

**On the Cover:** The initiation and development of shoot apical meristems (SAMs) determines plant and inflorescence architecture and thus grain yield in crop plants. SAMs give rise to vegetative structures, such as leaves and stems, and reproductive organs, such as inflorescences and flowers. The timing of developmental transitions determines the balance between vegetative versus reproductive growth, traits that have been strongly modified during domestication and crop improvement. It is consequently of great interest to identify the genes and genetic variants which influence the timing of meristem identity transitions and thereby the number leaves, flowers and seeds. The image shows the developing inflorescence of the barley mutant *many noded dwarf1 (mnd1)*. The transition from a vegetative SAM to a reproductive inflorescence is delayed and spikelet meristems at the base of the inflorescence revert to vegetative branch meristem-like organs (orange colored) and are subtended by outgrowing bracts which are leaf-like structures (green colored). The *mnd1* mutant serves as a model to study developmental phase changes and the balance of vegetative versus reproductive growth. Image credit: Rainer Franzen and Agatha Walla.

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## LETTERS

<sup>[OPEN]</sup>Distance-to-Time Conversion Using Gompertz Model Reveals Age-Dependent Aerenchyma Formation in Rice Roots. Takaki Yamauchi, Mikio Nakazono, Yoshiaki Inukai, and Nobuhiro Tsutsumi  
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<sup>[OPEN]</sup>Coordinated Systemic Stomatal Responses in Soybean. Sara I. Zandalinas, Itay Hamus Cohen, Felix B. Fritschi, and Ron Mittler  
*Rapid and coordinated systemic stomatal responses occur in the crop plant soybean and could be involved in acclimation to changes in light conditions occurring in the field as a result of sunflecks.* 1428

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*The quantification of auxin can be compromised by the breakdown of labile auxin-related compounds during sample preparation.* 1432

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[OPEN] Immunodetection of Cell Wall Pectin Galactan Opens up New Avenues for Phloem Research. *Dustin M. Ray and Jessica A. Savage*

*A galactan epitope is present in two woody plant cell walls and can be used for immunological analysis of sieve element anatomical characteristics.*

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## UPDATES

[OPEN] Organellar and Secretory Ribonucleases: Major Players in Plant RNA Homeostasis. *Gustavo C. MacIntosh and Benoît Castandet*

*Organellar and secretory RNases, associated with different cellular compartments, are essential to maintain cellular homeostasis during development and in stress responses.*

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[OPEN] Plant Genome Editing and the Relevance of Off-Target Changes. *Nathaniel Graham, Gunvant B. Patil, David M. Bubeck, Raymond C. Dobert, Kevin C. Glenn, Annie T. