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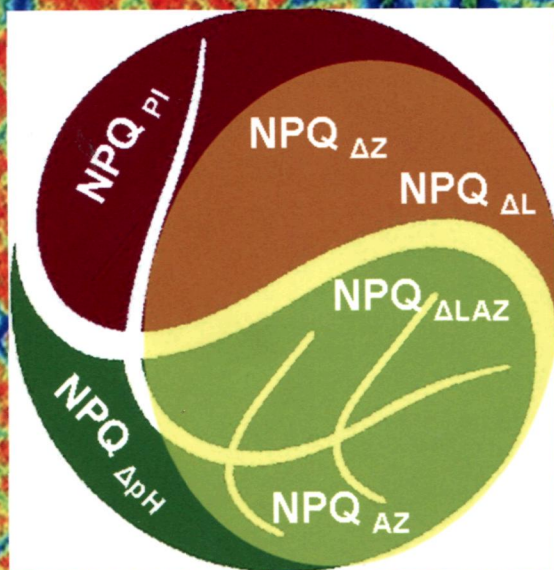
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**Irradiance  
Time**

**~2000  $\mu\text{E}$   
days**

**~20  $\mu\text{E}$   
minutes**

**~200  $\mu\text{E}$   
hours**



**Interacting Photoprotection and Photoinactivation in  
Old Shade Leaves of *Persea americana* (Avocado)**

The electronic form of this issue, available as of February 8, 2013, at [www.plantphysiol.org](http://www.plantphysiol.org), is considered the journal of record.

**On the Cover:** Non-photochemical quenching (NPQ) of chlorophyll fluorescence is a widely accepted indicator of diverse mechanisms that protect the photosynthetic apparatus against excess light and protect PSII reaction centers from photodamage. Old shade leaves of avocado (*Persea americana*) have very low rates of photosynthesis and are very sensitive to photodamage, but they also accumulate high levels of the  $\alpha$ -branch xanthophyll lutein epoxide relative to the more ubiquitous and structurally analogous  $\beta$ -branch xanthophyll violaxanthin. Jia et al. (pp. 836–852) show that with increasing irradiance and/or time the capacities for, and properties of, NPQ are modulated by deepoxidation of these pigments to lutein (L), and to antheraxanthin (A) and zeaxanthin (Z), respectively, within an hour of exposure to sunlight. The cover photo shows a full-size image of the remarkably heterogeneous (green to red = NPQ 0.3–1.6) increase in NPQ after the 2-min exposure of a shade leaf to approximately 5% sunlight in air. Heterogeneity is due to differential stomatal opening and access to CO<sub>2</sub> in adjacent vein-defined areas of the mesophyll (heterobaric anatomy) that produce transient increases in trans-thylakoid  $\Delta$ pH (hereafter termed NPQ <sub>$\Delta$ pH</sub>) during photosynthetic induction. However, the insert (from Fig. 8 in Jia et al.) summarizes the sequential engagement of differentially reversible forms of NPQ associated with these pigments (NPQ<sub>AZ</sub>, NPQ <sub>$\Delta$ LAZ</sub>, NPQ <sub>$\Delta$ L</sub>, and NPQ <sub>$\Delta$ Z</sub>). These forms of photoprotection are insufficient to fully mitigate photodamage in longer sunlight exposures. Independent measurements of the decline in functional fraction of PSII reaction centers suggest that their photoinactivation dominates the most slowly reversible form of NPQ (NPQ<sub>PI</sub>). Chlorophyll fluorescence image provided by Kotaro Takayama. Cover image designed by Barry Osmond.

## ON THE INSIDE

*Peter V. Minorsky*

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## BREAKTHROUGH TECHNOLOGIES

<sup>[C][W]</sup>The Perennial Ryegrass GenomeZipper: Targeted Use of Genome Resources for Comparative Grass Genomics. *Matthias Pfeifer, Mihaela Martis, Torben Asp, Klaus F.X. Mayer, Thomas Lübberstedt, Stephen Byrne, Ursula Frei, and Bruno Studer*

Summary: The GenomeZipper presented here is a model of the perennial ryegrass genome on the basis of conserved synteny to barley, Brachypodium, rice, and sorghum.

