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On the Cover: Secondary cell walls are of immense importance to our society as they provide raw material for the paper, textile, biomaterial, and fuel sectors. Secondary cell walls also sustain plant growth and the watertransporting capacity of the vasculature that support water and nutrient transport from the root to the aerial parts of a plant. A better understanding of how secondary walls are made is therefore of utmost importance. Li et al. (Vol. 172, pp. 1334-1351) and Ohtani et al. (this issue, pp. 1612-1624) used inducible secondary wall systems to explore metabolite and transcript changes after the onset of secondary wall production. They found dynamic changes associated with many different classes of metabolites, in particular amino acid biosynthesis and hormone signaling. These changes were put in context to transcript changes during the induction to generate a comprehensive map of how cells re-program to change their developmental fates. These data will lay a foundation for a better understanding of how secondary walls are synthesized in plants. The cover image shows an induced seedling that was torn to expose a secondary wall structure of a proto-xylem converted cell. The image was captured using a Olympus BX-51 epi-fluorescence microscope using a $20\times$ lens and was generated by Dr. Rene Schneider at the University of Melbourne.

ON THE INSIDE

1355 Peter V. Minorsky

COMMENTARY

Poor Evidence for C₄ Photosynthesis in the Wheat Grain. Florian A. Busch and Graham D. Farquhar

A critical comment to a recent paper claiming to have evidence for C_A photosynthesis in the wheat grain. 1357

BREAKTHROUGH TECHNOLOGIES

[OPEN] pheno Seeder - A Robot System for Automated Handling and Phenotyping of Individual Seeds. Siegfried Jahnke, Johanna Roussel, Thomas Hombach, Johannes Kochs, Andreas Fischbach, Gregor Huber, and Hanno Scharr

A robot system allows automated handling and phenotyping of individual seeds of different sizes, delivering biometric traits relevant for various aspects in seed biology.

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TOPICAL REVIEW

[OPEN] Rethinking Guard Cell Metabolism. Diana Santelia and Tracy Lawson

Recent research highlights the importance of both starch and sucrose for guard cell osmoregulation and its integration with carboxylate metabolism and membrane ion transport during stomatal movements.

RESEARCH REPORT

 ${}^{[\mathrm{OPEN}]}\!A\ Single\ Arabidopsis\ Gene\ Encodes\ Two\ Differentially\ Targeted\ Geranylgeranyl\ Diphosphate$ Synthase Isoforms. M. Aguila Ruiz-Sola, M. Victoria Barja, David Manzano, Briardo Llorente, Bert Schipper, Jules Beekwilder, and Manuel Rodriguez-Concepcion

GGPP synthase activity essential for chloroplast function and embryo development is provided by two differentially targeted enzyme isoforms encoded by the same gene in Arabidopsis.

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RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

[OPEN] Developmental Changes in Scots Pine Transcriptome during Heartwood Formation. Kean-Jin Lim, Tanja Paasela, Anni Harju, Martti Venäläinen, Lars Paulin, Petri Auvinen, Katri Kärkkäinen, and Teemu H. Teeri

The Scots pine heartwood formation takes place in the summer and is marked by programmed cell death.

