

The electronic form of this issue, available as of October 8, 2013, at www.plantphysiol.org, is considered the journal of record.

On the Cover: Ca^{2+} is a ubiquitous signalling molecule. This Focus Issue contains Updates and experimental reports describing new advances in the measurement of changes in intracellular free Ca^{2+} concentrations, the mechanisms by which dynamical alterations in intracellular free Ca^{2+} generated, and how these Ca^{2+} signals might be decoded. In this issue, Martí et al (pp. 625–634) describe the use of cell-specific enhancer trap lines of Arabidopsis to target the bioluminescent reporter aequorin to specific cell types. Their data demonstrate cell- and stimulus type-specific intracellular Ca^{2+} signals in the aerial parts of the plant, suggesting a mechanism to generate specificity in signaling pathways. The cover shows a confocal scanning laser microscopy image of APOEAQUORIN fused to YELLOW FLUORESCENT PROTEIN (red) in spongy mesophyll cells marked with ER-targeted GREEN FLUORESCENT PROTEIN (green) in the enhancer trap line JR11-2. Chlorophyll autofluorescence from the plastids is shown in blue. Image M.A. Stancombe.

FOCUS ISSUE ON CALCIUM SIGNALING

EDITORIAL

Focus Issue: Calcium Signaling. *Alex A.R. Webb*

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TOPICAL REVIEWS

There's More to the Picture Than Meets the Eye: Nitric Oxide Cross Talk with Ca^{2+} Signaling. *Sylvain Jeandroz, Olivier Lamotte, Jérémy Astier, Sumaira Rasul, Pauline Trapet, Angélique Besson-Bard, Stéphane Bourque, Valérie Nicolas-Francès, Wei Ma, Gerald A. Berkowitz, and David Wendehenne*

The complex cross talk between Ca^{2+} and nitric oxide involves components of the Ca^{2+} signaling machinery regulated through a nitric oxide-dependent process at the posttranslational and/or transcriptional levels.

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UPDATES

Calcium and Reactive Oxygen Species Rule the Waves of Signaling. *Leonie Steinhorst and Jörg Kudla*

Calcium signaling and reactive oxygen species signaling are directly connected, and both contribute to cell-to-cell signal propagation in plants.

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Calmodulin-Related Proteins Step Out from the Shadow of Their Namesake. *Kyle W. Bender and Wayne A. Snedden*

Emerging roles for these proteins in plant development and stress response highlight their importance in plant signaling, and their functional diversity underscores the significance of Ca^{2+} as a second messenger in plants.

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Nuclear Calcium Signaling in Plants. *Myriam Charpentier and Giles E.D. Oldroyd*

Plant cell nuclei can generate calcium responses to a variety of inputs, tantamount among them the response to signaling molecules from symbiotic microorganisms.

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^[W]Calcium-Dependent and -Independent Stomatal Signaling Network and Compensatory Feedback Control of Stomatal Opening via Ca^{2+} Sensitivity Priming. *Kristiina Laanemets, Benjamin Brandt, Junlin Li, Ebe Merilo, Yong-Fei Wang, Malik M. Keshwani, Susan S. Taylor, Hannes Kollist, and Julian I. Schroeder*

Guard cells use compensatory feedback controls to adapt to conditions that produce excessively open stomata.

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Plant Calcium-Permeable Channels. *Stéphanie M. Swarbreck, Renato Colaço, and Julia M. Davies*

Experimental and modeling breakthroughs will help establish the genetic identities of plant calcium channels.

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Calcium-Dependent Protein Kinases: Hubs in Plant Stress Signaling and Development. *Philipp Schulz, Marco Herde, and Tina Romeis*

These kinases are identified as integrators in plant signaling, with distinct as well as shared phosphorylation substrates mediating pathway specificity. 523

Recent Advances in Calcium/Calmodulin-Mediated Signaling with an Emphasis on Plant-Microbe Interactions. *B.W. Poovaliah, Liqun Du, Huizhong Wang, and Tianbao Yang*

Calcium/calmodulin-mediated signaling contributes in diverse roles in plant growth, development, and response to environmental stimuli. 531

