hormone regulation and defense gene activation, ultimately leading to hypersensitive cell death and defense response to bacterial pathogens.* 1298

[W] Mitochondrial Alternative Oxidase Maintains Respiration and Preserves Photosynthetic Capacity during Moderate Drought in *Nicotiana tabacum*. *Keshav Dahal, Jia Wang, Greg D. Martyn, Farkhunda Rahimy, and Greg C. Vanlerberghe*

*Alternative oxidase reduces feedback on the photosynthetic apparatus that can otherwise limit photosynthetic capacity during moderate drought.* 1560

[W][OPEN] Seed-Specific Expression of a Feedback-Insensitive Form of *CYSTATHIONINE- $\gamma$ -SYNTHASE* in *Arabidopsis* Stimulates Metabolic and Transcriptomic Responses Associated with Desiccation Stress. *Hagai Cohen, Hadasa Israeli, Ifat Matityahu, and Rachel Amir*

*Methionine metabolism in Arabidopsis seeds is strongly associated with stress-related metabolites and transcripts, suggesting that its content leads to desiccation stress during seed development.* 1575

### CELL BIOLOGY

[W][OPEN] Heterodimeric Capping Protein from *Arabidopsis* Is a Membrane-Associated, Actin-Binding Protein. *Jose C. Jimenez-Lopez, Xia Wang, Simeon O. Kotchoni, Shanjin Huang, Daniel B. Szymanski, and Christopher J. Staiger*

*A key regulator of the actin cytoskeleton is shown to be associated with endosomal membranes.* 1312

[W][OPEN] Peroxisomal Ubiquitin-Protein Ligases Peroxin2 and Peroxin10 Have Distinct But Synergistic Roles in Matrix Protein Import and Peroxin5 Retrotranslocation in *Arabidopsis*. *Sarah E. Burkhart, Yun-Ting Kao, and Bonnie Bartel*

*Two Arabidopsis membrane peroxins contribute to peroxisomal matrix protein import via distinct roles in recycling and degrading a matrix receptor protein.* 1329

[W][OPEN] Association of the P6 Protein of *Cauliflower mosaic virus* with Plasmodesmata and Plasmodesmal Proteins. *Andres Rodriguez, Carlos A. Angel, Lindy Lutz, Scott M. Leisner, Richard S. Nelson, and James E. Scholz*

*Inclusion bodies of Cauliflower mosaic virus function in delivery of virions to the plasmodesma for transport to adjacent cells.* 1345

[C][W][OPEN] *Arabidopsis* Myosin XI: A Motor Rules the Tracks. *Chao Cai, Jessica L. Henty-Ridilla, Daniel B. Szymanski, and Christopher J. Staiger*

*A myosin triple knockout mutant has altered cytoskeletal organization and single filament turnover.* 1359

### ECOPHYSIOLOGY AND SUSTAINABILITY

[C][W] Transient Silencing of *CHALCONE SYNTHASE* during Fruit Ripening Modifies Tomato Epidermal Cells and Cuticle Properties. *Laura España, José A. Heredia-Guerrero, José J. Reina-Pinto, Rafael Fernández-Muñoz, Antonio Heredia, and Eva Domínguez*

*Alteration of flavonoid accumulation during tomato fruit ripening affects cuticle wax accumulation, biomechanics, water permeability, and the molecular arrangement of cuticle components.* 1371

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[W][OPEN] Capturing Arabidopsis Root Architecture Dynamics with ROOT-FIT Reveals Diversity in Responses to Salinity. Magdalena M. Julkowska, Huub C.J. Hoefsloot, Selena Mol, Richard Feron, Gert-Jan de Boer, Michel A. Haring, and Christa Testerink

Natural variation in the dynamic response to salt stress of the Arabidopsis root system can be divided between four distinct strategies.

1387

[W][OPEN] Variation in Sulfur and Selenium Accumulation Is Controlled by Naturally Occurring Isoforms of the Key Sulfur Assimilation Enzyme ADENOSINE 5'-PHOSPHOSULFATE REDUCTASE2 across the Arabidopsis Species Range. Dai-Yin Chao, Patrycja Baraniecka, John Danku, Anna Koprivova, Brett Lahner, Hongbing Luo, Elena Yakubova, Brian Dilkes, Stanislav Kopriva, and David E. Salt

The ability of Arabidopsis to assimilate and accumulate sulfur varies widely across the species range and is controlled in part by diversity in a key reductase enzyme.