571

<sup>[W][OA]</sup>A Noninvasive Platform for Imaging and Quantifying Oil Storage in Submillimeter Tobacco Seed.

*Johannes Fuchs, Thomas Neuberger, Hardy Rolletschek, Silke Schiebold, Thuy Ha Nguyen, Nikolai Borisjuk, Andreas Börner, Gerd Melkus, Peter Jakob, and Ljudmilla Borisjuk*

Summary: This study describes a non-invasive NMR approach that enables counting of seeds inside the intact tobacco capsule, to measure seed sizes, to model the seed interior in three dimensions, to quantify the lipid content, and to visualize lipid gradients.

583

## SCIENTIFIC CORRESPONDENCE

<sup>[C]</sup>CSGRqtl, a Comparative Quantitative Trait Locus Database for Saccharinae Grasses. *Dong Zhang, Hui Guo, Changsoo Kim, Tae-Ho Lee, Jingping Li, Jon Robertson, Xiyin Wang, Zining Wang, and Andrew H. Paterson*

Summary: By aligning QTLs from many populations and several species, this study increases knowledge of the genetic control of agriculturally and developmentally important traits in the Saccharinae clade of grasses, expedites translation of knowledge from better-studied to less-studied species, and facilitates investigation of fundamental questions across the genomes and paleoduplicated “subgenomes” of divergent taxa.

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## RESEARCH ARTICLES

### BIOCHEMISTRY AND METABOLISM

<sup>[W][OA]</sup>Evolution of Conifer Diterpene Synthases: Diterpene Resin Acid Biosynthesis in Lodgepole Pine and Jack Pine Involves Monofunctional and Bifunctional Diterpene Synthases. *Dawn E. Hall, Philipp Zerbe, Sharon Jancsik, Alfonso Lara Quesada, Harpreet Dullat, Lina L. Madilao, Macaire Yuen, and Jörg Bohlmann*

Summary: The biosynthesis of diterpenoid specialized (i.e. secondary) metabolites in conifers is emerging as a modular metabolic network that is built from multiple diterpene synthases and cytochromes P450 of variable functions and activities to produce a diverse and dynamic array of metabolites for plant defense.

600

<sup>[W]</sup>Defense Activated by 9-Lipoxygenase-Derived Oxylipins Requires Specific Mitochondrial Proteins. *Tamara Vellosillo, Verónica Aguilera, Ruth Marcos, Michael Bartsch, Jorge Vicente, Tomas Cascón, Mats Hamberg, and Carmen Castresana*

Summary: 9-lipoxygenase-mediated defense and cell wall repair responses share common signaling processes that require specific mitochondrial proteins.

617

<sup>[W][OA]</sup>Alteration of the Interconversion of Pyruvate and Malate in the Plastid or Cytosol of Ripening Tomato Fruit Invokes Diverse Consequences on Sugar But Similar Effects on Cellular Organic Acid, Metabolism, and Transitory Starch Accumulation. *Sonia Osorio, José G. Vallarino, Marek Szczowka, Shai Ufaz, Vered Tzin, Ruthie Angelovici, Gad Galili, and Alisdair R. Fernie*

Summary: Normal tomato ripening is influenced by alterations on both cytosolic phosphoenolpyruvate carboxykinase and plastidic NADP-malic enzyme. This study provides compelling evidence of their roles in starch biosynthesis, respiration rates, and tricarboxylic acid cycle flux.

628

<sup>[C][W][OA]</sup>The Mitochondrial Folylpolyglutamate Synthetase Gene Is Required for Nitrogen Utilization during Early Seedling Development in Arabidopsis. *Ling Jiang, Yanyan Liu, Hong Sun, Yueting Han, Jinglai Li, Changkun Li, Wenzhu Guo, Hongyan Meng, Sha Li, Yunliu Fan, and Chunyi Zhang*

Summary: The mitochondrial folylpolyglutamate synthetase DFC is involved in nitrogen utilization through its participation in photorespiration during early seedling development in Arabidopsis.