RESEARCH ARTICLES

[W][OPEN] Analyses of a Gravistimulation-Specific Ca^{2+} Signature in Arabidopsis using Parabolic Flights. *Masatsugu Toyota, Takuya Furuichi, Masahiro Sokabe, and Hitoshi Tatsumi*

Parabolic flight experiments show that plants possess a gravistimulation-specific calcium signature and a rapid gravity-sensing mechanism that transduces a wide range of gravitational changes (0.5–2g) into Ca^{2+} signals on a subsecond time scale. 543

[W][OPEN] Teaching an Old Hormone New Tricks: Cytosolic Ca^{2+} Elevation Involvement in Plant Brassinosteroid Signal Transduction Cascades. *Yichen Zhao, Zhi Qi, and Gerald A. Berkowitz*

Ca^{2+} signaling is involved in brassinosteroid hormone-mediated gene expression and plant phenotypes. 555

[W][OPEN] PYR/PYL/RCAR Abscisic Acid Receptors Regulate K^+ and Cl^- Channels through Reactive Oxygen Species-Mediated Activation of Ca^{2+} Channels at the Plasma Membrane of Intact Arabidopsis Guard Cells. *Yizhou Wang, Zhong-Hua Chen, Ben Zhang, Adrian Hills, and Michael R. Blatt*

A new strategy for recording Ca^{2+} channels in intact guard cells demonstrates a central role for Ca^{2+} channel activation and elevated cytosol-free Ca^{2+} concentrations in signaling mediated by the PYR/PYL/RCAR family of abscisic acid receptors. 566

[W][OPEN] Identification of Cyclic GMP-Activated Nonselective Ca^{2+} -Permeable Cation Channels and Associated CNGC5 and CNGC6 Genes in Arabidopsis Guard Cells. *Yong-Fei Wang, Shintaro Munemasa, Noriyuki Nishimura, Hui-Min Ren, Nadia Robert, Michelle Han, Irina Puz̄rjova, Hannes Kollist, Stephen Lee, Izumi Mori, and Julian I. Schroeder*

Cyclic GMP activates Ca^{2+} -permeable cation channels in the plasma membrane of Arabidopsis guard cells. 578

[W][OPEN] Calcium-Dependent Protein Kinase CPK6 Positively Functions in Induction by Yeast Elicitor of Stomatal Closure and Inhibition by Yeast Elicitor of Light-Induced Stomatal Opening in Arabidopsis. *Wenxiu Ye, Daichi Muroyama, Shintaro Munemasa, Yoshimasa Nakamura, Izumi C. Mori, and Yoshiyuki Murata*

Calcium-dependent protein kinase CPK6 positively functions in induction by yeast elicitor of stomatal closure and inhibition by yeast elicitor of light-induced stomatal opening in Arabidopsis. 591

[W][OPEN] Difference in Abscisic Acid Perception Mechanisms between Closure Induction and Opening Inhibition of Stomata. *Ye Yin, Yuji Adachi, Wenxiu Ye, Maki Hayashi, Yoshimasa Nakamura, Toshinori Kinoshita, Izumi C. Mori, and Yoshiyuki Murata*

*Disruption of the ABA receptors *pyr1*, *pyl1*, *pyl2*, and *pyl4* does not impair ABA inhibition of stomatal opening.* 600

[C][W][OPEN]The Arabidopsis Cyclic Nucleotide-Gated Ion Channels AtCNGC2 and AtCNGC4 Work in the Same Signaling Pathway to Regulate Pathogen Defense and Floral Transition. Kimberley Chin, Thomas A. DeFalco, Wolfgang Moeder, and Keiko Yoshioka

Two Arabidopsis cyclic nucleotide-gated ion channels act in the same signaling pathway and possibly are part of the same channel complex to regulate both pathogen defense and floral transition.

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[W][OPEN]Cell- and Stimulus Type-Specific Intracellular Free Ca²⁺ Signals in Arabidopsis. María C. Martí, Matthew A. Stancombe, and Alex A.R. Webb

Enhancer trap targeting of aequorin to specific cell types identifies stimulus- and cell-specific signaling via cytosolic-free calcium concentration in Arabidopsis.