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Salinity. Katalin Gémes, Yu Jung Kim, Ky Young Park, Panagiotis N. Moschou, Efthimios Andronis, Chryssanthi Valassaki, Andreas Roussis, and Kalliopi A. Roubelakis-Angelakis	
The tobacco plasma membrane NADPH oxidase and the extracellular polyamine oxidase interact functionally to regulate the homeostasis of reactive oxygen species.	1418
[OPEN]SENSITIVE TO FREEZING2 Aids in Resilience to Salt and Drought in Freezing-Sensitive Tomato. Kun Wang, Hope Lynn Hersh, and Christoph Benning	
Lipid remodeling of chloroplast membranes mediated by SENSITIVE TO FREEZING 2 protects freezing-sensitive plants such as tomatoes against cellular dehydration brought on by drought and salt stress.	1432
[OPEN]Oxidation of P700 in Photosystem I Is Essential for the Growth of Cyanobacteria. <i>Ginga Shimakawa, Keiichiro Shaku, and Chikahiro Miyake</i>	
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The NDH-1L-PSI Supercomplex Is Important for Efficient Cyclic Electron Transport in Cyanobacteria. Fudan Gao, Jiaohong Zhao, Liping Chen, Natalia Battchikova, Zhaoxing Ran, Eva-Mari Aro, Teruo Ogawa, and Weimin Ma	
A novel NDH-1L-CpcG2-phycobilisome-PSI supercomplex essential to cyclic electron transport was identified in Synechocystis sp. strain PCC 6803.	1451
[OPEN]NAD Acts as an Integral Regulator of Multiple Defense Layers. Pierre Pétriacq, Jurriaan Ton, Oriane Patrit, Guillaume Tcherkez, and Bertrand Gakière	
NAD-mediated defense responses stimulate PAMP-triggered immunity in Arabidopsis by stimulating redox signaling and modulating the hormonal balance.	1465
Ferredoxin:NADP(H) Oxidoreductase Abundance and Location Influences Redox Poise and Stress Tolerance. Marina Kozuleva, Tatjana Goss, Manuel Twachtmann, Katherina Rudi, Jennifer Trapka, Jennifer Selinski, Boris Ivanov, Prashanth Garapati, Heinz-Juergen Steinhoff, Toshiharu Hase, Renate Scheibe, Johann P. Klare, and Guy T. Hanke	
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[OPEN]Carbon Supply and Photoacclimation Cross Talk in the Green Alga Chlamydomonas reinhardtii. Iryna Polukhina, Rikard Fristedt, Emine Dinc, Pierre Cardol, and Roberta Croce	
High-light acclimation strategies of Chlamydomonas reinhardtii cells grown in different carbon supply regimes show the high plasticity of the photosynthetic apparatus.	1494
[OPEN] Identification of Homogentisate Dioxygenase as a Target for Vitamin E Biofortification in Oilseeds. <i>Minviluz G. Stacey, Rebecca E. Cahoon, Hanh T. Nguyen, Yaya Cui, Shirley Sato, Cuong T. Nguyen, Nongnat Phoka, Kerry M. Clark, Yan Liang, Joe Forrester, Josef Batek, Phat Tien Do, David A. Sleper, Thomas E. Clemente, Edgar B. Cahoon, and Gary Stacey</i>	
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An NADPH-Oxidase/Polyamine Oxidase Feedback Loop Controls Oxidative Burst Under

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vitamin E production and herbicide tolerance in plants.