971

### CELL BIOLOGY

<sup>[W][OA]</sup>Acquisition, Conservation, and Loss of Dual-Targeted Proteins in Land Plants. *Lin Xu, Chris Carrie, Simon R. Law, Monika W. Murcha, and James Whelan*

Summary: The dual-targeting ability of proteins arose early in evolution, and although it is conserved in many cases, acquisition and loss still occur.

644

<sup>[C][W][OA]</sup>Rice *GLYCOSYLTRANSFERASE1* Encodes a Glycosyltransferase Essential for Pollen Wall Formation. *Sunok Moon, Sung-Ryul Kim, Guochao Zhao, Jakyung Yi, Youngchul Yoo, Ping Jin, Sang-Won Lee, Ki-hong Jung, Dabing Zhang, and Gynheung An*

Summary: This study elucidates functional roles of Golgi-localized rice Glycosyltransferase1 that is essential for intine construction and pollen maturation.

663

<sup>[W][OA]</sup>Recruitment of Arf1-GDP to Golgi by Glo3p-Type ArfGAPs Is Crucial for Golgi Maintenance and Plant Growth. *Myung Ki Min, Mihue Jang, Myounghui Lee, Junho Lee, Kyungyoung Song, Yongjik Lee, Kwan Yong Choi, David G. Robinson, and Inhwan Hwang*

Summary: Recruitment of GDP-bound Arf1 from the cytosol to the Golgi apparatus by Arf GAP proteins is essential in maintenance of the Golgi apparatus and protein trafficking through the Golgi apparatus.

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[W][OA] Direct Interaction between a Precursor Mature Domain and Transport Component Tha4 during Twin Arginine Transport of Chloroplasts. *Debjani Pal, Kristen Fite, and Carole Dabney-Smith*

Summary: Significant interaction between thylakoid twin arginine transport pathway component Tha4 and a twin arginine transport precursor under transport conditions suggests the point of passage across the membrane for the precursor is membrane protein dependent.

990

## ECOPHYSIOLOGY AND SUSTAINABILITY

[W][OA] Temporal Changes in Allocation and Partitioning of New Carbon as <sup>11</sup>C Elicited by Simulated Herbivory Suggest that Roots Shape Aboveground Responses in Arabidopsis. *Abigail P. Ferrieri, Beverly Agtuca, Heidi M. Appel, Richard A. Ferrieri, and Jack C. Schultz*

Summary: Radiotracer studies reveal how roots can regulate a plant's defensive responses to insect herbivory.

692

[W][OA] An RNA-Seq Transcriptome Analysis of Orthophosphate-Deficient White Lupin Reveals Novel Insights into Phosphorus Acclimation in Plants. *Jamie A. O'Rourke, S. Samuel Yang, Susan S. Miller, Bruna Bucciarelli, Junqi Liu, Ariel Rydeen, Zoltan Bozsoki, Claudia Uhde-Stone, Zheng Jin Tu, Deborah Allan, John W. Gronwald, and Carroll P. Vance*

Summary: Analysis of all the expressed genes in white lupin roots and leaves shows that acclimation to phosphorous deficiency involves changes in root development and modifications in metabolism.

705

[W][OA] Sulfite Reductase Protects Plants against Sulfite Toxicity. *Dmitry Yarmolinsky, Galina Brychkova, Robert Fluhr, and Moshe Sagi*

Summary: Sulfite oxidase, and the key elements of the sulfite network enzymes that include sulfite reductase, UDP-sulfoquinovose synthase,  $\beta$ -mercaptopyruvate sulfurtransferases, and adenosine-5'-phosphosulfate reductase, has a important role in maintaining sulfite homeostasis, where sulfite appears to act as an orchestrating signal molecule.

725

[W][OA] Multiple Roles for UV RESISTANCE LOCUS8 in Regulating Gene Expression and Metabolite Accumulation in Arabidopsis under Solar Ultraviolet Radiation. *Luis O. Morales, Mikael Brosché, Julia Vainonen, Gareth I. Jenkins, Jason J. Wargent, Nina Sipari, Åke Strid, Anders V. Lindfors, Riitta Tegelberg, and Pedro J. Aphalo*

Summary: Under natural sunlight, this study demonstrates multiple and complex roles for the UV-B photoreceptor UV RESISTANCE LOCUS8 in the acclimation of Arabidopsis plants to UV radiation.