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REGULAR ISSUE

ON THE INSIDE

Peter V. Minorsky

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BREAKTHROUGH TECHNOLOGIES

[W][OPEN]Multiscale Metabolic Modeling: Dynamic Flux Balance Analysis on a Whole-Plant Scale. Eva Grafahrend-Belau, Astrid Junker, André Eschenröder, Johannes Müller, Falk Schreiber, and Björn H. Junker

A multiscale metabolic modeling approach integrates a static multiorgan flux balance analysis model and a dynamic whole-plant multiscale functional plant model for dynamic flux balance analysis.

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[W][OPEN]Stable Transformation of Ferns Using Spores as Targets: *Pteris vittata* and *Ceratopteris thalictroides*. Balasubramaniam Muthukumar, Blake L. Joyce, Mark P. Elless, and C. Neal Stewart Jr.

Ferns are stably transformed by using spores as targets.

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[C][W][OPEN]Monitoring Meso-Scale Ordering of Cellulose in Intact Plant Cell Walls Using Sum Frequency Generation Spectroscopy. Yong Bum Park, Christopher M. Lee, Bon-Wook Koo, Sunky Park, Daniel J. Cosgrove, and Seong H. Kim

Sum frequency generation spectroscopy is sensitive to the ordering of cellulose microfibrils in plant cell walls at the meso scale (nm to μ m) that is important for cell wall architecture but cannot be probed by other spectroscopic or diffraction techniques.

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SCIENTIFIC CORRESPONDENCE

[W]Pathogen Infection Trial Increases the Secretion of Proteins Localized in the Endoplasmic Reticulum Body of Arabidopsis. Satoshi Watanabe, Takashi L. Shimada, Kei Hiruma, and Yoshitaka Takano

Endoplasmic reticulum structures facilitate the increased secretion of proteins during the plant immune response.

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[W]Regulating the Redox Gatekeeper: Vacuolar Sequestration Puts Glutathione Disulfide in Its Place. Graham Noctor, Amna Mhamdi, Guillaume Queval, and Christine H. Foyer

The case is made for the potential importance of compartmentalization in redox signaling with new data on the transporters that may be involved.

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BIOCHEMISTRY AND METABOLISM

[W]The Ureide-Degrading Reactions of Purine Ring Catabolism Employ Three Amidohydrolases and One Aminohydrolase in Arabidopsis, Soybean, and Rice. Andrea K. Werner, Nieves Medina-Escobar, Monika Zulawski, Imogen A. Sparkes, Feng-Qiu Cao, and Claus-Peter Witte

Aminohydrolases and amidohydrolases catalyze the last enzymatic steps of purine degradation in plants.

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[W][OPEN] Enzymatic Formation of β -Citraurin from β -Cryptoxanthin and Zeaxanthin by Carotenoid Cleavage Dioxygenase4 in the Flavedo of Citrus Fruit. *Gang Ma, Lancui Zhang, Asami Matsuta, Kazuki Matsutani, Kazuki Yamawaki, Masaki Yahata, Anung Wahyudi, Reiko Motohashi, and Masaya Kato*

The biosynthesis of β -citraurin from β -cryptoxanthin and zeaxanthin contribute to the reddish peel color of citrus fruits. 682

[C][W] The Green Microalga *Chlamydomonas reinhardtii* Has a Single ω -3 Fatty Acid Desaturase That Localizes to the Chloroplast and Impacts Both Plastidic and Extrplastidic Membrane Lipids. *Hoa Mai Nguyen, Stéphan Cuiné, Audrey Beyly-Adriano, Bertrand Légeret, Emmanuelle Billon, Pascaline Auroy, Fred Beisson, Gilles Peltier, and Yonghua Li-Beisson*

*A single ω -3 fatty acid desaturase in *Chlamydomonas reinhardtii* is sufficient to produce [omega]-3 polyunsaturated fatty acids for both plastidial and extrplastidial lipids.* 914

[W][OPEN] Gibberellin 3-oxidase Gene Expression Patterns Influence Gibberellin Biosynthesis, Growth, and Development in Pea. *Dennis M. Reinecke, Aruna D. Wickramarathna, Jocelyn A. Ozga, Leonid V. Kurepin, Alena L. Jin, Allen G. Good, and Richard P. Pharis*