1593

## GENES, DEVELOPMENT, AND EVOLUTION

[W][OPEN] Neofunctionalization of Duplicated *Tic40* Genes Caused a Gain-of-Function Variation Related to Male Fertility in *Brassica oleracea* Lineages. Xiaoling Dun, Wenhao Shen, Kaining Hu, Zhengfu Zhou, Shengqian Xia, Jing Wen, Bin Yi, Jinxiong Shen, Chaozhi Ma, Jinxing Tu, Tingdong Fu, and Ulf Lagercrantz

Divergent duplicated genes in the *Brassica oleracea* gain a novel function that could restore the fertility of a *Brassica napus* male-sterile mutant.

1403

## MEMBRANES, TRANSPORT, AND BIOENERGETICS

[W][OPEN] The Mitochondrial Protein Import Component, TRANSLOCASE OF THE INNER MEMBRANE17-1, Plays a Role in Defining the Timing of Germination in Arabidopsis. Yan Wang, Simon R. Law, Aneta Ivanova, Olivier van Aken, Szymon Kubiszewski-Jakubiak, Vindya Uggalla, Margaretha van der Merwe, Owen Duncan, Reena Narsai, James Whelan, and Monika W. Murcha

A mitochondrial import protein determines the timing of mitochondrial biogenesis during germination.

1420

[W][OPEN] Inducible Knockdown of MONOGALACTOSYLDIACYLGLYCEROL SYNTHASE1 Reveals Roles of Galactolipids in Organelle Differentiation in Arabidopsis Cotyledons. Sho Fujii, Koichi Kobayashi, Yuki Nakamura, and Hajime Wada

Biosynthesis of the major thylakoid membrane lipids coordinates the differentiation of chloroplasts with peroxisomes and mitochondria during the greening of Arabidopsis cotyledons.

1436

[C][W][OPEN] Elucidating the Role of Transport Processes in Leaf Glucosinolate Distribution. Svend Roesen Madsen, Carl Erik Olsen, Hussam Hassan Nour-Eldin, and Barbara Ann Halkier

Within-leaf allocation of glucosinolates implicates an intracellular route from site of biosynthesis to peripheral leaf layers.

1450

[W] Grain setting defect1, Encoding a Remorin Protein, Affects the Grain Setting in Rice through Regulating Plasmodesmatal Conductance. Jinshan Gui, Chang Liu, Junhui Shen, and Laigeng Li

A remorin protein plays a role in regulating photoassimilate translocation by modulating plasmodesmata permeability in rice.

1463

[C][W][OPEN] The Role of Plasma Membrane Aquaporins in Regulating the Bundle Sheath-Mesophyll Continuum and Leaf Hydraulics. Nir Sade, Arava Shatil-Cohen, Ziv Attia, Christophe Maurel, Yann Boursiac, Gilor Kelly, David Granot, Adi Yaaran, Stephen Lerner, and Menachem Moshelion

Silencing aquaporins of the xylem bundle sheath cells reduces leaf hydraulic conductance and affects the water permeability of adjacent mesophyll cells, suggesting a bundle sheath-mesophyll feed-forward hydraulic control.

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## SIGNALING AND RESPONSE

[C][W][OPEN] Identification of Phosphatin, a Drug Alleviating Phosphate Starvation Responses in Arabidopsis. Carole Arnaud, Mathilde Clément, Marie-Christine Thibaud, H  l  ne Javot, Serge Chiarenza, Etienne Delannoy, Julia Revol, Paul Soreau, Sandrine Balzergue, Maryse A. Block, Eric Mar  chal, Thierry Desnos, and Laurent Nussaume

*A family of drugs reduces the growth response, the lipid modifications, and the pattern of gene expression triggered by inorganic phosphate starvation.*

1479

[W][OPEN] Enhanced Oxidative Stress Resistance through Activation of a Zinc Deficiency Transcription Factor in *Brachypodium distachyon*. Kira M. Glover-Cutter, Stephen Alderman, James E. Dombrowski, and Ruth C. Martin