744

## GENES, DEVELOPMENT, AND EVOLUTION

[W][OA] The Impact of the Long-Distance Transport of a BEL1-Like Messenger RNA on Development. *Tian Lin, Pooja Sharma, Daniel H. Gonzalez, Ivana L. Viola, and David J. Hannapel*

Summary: Through regulation by light, a mobile mRNA of potato is involved in controlling processes of growth and in mediating the activation of its own gene.

760

[W][OA] Functional Divergence of the Glutathione S-Transferase Supergene Family in *Physcomitrella patens* Reveals Complex Patterns of Large Gene Family Evolution in Land Plants. *Yan-Jing Liu, Xue-Min Han, Lin-Ling Ren, Hai-Ling Yang, and Qing-Yin Zeng*

Summary: This study characterized the functional divergence of the GST gene family in *Physcomitrella patens*, and revealed complex patterns of evolutionary divergence among the GST gene family in land plants.

773

[W] Functional Genomics Reveals That a Compact Terpene Synthase Gene Family Can Account for Terpene Volatile Production in Apple. *Niels J. Nieuwenhuizen, Sol A. Green, Xiuyin Chen, Estelle J.D. Bailleul, Adam J. Matich, Mindy Y. Wang, and Ross G. Atkinson*

Summary: Apple is shown to contain only a small number of functional terpene synthase genes whose evolution appears to have been shaped by genome-wide duplication events and commercial breeding strategies.

787

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<sup>[W][OA]</sup>Tissue-Specific Silencing of Arabidopsis *SU(VAR)3-9 HOMOLOG8* by miR171a\*. *Pablo A. Manavella, Daniel Koenig, Ignacio Rubio-Somoza, Hernán A. Burbano, Claude Becker, and Detlef Weigel*

Summary: Active miR171a\* complexes are common in Arabidopsis and trigger silencing of *SUVH8*, a new microRNA target that was acquired very recently in the Arabidopsis lineage.

805

<sup>[W][OA]</sup>Early Cone Setting in *Picea abies* *acrocona* Is Associated with Increased Transcriptional Activity of a MADS Box Transcription Factor. *Daniel Uddenberg, Johan Reimegård, David Clapham, Curt Almqvist, Sara von Arnold, Olof Emanuelsson, and Jens F. Sundström*

Summary: Transcriptome analysis of an early cone-setting mutant identified candidate genes active during reproductive phase change in the conifer *Picea abies*.

813

<sup>[C][W][OA]</sup>*SAUR36*, a SMALL AUXIN UP RNA Gene, Is Involved in the Promotion of Leaf Senescence in Arabidopsis. *Kai Hou, Wei Wu, and Su-Sheng Gan*

Summary: Auxin induces the expression of *SAUR36* that positively regulates leaf senescence in Arabidopsis.

1002

## MEMBRANES, TRANSPORT, AND BIOENERGETICS

<sup>[C][W]</sup>Comparative Analysis of 126 Cyanobacterial Genomes Reveals Evidence of Functional Diversity Among Homologs of the Redox-Regulated CP12 Protein. *Desirée N. Stanley, Christine A. Raines, and Cheryl A. Kerfeld*

Summary: Comparative analysis of 126 cyanobacterial genomes reveals evidence of functional diversity among homologs of CP12, a protein found almost universally among photosynthetic organisms.

824

<sup>[W]</sup>Decreased Photochemical Efficiency of Photosystem II following Sunlight Exposure of Shade-Grown Leaves of Avocado: Because of, or in Spite of, Two Kinetically Distinct Xanthophyll Cycles? *Husen Jia, Britta Förster, Wah Soon Chow, Barry James Pogson, and C. Barry Osmond*

Summary: Photoprotection in sunlight by two xanthophyll pigment systems is not enough to prevent inactivation of photochemical efficiency in avocado shade leaves.