GA biosynthesis and catabolism regulation at the plant tissue and organ level is important for the timing/localization of gene expression for the production of bioactive GA, and thereby plant growth. 929

[W][OPEN] Eugenol Production in Achenes and Receptacles of Strawberry Fruits Is Catalyzed by Synthases Exhibiting Distinct Kinetics. *Irene Aragüez, Sonia Osorio, Thomas Hoffmann, José Luis Rambla, Nieves Medina-Escobar, Antonio Granell, Miguel Ángel Botella, Wilfried Schwab, and Victoriano Valpuesta*

Two different synthases are responsible for the high production of eugenol in the green achene and the ripe receptacle of the strawberry fruit. 946

[C][W][OPEN] Successful Fertilization Requires the Presence of at Least One Major O-Acetylserine(thiol)lyase for Cysteine Synthesis in Pollen of Arabidopsis. *Hannah Birke, Corinna Heeg, Markus Wirtz, and Rüdiger Hell*

The major cysteine-synthesizing enzymes have specific functions in different subcellular compartments of Arabidopsis leaf cells and are essential for male gametophyte function. 959

[C][W][OPEN] Alterations in Seed Development Gene Expression Affect Size and Oil Content of Arabidopsis Seeds. *Abdelhak Fatihi, Anna Maria Zbierzak, and Peter Dörmann*

Analysis of mutant and overexpressing lines of Arabidopsis seed development genes uncovers the impact of a leucine-rich repeat kinase on seed size and oil content. 973

[C][W][OPEN] Dissection of Tomato Lycopene Biosynthesis through Virus-Induced Gene Silencing. *Elio Fantini, Giulia Falcone, Sarah Frusciante, Leonardo Giliberto, and Giovanni Giuliano*

A reverse genetic dissection of a carotenoid biosynthesis pathway is achieved through systematic gene silencing analysis. 986

CELL BIOLOGY

[C][W][OPEN] Arabidopsis Tetraspanins Are Confined to Discrete Expression Domains and Cell Types in Reproductive Tissues and Form Homo- and Heterodimers When Expressed in Yeast. *Leonor C. Boavida, Peng Qin, Miranda Broz, Jörg D. Becker, and Sheila McCormick*

Arabidopsis tetraspanins show conserved cellular and molecular features with functional relevance in the context of intercellular interactions, with specificity that might be determined by the composition of tetraspanin complexes and their binding partners at the cell surface of specific cell types. 696

[W][OPEN]ROOT HAIR DEFECTIVE3 Family of Dynamin-Like GTPases Mediates Homotypic Endoplasmic Reticulum Fusion and Is Essential for Arabidopsis Development. *Miao Zhang, Fuyun Wu, Juanming Shi, Yimeng Zhu, Zhengmao Zhu, Qingqiu Gong, and Junjie Hu*

RHD3 proteins mediate ER fusion and are essential for plant development and the formation of the tubular ER network. 713

[C][W]Fertilization and Uniparental Chromosome Elimination during Crosses with Maize Haploid Inducers. *Xin Zhao, Xiaowei Xu, Hongxia Xie, Shaojiang Chen, and Weiwei Jin*

Selective elimination of uniparental chromosomes occurred in both embryo and endosperm during the formation of haploid in maize. 721

ECOPHYSIOLOGY AND SUSTAINABILITY

[W]A Novel Proteinase, SNOWY COTYLEDON4, Is Required for Photosynthetic Acclimation to Higher Light Intensities in Arabidopsis. *Verónica Albrecht-Borth, Dominika Kauss, Dayong Fan, Yuanyuan Hu, Derek Collinge, Shashikanth Marri, Monique Liebers, Klaus Apel, Thomas Pfannschmidt, Wah S. Chow, and Barry J. Pogson*

A plant-specific chloroplast endopeptidase is identified that functions in protection of the photosynthetic apparatus from photo-oxidative stress. 732

[C]Impact of Electroviscosity on the Hydraulic Conductance of the Bordered Pit Membrane: A Theoretical Investigation. *Michael Santiago, Vinay Pagay, and Abraham D. Stroock*

Electroviscous effects in the bordered pit membrane may impact the overall hydraulic conductance of xylem and explain ion-mediated changes in conductance observed in perfusion experiments. 999

