

**On the Cover:** The cover image, entitled “The shape of roots to come,” was composed by Alexander Bucksch from the computed binary image masks of cowpea roots. The image conveys the diversity of root shapes of an emerging crop and the increasingly important algorithmic advances enabled by computational plant sciences. As described in Bucksch et al. (pp. 470–486), computational analysis of root systems excavated and imaged in field conditions enabled the phenotypic differentiation of 188 cowpea genotypes.

## FOCUS ON ROOTS

### EDITORIAL

Focus on Roots. *Niko Geldner and David E. Salt*

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### BREAKTHROUGH TECHNOLOGIES

<sup>[W][OPEN]</sup>Hairy Root Transformation Using *Agrobacterium rhizogenes* as a Tool for Exploring Cell Type-Specific Gene Expression and Function Using Tomato as a Model. *Mily Ron, Kaisa Kajala, Germain Pauluzzi, Dongxue Wang, Mauricio A. Reynoso, Kristina Zumstein, Jasmine Garcha, Sonja Winte, Helen Masson, Soichi Inagaki, Fernán Federici, Neelima Sinha, Roger B. Deal, Julia Bailey-Serres, and Siobhan M. Brady*

*Testing tomato gene expression with tagged nuclei and ribosomes and CRISPR/Cas9 genome editing shows conservation of SHORT-ROOT gene function.*

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<sup>[W][OPEN]</sup>Image-Based High-Throughput Field Phenotyping of Crop Roots. *Alexander Bucksch, James Burrridge, Larry M. York, Abhiram Das, Eric Nord, Joshua S. Weitz, and Jonathan P. Lynch*

*Automatic methods developed or reproducible field-based phenotyping allow distinction of genotypes, including 13 newly accessible plant root traits.*

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<sup>[C]</sup>Visualization of Root Water Uptake: Quantification of Deuterated Water Transport in Roots Using Neutron Radiography and Numerical Modeling. *Mohsen Zarebanadkouki, Eva Kroener, Anders Kaestner, and Andrea Carminati*

*Neutron radiography traces the transport of deuterated water in soil and roots to reconstruct the water flow across the root tissue and along the xylem.*

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### UPDATES

Plant Nutrition: Root Transporters on the Move. *Enric Zelazny and Grégory Vert*

*The dynamics of nutrient transporters and channels emerges as a critical and highly regulated cellular process controlling nutrient uptake and distribution in plant roots.*

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Root Nutrient Foraging. *Ricardo F.H. Giehl and Nicolaus von Wirén*

*Root morphological traits that are relevant for nutrient acquisition are regulated by nutrients and the plant's nutritional status.*

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Natural Variation of Root Traits: From Development to Nutrient Uptake. *Daniela Ristova and Wolfgang Busch*

*Natural variation of root growth informs on processes that govern root development, responses to nutrient availability, and ion uptake and homeostasis.*

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Radial Transport of Nutrients: The Plant Root as a Polarized Epithelium. *Marie Barberon and Niko Geldner*

*Different routes underlie radial transport of nutrients in plant roots and are influenced by the endodermis permeability and the polarity of transporters.* 528

Branching Out in Roots: Uncovering Form, Function, and Regulation. *Jonathan A. Atkinson, Amanda Rasmussen, Richard Traini, Ute Voß, Craig Sturrock, Sacha J. Mooney, Darren M. Wells, and Malcolm J. Bennett*

*The diversity of postembryonic root forms and their functions add to our understanding of the genes, signals and mechanisms regulating lateral and adventitious root branching in the plant models Arabidopsis and rice.* 538

Beyond the Barrier: Communication in the Root through the Endodermis. *Neil E. Robbins II, Charlotte Trontin, Lina Duan, and José R. Dinneny*

*The endodermis acts as a barrier to solute and water movement but also has important functions in signaling and morphogenesis.* 551

Strigolactone Involvement in Root Development, Response to Abiotic Stress, and Interactions with the Biotic Soil Environment. *Yoram Kapulnik and Hinanit Koltai*

*Strigolactones play a role in root development, root response to nutrient deficiency, and plant interactions in the rhizosphere.* 560

The Origin and Early Evolution of Roots. *Paul Kenrick and Christine Strullu-Derrien*

*Exceptionally well-preserved fossils shed light on the earliest roots and their interactions with the environment.* 570

<sup>[C]</sup>Functional Soil Microbiome: Belowground Solutions to an Aboveground Problem. *Venkatachalam Lakshmanan, Gopinath Selvaraj, and Harsh P. Bais*

*The functional soil microbiome is an important parameter in developing a sustainable and effective strategy to increase crop yield and food security.* 689