836

<sup>[W][OA]</sup>High Light Acclimation in the Secondary Plastids Containing Diatom *Phaeodactylum tricornutum* is Triggered by the Redox State of the Plastoquinone Pool. *Bernard Lepetit, Sabine Sturm, Alessandra Rogato, Ansgar Gruber, Matthias Sachse, Angela Falciatore, Peter G. Kroth, and Johann Lavaud*

Summary: The redox state of the plastidic plastoquinone pool triggers a retrograde signal in diatoms, organisms with plastids evolved by secondary endosymbiosis.

853

<sup>[W]</sup>Expression of the Minor Isoform Pea Ferredoxin in Tobacco Alters Photosynthetic Electron Partitioning and Enhances Cyclic Electron Flow. *Nicolás E. Blanco, Romina D. Ceccoli, María V. Dalla Vía, Ingo Voss, María E. Segretin, Fernando F. Bravo-Almonacid, Michael Melzer, Mohammad-Reza Hajirezaei, Renate Scheibe, and Guy T. Hanke*

Summary: Characterization of ferredoxin overexpressor transplastomic tobacco plants provides new evidence about the different roles of this protein and the effect of this feature on the regulation of the photosynthetic electron flow to produce alternative electron partitioning between linear and cyclic flow.

866

<sup>[W]</sup>Transposon-Mediated Alteration of *TaMATE1B* Expression in Wheat Confers Constitutive Citrate Efflux from Root Apices. *Andriy Tovkach, Peter R. Ryan, Alan E. Richardson, David C. Lewis, Tina M. Rathjen, Sunita Ramesh, Stephen D. Tyerman, and Emmanuel Delhaize*

Summary: This research describes how a mobile genetic element recruits the *TaMATE1B* gene into a role associated with aluminum tolerance by altering its expression level and pattern.

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## SIGNALING AND RESPONSE

[W][OA] Reciprocal Interaction of the Circadian Clock with the Iron Homeostasis Network in Arabidopsis. *Sunghyun Hong, Sun A. Kim, Mary Lou Guerinot, and C. Robertson McClung*

Summary: Description of a novel feedback loop between the circadian clock and the iron homeostasis network in which the circadian clock regulates the transcription of multiple iron homeostasis genes and iron nutritional status feeds back on the clock to modulate circadian period.

893

[C][W][OA] Functional Phosphoproteomic Analysis Reveals That a Serine-62-Phosphorylated Isoform of Ethylene Response Factor110 Is Involved in Arabidopsis Bolting. *Lin Zhu, Dandan Liu, Yaojun Li, and Ning Li*

Summary: The simple gaseous plant hormone ethylene regulates Arabidopsis flowering via Yin-and-Yang signal transduction pathways.

904

[W][OA] Proteome Analysis in Arabidopsis Reveals Shoot- and Root-Specific Targets of Cytokinin Action and Differential Regulation of Hormonal Homeostasis. *Markéta Žd'árská, Paolína Zatloukalová, Mariana Benítez, Ondrej Šedo, David Potěšil, Ondřej Novák, Jana Svačinová, Bedřich Pešek, Jiří Malbeck, Jana Vašíčková, Zbyněk Zdráhal, and Jan Hejátko*

Summary: The plant hormone cytokinin regulates the Arabidopsis proteome in a shoot- and root-specific way, and the cytokinin-mediated tissue-specific modulation of hormonal metabolism is an intrinsic component of the Arabidopsis response to cytokinins.

918

[C][W][OA] PYRABACTIN RESISTANCE1-LIKE8 Plays an Important Role for the Regulation of Abscisic Acid Signaling in Root. *Regina Antoni, Miguel Gonzalez-Guzman, Lesia Rodriguez, Marta Peirats-Llobet, Gaston A. Pizzio, Maria A. Fernandez, Nancy De Winne, Geert De Jaeger, Daniela Dietrich, Malcom J. Bennett, and Pedro L. Rodriguez*

Summary: The abscisic acid receptor PYL8 plays an important role for regulation of root abscisic acid sensitivity, and abscisic acid-dependent inhibition of PP2Cs by PYR/PYLs is required for root hydrotropism.