*A zinc deficiency transcription factor moderates oxidative stress resistance.*

1492

[C][W] The Receptor Kinase IMPAIRED OOMYCETE SUSCEPTIBILITY1 Attenuates Abscisic Acid Responses in Arabidopsis. Sophie Hok, Val  rie Allasia, Emilie Andrio, Elodie Naessens, Elsa Ribes, Franck Panabi  res, Agn  s Attard, Nicolas Ris, Mathilde Cl  ment, Xavier Barlet, Yves Marco, Erwin Grill, Ruth Eichmann, Corina Weis, Ralph H  ckelhoven, Alexandra Ammon, Jutta Ludwig-M  ller, Lars M. Voll, and Harald Keller

*An Arabidopsis receptor-like kinase negatively regulates abscisic acid signaling and promotes infection by filamentous (hemi)biotrophs.*

1506

[W][OPEN] Arabidopsis PHOSPHOTYROSYL PHOSPHATASE ACTIVATOR Is Essential for PROTEIN PHOSPHATASE 2A Holoenzyme Assembly and Plays Important Roles in Hormone Signaling, Salt Stress Response, and Plant Development. Jian Chen, Rongbin Hu, Yinfeng Zhu, Guoxin Shen, and Hong Zhang

*An Arabidopsis phosphotyrosyl phosphatase activator is essential for assembly of a protein phosphatase and plays important roles in hormone signaling, salt stress response, and plant development.*

1519

[W][OPEN] PINOID AGC Kinases Are Necessary for Phytochrome-Mediated Enhancement of Hypocotyl Phototropism in Arabidopsis. Ken Haga, Ken-ichiro Hayashi, and Tatsuya Sakai

*Phytochrome-mediated phototropic enhancement depends on PINOID family kinases.*

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[C][W] Evolutionary Conserved Function of Barley and Arabidopsis 3-KETOACYL-CoA SYNTHASES in Providing Wax Signals for Germination of Powdery Mildew Fungi. Denise Weidenbach, Marcus Jansen, Rochus B. Franke, Goetz Hensel, Wiebke Weissgerber, Sylwia Ulferts, Irina Jansen, Lukas Schreiber, Viktor Korzun, Rolf Pontzen, Jochen Kumlehn, Klaus Pillen, and Ulrich Schaffrath

*An orthologous pair of genes from barley and Arabidopsis is involved in long-chain fatty acid signaling that is required for germination of conidia from distantly related powdery mildews.*

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[C][W][OPEN] Rice GROWTH UNDER DROUGHT KINASE Is Required for Drought Tolerance and Grain Yield under Normal and Drought Stress Conditions. Venkategowda Ramegowda, Supratim Basu, Arjun Krishnan, and Andy Pereira

*A drought stress-inducible receptor-like kinase is important for plant growth and grain yield in rice.*

1634

[C][W][OPEN] Intergenic Sequence between Arabidopsis Caseinolytic Protease B-Cytoplasmic/Hsp100 and Choline Kinase Genes Functions as a Heat-Inducible Bidirectional Promoter. Ratnesh Chandra Mishra and Anil Grover

*Two Arabidopsis genes with a role in thermotolerance are oriented in a head-to-head manner in the genome and the intergenic region between these genes functions as a heat-inducible bidirectional promoter.*

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## SYSTEMS AND SYNTHETIC BIOLOGY

[W][OPEN] Systematic Phenotypic Screen of Arabidopsis Peroxisomal Mutants Identifies Proteins Involved in  $\beta$ -Oxidation. *Gaëlle Cassin-Ross and Jianping Hu*

*Recently discovered Arabidopsis peroxisomal mutants identify proteins involved in  $\beta$ -oxidation.*

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[C][W][OPEN] Assessing the Metabolic Impact of Nitrogen Availability Using a Compartmentalized Maize Leaf Genome-Scale Model. *Margaret Simons, Rajib Saha, Nardjis Amour, Akhil Kumar, Lenaïg Guillard, Gilles Climent, Martine Miquel, Zhenni Li, Gregory Mouille, Peter J. Lea, Bertrand Hirel, and Costas D. Maranas*

*A cell type- and leaf tissue-specific model provides new insights into nitrogen metabolism in the maize leaf.*

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