<sup>[C]</sup>Biotic Interactions in the Rhizosphere: A Diverse Cooperative Enterprise for Plant Productivity. *Clelia De-la-Peña and Víctor M. Loyola-Vargas*

*Roots and microbes secrete organic compounds into the rhizosphere that influence plant productivity.* 701

<sup>[C]</sup>Perennial Roots to Immortality. *Sergi Munné-Bosch*

*Roots play a key role in determining long life in perennials.* 720

## RESEARCH ARTICLES

<sup>[W]</sup><sup>[OPEN]</sup>Low Crown Root Number Enhances Nitrogen Acquisition from Low-Nitrogen Soils in Maize. *Patompong Saengwilai, Xiaoli Tian, and Jonathan Paul Lynch*

*Low crown root number improves nitrogen acquisition in maize by enhancing deep soil exploration in low-nitrogen soils.* 581

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[C][W][OPEN]The Optimal Lateral Root Branching Density for Maize Depends on Nitrogen and Phosphorus Availability. Johannes Auke Postma, Annette Dathe, and Jonathan Paul Lynch

*The optimal lateral root branching density in the maize root system depends on the relative availability of nitrate (a mobile soil resource) and phosphorus (an immobile soil resource), with the optimum shifting to more branches when the nitrate-to-phosphorus ratio is high.*

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[W][OPEN]Origin and Development of the Root Cap in Rice. Likai Wang, Huangwei Chu, Zhiyong Li, Juan Wang, Jintao Li, Yang Qiao, Yanru Fu, Tongmin Mou, Chunli Chen, and Jian Xu

*Cellular and molecular events are inherent to the formation and development of the root cap in rice.*

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[W][OPEN]The anthocyanin reduced Tomato Mutant Demonstrates the Role of Flavonols in Tomato Lateral Root and Root Hair Development. Gregory S. Maloney, Kathleen T. DiNapoli, and Gloria K. Muday

*Flavonols contribute to lateral root development through the regulation of auxin transport and root hair and they modulate the levels of reactive oxygen species.*

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[W][OPEN]The ASH1-RELATED3 SET-Domain Protein Controls Cell Division Competence of the Meristem and the Quiescent Center of the Arabidopsis Primary Root. Robert Kumpf, Tage Thorstensen, Mohummad Aminur Rahman, Jefri Heyman, H. Zeynep Nenseth, Tim Lammens, Ullrich Herrmann, Ranjan Swarup, Silje Veie Veiseth, Gitika Emberland, Malcolm J. Bennett, Lieven De Veylder, and Reidunn B. Aalen

*A histone Lys methyltransferase gene is expressed in the root stem cell niche and contributes to coordinated divisions in the immediate cell lineage originating from the same stem cell.*

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[W][OPEN]Abscisic Acid and LATERAL ROOT ORGAN DEFECTIVE/NUMEROUS INFECTIONS AND POLYPHENOLICS Modulate Root Elongation via Reactive Oxygen Species in *Medicago truncatula*. Chang Zhang, Amanda Bousquet, and Jeanne M. Harris

*Both abscisic acid and a nitrate transporter regulate the production of ROS and the expression of superoxide-generating NADPH oxidase enzymes to regulate root elongation.*

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[C][W][OPEN]Duplicate and Conquer: Multiple Homologs of PHOSPHORUS-STARVATION TOLERANCE1 Enhance Phosphorus Acquisition and Sorghum Performance on Low-Phosphorus Soils. Barbara Hufnagel, Sylvia M. de Sousa, Lidianne Assis, Claudia T. Guimaraes, Willmar Leiser, Gabriel C. Azevedo, Barbara Negri, Brandon G. Larson, Jon E. Shaff, Maria Marta Pastina, Beatriz A. Barros, Eva Weltzien, Henry Frederick W. Rattunde, Joao H. Viana, Randy T. Clark, Alexandre Falcão, Rodrigo Gazaffi, Antonio Augusto F. Garcia, Robert E. Schaffert, Leon V. Kochian, and Jurandir V. Magalhaes

*Sorghum homologs of a rice gene contributing to P-starvation tolerance enhance P uptake and crop performance in low-P soils via modulation of root system morphology and architecture.*

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[W][OPEN]Activity of the Brassinosteroid Transcription Factors BRASSINAZOLE RESISTANT1 and BRASSINOSTEROID INSENSITIVE1-ETHYL METHANESULFONATE-SUPPRESSOR1/BRASSINAZOLE RESISTANT2 Blocks Developmental Reprogramming in Response to Low Phosphate Availability. Amar Pal Singh, Yulia Fridman, Lilach Friedlander-Shani, Danuse Tarkowska, Miroslav Strnad, and Sigal Savaldi-Goldstein