[OPEN] Comparative Analysis of Light-Harvesting Antennae and State Transition in chlorina and cpSRP Mutants. Peng Wang and Bernhard Grimm Comparative analysis of chlorina and cpSRP mutants provides the novel genetic evidence for the flexible organization of light-harvesting complexes and their dynamic and reversible allocation to the two photosystems. 1519 A NAC Transcription Factor Represses Putrescine Biosynthesis and Affects Drought Tolerance. Hao Wu, Bing Fu, Peipei Sun, Chang Xiao, and Ji-Hong Liu The NAC transcription factor of Poncirus trifoliata, PtrNAC72, interacts in arginine decarboxylase gene expression. 1532 Ethylene-Regulated Glutamate Dehydrogenase Fine-Tunes Metabolism during Anoxia-Reoxygenation. Kuen-Jin Tsai, Chih-Yu Lin, Chen-Yun Ting, and Ming-Che Shih Ethylene participates in the regulation of glutamate dehydrogenase genes during anoxia-reoxygenation and modulates metabolism by enhancing tricarboxylic acid cycle replenishment to aid recovery in Arabidopsis. 1548 Class II Cytochrome P450 Reductase Governs the Biosynthesis of Alkaloids. Claire Parage, Emilien Foureau, Franziska Kellner, Vincent Burlat, Samira Mahroug, Arnaud Lanoue, Thomas Dugé de Bernonville, Monica Arias Londono, Inês Carqueijeiro, Audrey Oudin, Sébastien Besseau, Nicolas Papon, Gaëlle Glévarec, Lucia Atehortùa, Nathalie Giglioli-Guivarc'h, Benoit St-Pierre, Marc Clastre, Sarah E. O'Connor, and Vincent Courdavault Class II cytochrome P450 reductase in Madagascar periwinkle displays a prominent contribution toward specialized metabolism by acting as the main partner of P450s dedicated to alkaloid biosynthesis. 1563 ${}^{[OPEN]}Phosphorylation\ of\ GENOMES\ UNCOUPLED\ 4\ Alters\ Stimulation\ of\ Mg\ Chelatase\ Activity\ in$ Angiosperms. Andreas Sven Richter, Caroline Hochheuser, Christian Fufezan, Laura Heinze, Franziska Kuhnert, and Bernhard Grimm GENOMES UNCOUPLED 4, a positive regulator of tetrapyrrole biosynthesis, is phosphorylated at serine 264 within a conserved C-terminal motif leading to altered stimulation of Mg chelatase in angiosperms. 1578 A Tomato Vacuolar Invertase Inhibitor Mediates Sucrose Metabolism and Influences Fruit Ripening. Guozheng Qin, Zhu Zhu, Weihao Wang, Jianghua Cai, Yong Chen, Li Li, and Shiping Tian A tomato vacuolar invertase inhibitor regulated by the global fruit ripening regulator RIPENING INHIBITOR is responsible for sucrose metabolism and fruit ripening. 1596 **CELL BIOLOGY** [OPEN] Primary Metabolism during Biosynthesis of Secondary Wall Polymers of Protoxylem Vessel Elements. Misato Ohtani, Keiko Morisaki, Yuji Sawada, Ryosuke Sano, Abigail Loren Tung Uy, Atsushi Yamamoto, Tetsuya Kurata, Yoshimi Nakano, Shiro Suzuki, Mami Matsuda, Tomohisa Hasunuma, Masami Yokota Hirai, and Taku Demura Primary metabolism is actively regulated for the biosynthesis of secondary wall polymers during the differentiation of protoxylem vessel elements. 1612 [OPEN] Secretory COPII Protein SEC31B Is Required for Pollen Wall Development. Bingchun Zhao, Haidan Shi, Wanlei Wang, Xiaoyu Liu, Hui Gao, Xiaoxiao Wang, Yinghui Zhang, Meidi Yang, Rui Li, and Yi Guo Sec31B protein is crucial for pollen wall formation by participating in COPII-coated vesicle trafficking in the tapetum in Arabidopsis. 1625 [OPEN] Genetic Interactions between PEROXIN12 and Other Peroxisome-Associated Ubiquitination Components. *Yun-Ting Kao, Wendell A. Fleming, Meredith J. Ventura, and Bonnie Bartel*

A pex12-1 mutation creating an ectopic lysine causes degradation of the RING peroxin complex and reveals PEX12 involvement in retrotranslocating peroxisome matrix protein receptors.

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ECOPHYSIOLOGY AND SUSTAINABILITY

[OPEN] Evidence for Hydraulic Vulnerability Segmentation and Lack of Xylem Refilling under Tension.

Guillaume Charrier, José M. Torres-Ruiz, Eric Badel, Regis Burlett, Brendan Choat, Herve Cochard, Chloe E. L. Delmas, Jean-Christophe Domec, Steven Jansen, Andrew King, Nicolas Lenoir, Nicolas Martin-StPaul, Gregory Alan Gambetta, and Sylvain Delzon

Direct, noninvasive observations of embolism formation and repair reveal a lack of refilling under negative pressure and a xylem hydraulic vulnerability segmentation in grapevine.

1657

[OPEN] Mechanical Failure of Fine Root Cortical Cells Initiates Plant Hydraulic Decline during Drought. Italo F. Cuneo, Thorsten Knipfer, Craig R. Brodersen, and Andrew J. McElrone

Drought-induced mechanical failure (lacunae formation) in fine root cortical cells initiates hydraulic decline under drought stress and precedes xylem embolism and root shrinkage.

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[OPEN] An Oxalyl-CoA Synthetase Is Involved in Oxalate Degradation and Aluminum Tolerance. He Qiang Lou, Wei Fan, Jia Meng Xu, Yu Long Gong, Jian Feng Jin, Wei Wei Chen, Ling Yu Liu, Mei Rong Hai, Jian Li Yang, and Shao Jian Zheng

A Vigna umbellata oxalyl-CoA synthetase, VuAAE3, confers tolerance to Al stress by regulating cytosolic oxalate metabolism.

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^[CC-BY]Developmental Control and Plasticity of Fruit and Seed Dimorphism in Aethionema arabicum.