931

[W][OA] Role of the Putative Osmosensor Arabidopsis *Histidine Kinase1* in Dehydration Avoidance and Low-Water-Potential Response. *M. Nagaraj Kumar, Wann-Neng Jane, and Paul E. Verslues*

Summary: AHK1 mutants had increased stomatal density and faster leaf water loss; however, AHK1 mutants were not more sensitive to controlled low water potential stress and not impaired in abscisic acid, Pro, or osmoregulatory solute accumulation, thus indicating that AHK1 is not the main plant osmosensor controlling these drought tolerance-associated phenotypes.

942

[W][OA] Transcriptional and Functional Classification of the GOLVEN/ROOT GROWTH FACTOR/CLE-Like Signaling Peptides Reveals Their Role in Lateral Root and Hair Formation. *Ana Fernandez, Andrzej Drozdzecki, Kurt Hoogewijs, Anh Nguyen, Tom Beeckman, Annemieke Madder, and Pierre Hilson*

Summary: The expression domains and phenotypes associated with distinct members of the GLV/RFG/CLEL secreted peptide family indicate that they function in multiple developmental programs, including meristem maintenance, gravitropism, lateral root emergence, and the formation of root hairs.

954

[W][OA] A Cyclic Nucleotide-Gated Channel (CNGC16) in Pollen Is Critical for Stress Tolerance in Pollen Reproductive Development. *Meral Tunc-Ozdemir, Chong Tang, Maryam Rahmati Ishka, Elizabeth Brown, Norman R. Groves, Candace T. Myers, Claudia Rato, Lisbeth R. Poulsen, Stephen McDowell, Gad Miller, Ron Mittler, and Jeffrey F. Harper*

Summary: A genetic knockout of a pollen-expressed cyclic nucleotide-gated ion channel (cngc16) provides evidence for a signaling pathway that links a cyclic nucleotide signal to changes in gene expression that are critical for heat or drought stress tolerance during reproductive development.

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## SYSTEMS AND SYNTHETIC BIOLOGY

<sup>[W]</sup><sup>[OA]</sup> Recombinant Antibody Production in Arabidopsis Seeds Triggers an Unfolded Protein Response. *Kirsten De Wilde, Sylvie De Buck, Kevin Vanneste, and Ann Depicker*

Summary: This study shows that seed-specific recombinant antibody production evokes endoplasmic reticulum stress, triggering the unfolded protein response without greatly affecting seed germination and seedling growth, however, making the *PPHAS*-driven expression cassette a suitable system for molecular farming.

1021

<sup>[C]</sup><sup>[W]</sup><sup>[OA]</sup> Gene Regulation of Carbon Fixation, Storage, and Utilization in the Diatom *Phaeodactylum tricornutum* Acclimated to Light/Dark Cycles. *Matilde Skogen Chauton, Per Winge, Tore Brembu, Olav Vadstein, and Atle M. Bones*

Summary: Analyses of gene regulation and cell chemistry in acclimated fed batch cultures of *Phaeodactylum tricornutum* identify genes and metabolic pathways of carbon metabolism, and the subcellular localization and timing of genes and processes during light/dark cycles.

1034

<sup>[C]</sup><sup>[W]</sup><sup>[OA]</sup> Alteration of the Alkaloid Profile in Genetically Modified Tobacco Reveals a Role of Methylene tetrahydrofolate Reductase in Nicotine *N*-Demethylation. *Chiu-Yueh Hung, Longjiang Fan, Farooqahmed S. Kittur, Kehan Sun, Jie Qiu, She Tang, Bronwyn M. Holliday, Bingguang Xiao, Kent O. Burkey, Lowell P. Bush, Mark A. Conkling, Sanja Roje, and Jiahua Xie*

Summary: The primary metabolic pathway gene *NiMTHFR* negatively regulates the secondary metabolism pathway nicotine demethylation gene to potentially recycle methyl groups from alkaloids.

1049

<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.