*Pi deprivation shifts the subcellular distribution of two key brassinosteroid-related transcriptional effectors to trigger shallower root system architecture.*

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- [W][OPEN]Root Cortical Aerenchyma Enhances Nitrogen Acquisition from Low-Nitrogen Soils in Maize. *Patompong Saengwilai, Eric A. Nord, Joseph G. Chimungu, Kathleen M. Brown, and Jonathan Paul Lynch*  
*Abundant root cortical aerenchyma improves plant growth under nitrogen-limiting conditions by decreasing root metabolic costs, enhancing soil exploration in deep soil strata, thereby increasing nitrogen acquisition at greater depths.* 726
- [W][OPEN]It's Complicated: Intraroot System Variability of Respiration and Morphological Traits in Four Deciduous Tree Species. *Boris Rewald, Andreas Rechenmacher, and Douglas L. Godbold*  
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- [C][W][OPEN]Loss of Cytosolic Phosphoglucose Isomerase Affects Carbohydrate Metabolism in Leaves and Is Essential for Fertility of Arabidopsis. *Hans-Henning Kunz, Shirin Zamani-Nour, Rainer E. Häusler, Katja Ludewig, Julian I. Schroeder, Irina Malinova, Joerg Fettke, Ulf-Ingo Flügge, and Markus Gierth*  
*An enzyme of cytosolic hexose phosphate metabolism is essential for plant reproduction and important for photosynthesis.* 753
- [W]A Secreted Protein with Plant-Specific Cysteine-Rich Motif Functions as a Mannose-Binding Lectin That Exhibits Antifungal Activity. *Takuya Miyakawa, Ken-ichi Hatano, Yumiko Miyauchi, You-ichi Suwa, Yoriko Sawano, and Masaru Tanokura*  
*Ginkbilobin2 is shown to exert antifungal activity through its interaction with  $\alpha$ 1,2-linked mannose chains of fungal cell-wall mannan, which provides clues to the molecular function of the DUF26 protein family.* 766
- [W]Ectopic Terpene Synthase Expression Enhances Sesquiterpene Emission in *Nicotiana attenuata* without Altering Defense or Development of Transgenic Plants or Neighbors. *Meredith C. Schuman, Evan C. Palmer-Young, Axel Schmidt, Jonathan Gershenzon, and Ian T. Baldwin*  
*Plants expressing two sesquiterpene synthases emitted increased quantities of target volatiles without changes to other volatiles, defense, growth, or yield in transformants or neighboring plants.* 779

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[C][W] Unraveling the Mechanism Underlying the Glycosylation and Methylation of Anthocyanins in Peach. Jun Cheng, Guochao Wei, Hui Zhou, Chao Gu, Sornkanok Vimolmangkang, Liao Liao, and Yuepeng Han

*Diversification of anthocyanins in peach is attributed to glycosylation and methylation.*

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## CELL BIOLOGY

[W][OPEN] Laccases Direct Lignification in the Discrete Secondary Cell Wall Domains of Protoxylem. Mathias Schuetz, Anika Benske, Rebecca A. Smith, Yoichiro Watanabe, Yuki Tobimatsu, John Ralph, Taku Demura, Brian Ellis, and A. Lacey Samuels

*The discrete localization of laccases to secondary cell walls directs lignification in protoxylem.*

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[W][OPEN] FRIENDLY Regulates Mitochondrial Distribution, Fusion, and Quality Control in Arabidopsis. Amr M. El Zawily, Markus Schwarzländer, Iris Finkemeier, Iain G. Johnston, Abdelilah Benamar, Yongguo Cao, Clémence Gissot, Andreas J. Meyer, Ken Wilson, Raju Datla, David Macherel, Nick S. Jones, and David C. Logan

*Disruption of intermitochondrial association affects mitochondrial quality control, leading to mitochondrial stress, cell death, and strong growth defects.*

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## ECOPHYSIOLOGY AND SUSTAINABILITY

[W][OPEN] Leaf Vein Length per Unit Area Is Not Intrinsically Dependent on Image Magnification: Avoiding Measurement Artifacts for Accuracy and Precision. Lauren Sack, Marissa Caringella, Christine Scoffoni, Chase Mason, Michael Rawls, Lars Markesteijn, and Lourens Poorter

*Measurements of leaf vein length per area do not increase systematically with image magnification, contrary to a recent claim, given appropriate attention toward accuracy and precision.*