Teresa Lenser, Kai Graeber, Özge Selin Cevik, Nezaket Adigüzel, Ali A. Dönmez, Christopher Grosche, Marcel Kettermann, Sara Mayland-Quellhorst, Zsuzsanna Mérai, Setareh Mohammadin, Thu-Phuong Nguyen, Florian Rümpler, Christina Schulze, Katja Sperber, Tina Steinbrecher, Nils Wiegand, Miroslav Strnad, Ortrun Mittelsten Scheid, Stefan A. Rensing, Michael Eric Schranz, Günter Theißen, Klaus Mummenhoff, and Gerhard Leubner-Metzger

Aethionema arabicum produces two different fruit and seed types with distinct anatomical, biomechanical, and physiological properties.

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OsHAC1;1 and OsHAC1;2 Function as Arsenate Reductases and Regulate Arsenic Accumulation. Shulin Shi, Tao Wang, Ziru Chen, Zhong Tang, Zhongchang Wu, David E. Salt, Dai-Yin Chao, and Fang-Jie Zhao

OsHAC1;1 and OsHAC1;2 function as arsenate reductases that play an important role in restricting As accumulation in rice shoots and grain when plants are exposed to arsenate.

1708

GENES, DEVELOPMENT, AND EVOLUTION

^[OPEN]Optimization of Light-Harvesting Pigment Improves Photosynthetic Efficiency. Honglei Jin, Mengshu Li, Sujuan Duan, Mei Fu, Xiaoxiao Dong, Bing Liu, Dongru Feng, Jinfa Wang, and Hong-Bin Wang

Characterization of Arabidopsis hpe1 mutants revealed a novel strategy to optimize light-harvesting pigments that improved photosynthetic efficiency and biomass production.

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 ${}^{
m [OPEN]}$ TWS1, a Novel Small Protein, Regulates Various Aspects of Seed and Plant Development. Elisa Fiume, Virginie Guyon, Carine Remoué, Enrico Magnani, Martine Miquel, Damaris Grain, and Loïc Lepiniec TWISTED SEED1 is a novel small protein located in the endomembrane system of Arabidopsis that regulates various aspects of seed and plant development. 1732 [OPEN]ZRF1 Chromatin Regulators Have Polycomb Silencing and Independent Roles in Development. Jing Feng, Donghong Chen, Alexandre Berr, and Wen-Hui Shen AtZRF1a/b play both PRC1-related and PRC1-unrelated functions in regulating transcription and multiple processes of plant growth and development. 1746 [OPEN] Histone Modifications Define Expression Bias of Homoeologous Genomes in Allotetraploid Cotton. Dewei Zheng, Wenxue Ye, Qingxin Song, Fangpu Han, Tianzhen Zhang, and Z. Jeffrey Chen Comparative analysis of immunostained metaphase chromosomes at the single cell level with ChIP-seq of individual genes reveals a chromatin basis for biased homoeolog gene expression in polyploids. 1760 [OPEN] A Rice Ca²⁺ Binding Protein Is Required for Tapetum Function and Pollen Formation. *Jing Yu*, Zhaolu Meng, Wanqi Liang, Smrutisanjita Behera, Jörg Kudla, Matthew R. Tucker, Zhijing Luo, Mingjiao Chen, Dawei Xu, Guochao Zhao, Jie Wang, Siyi Zhang, Yu-Jin Kim, and Dabing Zhang OsDEX1 binds Ca²⁺ and plays a conserved role in the development of tapetal cells and pollen formation in rice. 1772 [OPEN] The Genetics of Leaf Flecking in Maize and Its Relationship to Plant Defense and Disease Resistance. Bode A. Olukolu, Yang Bian, Brian De Vries, William F. Tracy, Randall J. Wisser, James B. Holland, and Peter J. Balint-Kurti Leaf flecking in maize may be related to disease resistance and to a diverse set of metabolic pathways. 1787 Evolutionary and Functional Analysis of Membrane-Bound NAC Transcription Factor Genes in Soybean. Shuo Li, Nan Wang, Dandan Ji, Zheyong Xue, Yanchong Yu, Yupei Jiang, Jinglin Liu, Zhenhua Liu, and Fengning Xiang Multiple levels of functional divergence contributed to gene retention after whole-genome duplication in the soybean membrane-bound NAC transcription factors gene family. 1804 Disclosing the Molecular Basis of the Postharvest Life of Berry in Different Grapevine Genotypes. Sara Zenoni, Marianna Fasoli, Flavia Guzzo, Silvia Dal Santo, Alessandra Amato, Andrea Anesi, Mauro Commisso, Markus Herderich, Stefania Ceoldo, Linda Avesani, Mario Pezzotti, and Giovanni Battista Tornielli Transcriptomic and metabolomic profiling of grapevine berries after harvest in different Vitis vinifera genotypes reveals the molecular basis of cluster detachment, senescence and dehydration stress. 1821 Phloem Transport of the Receptor DWARF14 Protein Is Required for Full Function of Strigolactones. Hiromu Kameoka, Elizabeth A. Dun, Mauricio Lopez-Obando, Philip B. Brewer, Alexandre de Saint Germain, Catherine Rameau, Christine A. Beveridge, and Junko Kyozuka