GENES, DEVELOPMENT, AND EVOLUTION

[W][OPEN]The Single-Stranded DNA-Binding Protein WHIRLY1 Represses WRKY53 Expression and Delays Leaf Senescence in a Developmental Stage-Dependent Manner in Arabidopsis. *Ying Miao, Jingjing Jiang, Yujun Ren, and Ziwei Zhao*

A single-stranded DNA-binding protein represses expression and delays leaf senescence in a developmental stage-dependent manner in Arabidopsis. 746

[C][W][OPEN]A Regulatory Network-Based Approach Dissects Late Maturation Processes Related to the Acquisition of Desiccation Tolerance and Longevity of *Medicago truncatula* Seeds. *Jerome Verdier, David Lalanne, Sandra Pelletier, Ivone Torres-Jerez, Karima Righetti, Kaustav Bandyopadhyay, Olivier Leprince, Emilie Chatelain, Benoit Ly Vu, Jerome Gouzy, Pascal Gamas, Michael K. Udvardi, and Julia Buitink*

A network analysis approach to gene regulation during seed maturation of Medicago truncatula uncovers distinct temporal regulatory programs related to desiccation tolerance, longevity, and pod abscission and the key regulators governing these programs. 757

[C][W][OPEN]An NAC Transcription Factor Controls Ethylene-Regulated Cell Expansion in Flower Petals. *Haixia Pei, Nan Ma, Ji Tian, Jing Luo, Jiwei Chen, Jing Li, Yi Zheng, Xiang Chen, Zhangjun Fei, and Junping Gao*

Transcriptome sequencing and microarray analysis identifies an miR164-regulated, ethylene-responsive transcription factor that mediates floral organ size through direct regulation of cell expansion-related genes. 775

[W][OPEN]FLOWERING LOCUS T/TERMINAL FLOWER1-Like Genes Affect Growth Rhythm and Bud Set in Norway Spruce. *Anna Karlgren, Niclas Gyllenstrand, David Clapham, and Ulf Lagercrantz*

Phosphatidylethanolamine-binding proteins have a role in the control of annual growth rhythm in the conifer Norway spruce. 792

[W]Phytochrome C Is A Key Factor Controlling Long-Day Flowering in Barley. *Hidetaka Nishida, Daisuke Ishihara, Makoto Ishii, Takuma Kaneko, Hiroyuki Kawahigashi, Yukari Akashi, Daisuke Saisho, Katsunori Tanaka, Hirokazu Handa, Kazuyoshi Takeda, and Kenji Kato*

A red/far-red light photoreceptor controls flowering time in barley by stimulating a flowering promoter gene in the most downstream part of the genetic pathways for flowering. 804

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- ^{[C][W]}Strigolactones Stimulate Internode Elongation Independently of Gibberellins. *Alexandre de Saint Germain, Yasmine Ligerot, Elizabeth A. Dun, Jean-Paul Pillot, John J. Ross, Christine A. Beveridge, and Catherine Rameau*
Strigolactones stimulate internode elongation by regulating cell division using a gibberellin-independent pathway. 1012
- ^{[C][W]}A Tomato MADS-Box Transcription Factor, SIMADS1, Acts as a Negative Regulator of Fruit Ripening. *Tingting Dong, Zongli Hu, Lei Deng, Yi Wang, Mingku Zhu, Jianling Zhang, Guoping Chen*
A tomato MADS-box gene, SIMADS1, impacts fruit ripening as a negative regulator. 1026