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[W][OPEN] Root-Secreted Nicotianamine from *Arabidopsis halleri* Facilitates Zinc Hypertolerance by Regulating Zinc Bioavailability. Munkhtsetseg Tsednee, Shun-Chung Yang, Der-Chuen Lee, and Kuo-Chen Yeh

*Root secretion of nicotianamine from zinc-hyperaccumulating Arabidopsis halleri facilitates zinc hypertolerance through coordinating zinc uptake and iron homeostasis in roots.*

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[W][OPEN] Increased Ratio of Electron Transport to Net Assimilation Rate Supports Elevated Isoprenoid Emission Rate in Eucalypts under Drought. Kaidala Ganesha Srikanta Dani, Ian McLeod Jamie, Iain Colin Prentice, and Brian James Atwell

*Volatile isoprenoids emitted by plants, enhanced by photosynthesis under drought, have a significant influence on ozone pollution and global climate.*

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## GENES, DEVELOPMENT, AND EVOLUTION

[C][W][OPEN] TRANSLOCASE OF THE INNER MEMBRANE9 and 10 Are Essential for Maintaining Mitochondrial Function during Early Embryo Cell and Endosperm Free Nucleus Divisions in Arabidopsis. Yingtian Deng, Wenxuan Zou, Gang Li, and Jie Zhao

*Two mitochondrial translocases are essential for the division during early embryo and endosperm development in Arabidopsis.*

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[C][W] Digital Inventory of Arabidopsis Transcripts Revealed by 61 RNA Sequencing Samples. Xiaoyong Sun, Qiuying Yang, Zhiping Deng, and Xinfu Ye

*Analysis of 61 RNA-seq samples reveals the existence of common, rare, and nondetectable transcripts, including ubiquitous transcripts, dominant/subordinate transcripts, and switch transcripts, in terms of their expression and transcript ratio.*

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[W][OPEN] ATP-Dependent Binding Cassette Transporter G Family Member 16 Increases Plant Tolerance to Abscisic Acid and Assists in Basal Resistance against *Pseudomonas syringae* DC3000. Hao Ji, Yanhui Peng, Nicole Meckes, Sara Allen, C. Neal Stewart Jr, and M. Brian Traw

*An ATP-dependent binding cassette transporter contributes to plant resistance to infection by *Pseudomonas syringae* and tolerance of abscisic acid.*

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[C][W][OPEN] The VASCULATURE COMPLEXITY AND CONNECTIVITY Gene Encodes a Plant-Specific Protein Required for Embryo Provasculature Development. Hannetz Roschttardtz, Julio Paez-Valencia, Tejasvi Dittakavi, Sathya Jali, Francisca C. Reyes, Gary Baisa, Pauline Anne, Lionel Gissot, Jean-Christophe Palauqui, Patrick H. Masson, Sebastian Y. Bednarek, and Marisa S. Otegui

*A plant-specific protein controls the complexity and connectivity of veins in cotyledons.*

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[C][W][OPEN] Genetic Analysis of DEFECTIVE KERNEL1 Loop Function in Three-Dimensional Body Patterning in *Physcomitrella patens*. Viktor Demko, Pierre-François Perroud, Wenche Johansen, Charles F. Delwiche, Endymion D. Cooper, Pål Remme, Ako Eugene Ako, Karl G. Kugler, Klaus F.X. Mayer, Ralph Quatrano, and Odd-Arne Olsen

*A proposed regulatory loop segment of the DEK1 transmembrane domain is required for gametophore patterning in *Physcomitrella patens*.*

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## MEMBRANES, TRANSPORT, AND BIOENERGETICS

[W][OPEN] Tomato Fruit Chromoplasts Behave as Respiratory Bioenergetic Organelles during Ripening. Marta Renato, Iринi Pateraki, Albert Boronat, and Joaquín Azcón-Bieto

*Tomato fruit chromoplasts exhibit a respiratory process linked to ATP synthesis that uses NAD(P)H as electron donors and represents 25% of total ripe fruit respiration.*

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[C][W] Inhibition of Nitrate Transporter 1.1-Controlled Nitrate Uptake Reduces Cadmium Uptake in Arabidopsis. Qian Qian Mao, Mei Yan Guan, Kai Xing Lu, Shao Ting Du, Shi Kai Fan, Yi-Quan Ye, Xian Yong Lin, and Chong Wei Jin

*Cadmium inhibits controlled nitrate uptake by roots, but this has the beneficial effect of reducing cadmium entry into roots.*