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DWARF 14 protein, a strigolactone receptor, is transported through phloem to axillary buds and the transport is

required for full function of strigolactones to suppress shoot branching.

^[OPEN]Developmental Defects Mediated by the P1/HC-Pro Potyviral Silencing Suppressor Are Not Due to Misregulation of AUXIN RESPONSE FACTOR 8. Sizolwenkosi Mlotshwa, Gail J. Pruss, John L. MacArthur, Jason W. Reed, and Vicki Vance

Misregulation of ARF8 does not underlie developmental defects in Arabidopsis expressing a P1/HC-Pro transgene.

1853

[OPEN] Analysis of Arabidopsis Accessions Hypersensitive to a Loss of Chloroplast Translation. *Nicole Parker, Yixing Wang, and David Meinke*

Genetic analysis of sequenced Arabidopsis accessions highlights the mutational landscape of an essential metabolic enzyme, with implications for chloroplast transformation and plastid protein import.

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MEMBRANES, TRANSPORT, AND BIOENERGETICS

[OPEN]Sucrose Transporter *ZmSut1* Expression and Localization Uncover New Insights into Sucrose Phloem Loading. *R. Frank Baker, Kristen A. Leach, Nathanial R. Boyer, Michael J. Swyers, Yoselin Benitez-Alfonso, Tara Skopelitis, Anding Luo, Anne Sylvester, David Jackson, and David M. Braun*

Maize SUCROSE TRANSPORTER1 functions to load sucrose into phloem companion cells, restrict its accumulation in the apoplasm, and prevent its loss during long-distance transport.

1876

[OPEN] The HvNramp5 Transporter Mediates Uptake of Cadmium and Manganese, But Not Iron. Dezhi Wu, Naoki Yamaji, Miki Yamane, Miho Kashino-Fujii, Kazuhiro Sato, and Jian Feng Ma

HvNramp5 is a plasma membrane-localized transporter, which is responsible for Mn and Cd uptake in barley.

1899

[OPEN] The Nonspecific Lipid Transfer Protein AtLtpI-4 Is Involved in Suberin Formation of *Arabidopsis thaliana* Crown Galls. *Rosalia Deeken, Stefanie Saupe, Joern Klinkenberg, Michael Riedel, Jana Leide, Rainer Hedrich, and Thomas D. Mueller*

AtLtpI-4 involvement in suberin formation is essential for crown gall growth, while ectopic expression in epidermal cells provides evidence for AtLp-I-4 functioning in extracellular lipid deposition.

1911

[OPEN] Hydrocarbons Are Essential for Optimal Cell Size, Division, and Growth of Cyanobacteria. David J. Lea-Smith, Maite L. Ortiz-Suarez, Tchern Lenn, Dennis J. Nürnberg, Laura L. Baers, Matthew P. Davey, Lucia Parolini, Roland G. Huber, Charles A. R. Cotton, Giulia Mastroianni, Paolo Bombelli, Petra Ungerer, Tim J. Stevens, Alison G. Smith, Peter J. Bond, Conrad W. Mullineaux, and Christopher J. Howe

Optimal growth and division of cyanobacteria depends upon hydrocarbon induced flexibility in the thylakoid membranes of cyanobacteria, via accumulation of these compounds within the lipid bilayer.