MEMBRANES, TRANSPORT, AND BIOENERGETICS

- ^{[C][OPEN]}Effect of Temperature on Photosynthesis and Growth in Marine *Synechococcus* spp.. *Katherine R.M. Mackey, Adina Paytan, Ken Caldeira, Arthur R. Grossman, Dawn Moran, Matthew McIlvin, and Mak A. Saito*
Marine Synechococcus regulates state transitions and photosynthetic protein content for temperature acclimation. 815
- ^{[W][OPEN]}Identification of a Probable Pore-Forming Domain in the Multimeric Vacuolar Anion Channel AtALMT9. *Jingbo Zhang, Ulrike Baetz, Undine Krügel, Enrico Martinoia, and Alexis De Angeli*
Several subunits participate in forming the permeation pathway of a vacuolar anion channel. 830
- ^{[C][W][OPEN]}Two Phloem Nitrate Transporters, NRT1.11 and NRT1.12, Are Important for Redistributing Xylem-Borne Nitrate to Enhance Plant Growth. *Po-Kai Hsu and Yi-Fang Tsay*
The property of two nitrate transporters suggests a new strategy to enhance nitrate supply into developing tissues with low transpiration rate by redistributing xylem-borne nitrate. 844
- Thylakoid Membrane Maturation and PSII Activation Are Linked in Greening *Synechocystis* sp. PCC 6803 Cells. *Sandra Barthel, Gábor Bernát, Tobias Seidel, Eva Rupprecht, Uwe Kahmann, and Dirk Schneider*
Thylakoid membrane formation and photosynthetic electron transfer reactions are linked in greening cyanobacteria. 1037

SIGNALING AND RESPONSE

- ^{[C][W][OPEN]}FAR-RED ELONGATED HYPOCOTYL3 and FAR-RED IMPAIRED RESPONSE1 Transcription Factors Integrate Light and Abscisic Acid Signaling in Arabidopsis. *Weijiang Tang, Qiang Ji, Yongping Huang, Zhimin Jiang, Manzhu Bao, Haiyang Wang, and Rongcheng Lin*
Two transcription factors link light and abscisic acid networks to regulate plant growth and development. 857
- ^{[C][W][OPEN]}Plastid Genome Instability Leads to Reactive Oxygen Species Production and Plastid-to-Nucleus Retrograde Signaling in Arabidopsis. *Étienne Lepage, Éric Zampini, and Normand Brisson*
Instability of the plastid genome leads to the production of reactive oxygen species and to nuclear genetic reprogramming. 867
- ^{[C][W]}Antiphase Light and Temperature Cycles Affect PHYTOCHROME B-Controlled Ethylene Sensitivity and Biosynthesis, Limiting Leaf Movement and Growth of Arabidopsis. *Ralph Bours, Martijn van Zanten, Ronald Pierik, Harro Bouwmeester, and Alexander van der Krol*
Light and temperature cycles influence the amplitude and phase of diurnal leaf movement rhythms by regulating ethylene biosynthesis in the petiole. 882
- ^[W]Arabidopsis Phospholipase D δ Is Involved in Basal Defense and Nonhost Resistance to Powdery Mildew Fungi. *Francesco Pinosa, Nathalie Buhot, Mark Kwaktaal, Per Fahlberg, Hans Thordal-Christensen, Mats Ellerström, and Mats X. Andersson*
An Arabidopsis family of phospholipases, probed using reverse genetics for involvement in cell wall-based defense to nonhost powdery mildew, identifies one isoform as a component in the defense reaction. 896

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^{[C][W][OPEN]} Abscisic Acid Regulates Axillary Bud Outgrowth Responses to the Ratio of Red to Far-Red Light. *Srirama Krishna Reddy, Srinidhi V. Holalu, Jorge J. Casal, and Scott A. Finlayson*

ABA regulates bud outgrowth responses to the ratio of red to far-red light, extending the known hormonal pathways associated with the regulation of branching and shade avoidance.

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^{[C][W]} LESION SIMULATING DISEASE1 Interacts with Catalases to Regulate Hypersensitive Cell Death in Arabidopsis. *Yansha Li, Lichao Chen, Jinye Mu, and Jianru Zuo*

A zinc finger-domain protein interacts with catalases to regulate hypersensitive cell death in Arabidopsis.

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SYSTEMS AND SYNTHETIC BIOLOGY

^{[C][W][OPEN]} ROSMETER: A Bioinformatic Tool for the Identification of Transcriptomic Imprints Related to Reactive Oxygen Species Type and Origin Provides New Insights into Stress Responses. *Shilo Rosenwasser, Robert Fluhr, Janak Raj Joshi, Noam Leviatan, Noa Sela, Amotz Hetzroni, and Haya Friedman*

The bioinformatic tool, ROSMETER, differentiates different reactive oxygen species, their subcellular origin, to give new insight into senescence and biotic and abiotic stresses.

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