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[W][OPEN] The Role of a Potassium Transporter OsHAK5 in Potassium Acquisition and Transport from Roots to Shoots in Rice at Low Potassium Supply Levels. Tianyuan Yang, Song Zhang, Yibing Hu, Fachi Wu, Qingdi Hu, Guang Chen, Jing Cai, Ting Wu, Nava Moran, Ling Yu, and Guohua Xu

*A high-affinity rice potassium transporter plays a major role in K acquisition by roots faced with low external K and in K upward transport from roots to shoots in K-deficient rice plants.*

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[W][OPEN] Voltage-Sensor Transitions of the Inward-Rectifying K<sup>+</sup> Channel KAT1 Indicate a Latching Mechanism Biased by Hydration within the Voltage Sensor. *Cécile Lefoulon, Rucha Karnik, Annegret Honsbein, Paul Vijay Gutla, Christopher Grefen, Janin Riedelsberger, Tomás Poblete, Ingo Dreyer, Wendy Gonzalez, and Michael R. Blatt*

*Manipulating the electrostatic charge network that stabilizes the voltage sensor of the KAT1 K<sup>+</sup> channel displaces channel gating across more than 140 mV within the physiological voltage range.*

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[W][OPEN] Dynamics of Carbon-Concentrating Mechanism Induction and Protein Relocalization during the Dark-to-Light Transition in Synchronized *Chlamydomonas reinhardtii*. *Madeline C. Mitchell, Moritz T. Meyer, and Howard Griffiths*

*In synchronized Chlamydomonas reinhardtii cells, the carbon-concentrating mechanism is induced prior to dawn, which coincides with the relocalization of key proteins to the chloroplast pyrenoid.*

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## SIGNALING AND RESPONSE

[OPEN] Distinct Signaling Mechanisms in Multiple Developmental Pathways by the SCRAMBLED Receptor of Arabidopsis. *Su-Hwan Kwak, Sooah Woo, Myeong Min Lee, and John Schiefelbein*

*A single receptor-like kinase exhibits distinct signaling requirements to mediate different developmental events in Arabidopsis.*

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[W][OPEN] Distinct Roles for Mitogen-Activated Protein Kinase Signaling and CALMODULIN-BINDING TRANSCRIPTIONAL ACTIVATOR3 in Regulating the Peak Time and Amplitude of the Plant General Stress Response. *Marta Bjornson, Geoffrey Benn, Xingshun Song, Luca Comai, Annaliese K. Franz, Abhaya M. Dandekar, Georgia Drakakaki, and Katayoon Dehesh*

*Unbiased screening through forward and chemical genetics unveils components distinctly regulating the peak time and amplitude of the plant general stress responses.*

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[W] Oxidative Stress Contributes to Autophagy Induction in Response to Endoplasmic Reticulum Stress in *Chlamydomonas reinhardtii*. *Marta Pérez-Martín, María Esther Pérez-Pérez, Stéphane D. Lemaire, and José L. Crespo*

*Alteration of the intracellular redox state during endoplasmic reticulum stress contributes to autophagy activation in Chlamydomonas reinhardtii.*

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[W][OPEN] Arabidopsis Triphosphate Tunnel Metalloenzyme2 Is a Negative Regulator of the Salicylic Acid-Mediated Feedback Amplification Loop for Defense Responses. *Huoi Ung, Wolfgang Moeder, and Keiko Yoshioka*

*A triphosphate tunnel metalloenzyme is a negative regulator in amplification of SA-dependent defense responses.*

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[C][W] Large-Scale Identification of Gibberellin-Related Transcription Factors Defines Group VII ETHYLENE RESPONSE FACTORS as Functional DELLA Partners. *Nora Marín-de la Rosa, Berta Sotillo, Pal Miskolczi, Daniel J. Gibbs, Jorge Vicente, Pilar Carbonero, Luis Oñate-Sánchez, Michael J. Holdsworth, Rishikesh Bhalerao, David Alabadí, and Miguel A. Blázquez*

*Transcription factors of the APETALA2 superfamily are regulated by DELLAs which represents a cross regulatory node for gibberellins and ethylene to control apical hook opening.*

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## SYSTEMS AND SYNTHETIC BIOLOGY

<sup>[W]</sup>Label-Free Protein Quantification for Plant Golgi Protein Localization and Abundance. *Nino Nikolovski, Pavel V. Shliaha, Laurent Gatto, Paul Dupree, and Kathryn S. Lilley*

*A quantitative proteomic approach enables unambiguous protein localization to the plant Golgi apparatus and rank ordering of the Golgi resident proteins by abundance, providing a unique view on the organization of this organelle.*

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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> The online version of this article contains Web-only data.

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