1928

SIGNALING AND RESPONSE

[OPEN] The Proteasome Acts as a Hub for Plant Immunity and Is Targeted by *Pseudomonas* Type III Effectors. Suayib Üstün, Arsheed Sheikh, Selena Gimenez-Ibanez, Alexandra Jones, Vardis Ntoukakis, and Frederik Börnke

The proteasome is required for local and systemic immune responses and is targeted by Pseudomonas type III effectors.

1941

[OPEN]Two Different Transcripts of a LAMMER Kinase Gene Play Opposite Roles in Disease Resistance. Liu Duan, Wenfei Xiao, Fan Xia, Hongbo Liu, Jinghua Xiao, Xianghua Li, and Shiping Wang

A LAMMER kinase gene generates two types of transcripts, the long OsDR11L and the short OsDR11S, which have opposite functions in rice resistance to a bacterial pathogen.

1959

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degrading MdbHLH104 proteins in response to Fe status in apple.

[OPEN] Ubiquitination-Related MdBT Scaffold Proteins Target a bHLH Transcription Factor for Iron Homeostasis. Qiang Zhao, Yi-Ran Ren, Qing-Jie Wang, Xiao-Fei Wang, Chun-Xiang You, and Yu-Jin Hao
BTB-TAZ proteins bridge and scaffold the CRL3 complex to modulate iron homeostasis by ubiquitinating and

^[OPEN]Arabidopsis Responds to *Alternaria alternata* Volatiles by Triggering Plastid Phosphoglucose Isomerase-Independent Mechanisms. *Ángela María Sánchez-López, Abdellatif Bahaji, Nuria De Diego, Marouane Baslam, Jun Li, Francisco José Muñoz, Goizeder Almagro, Pablo García-Gómez, Kinia Ameztoy, Adriana Ricarte-Bermejo, Ondřej Novák, Jan F. Humplík, Lukáš Spíchal, Karel Doležal, Sergio Ciordia, María Carmen Mena, Rosana Navajas, Edurne Baroja-Fernández, and Javier Pozueta-Romero*

Cytokinin-mediated responses of Arabidopsis to volatile compounds emitted by pathogenic microorganisms involve the activation of plastidic phosphoglucose isomerase-independent mechanisms.

1989

1973

[OPEN] A Legume TOR Protein Kinase Regulates *Rhizobium* Symbiosis and Is Essential for Infection and Nodule Development. *Kalpana Nanjareddy, Lourdes Blanco, Manoj-Kumar Arthikala, Xóchitl Alvarado-Affantranger, Carmen Quinto, Federico Sánchez, and Miguel Lara*

Target of rapamycin regulates infection and nodule development during rhizobial symbiosis in Phaseolus vulgaris.

2002

[OPEN] Regulation of Stomatal Defense by Air Relative Humidity. Shweta Panchal, Reejana Chitrakar, Blaine K. Thompson, Nisita Obulareddy, Debanjana Roy, W. Sealy Hambright, and Maeli Melotto

High relative humidity suppresses Pseudomonas syringae-triggered stomatal closure by regulating hormone signaling in guard cells.

2021

The Thiamine Biosynthesis Gene *THI1* Promotes Nodule Growth and Seed Maturation. *Miwa Nagae, Martin Parniske, Masayoshi Kawaguchi, and Naoya Takeda*

A mutant in the thiamine biosynthesis gene THI1 reduces the size of root nodules and leads to high frequency of immature seeds in Lotus japonicus.

2033

[OPEN] Phytoglobins Improve Hypoxic Root Growth by Alleviating Apical Meristem Cell Death. *Mohamed M. Mira, Robert D. Hill, and Claudio Stasolla*

Phytoglobin expression in hypoxic root apical meristems alleviates programmed cell death by removing NO and moderating ethylene and ROS in the maize meristematic cells.

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SYSTEMS AND SYNTHETIC BIOLOGY

[OPEN] Central Metabolic Responses to Ozone and Herbivory Affect Photosynthesis and Stomatal Closure. Stefano Papazian, Eliezer Khaling, Christelle Bonnet, Steve Lassueur, Philippe Reymond, Thomas Moritz, James D. Blande, and Benedicte R. Albrectsen

When confronted with sequential abiotic and biotic stress, black mustard regulates glycerol and central energy metabolism to prioritize processes of photosynthesis and stomatal osmoregulation.

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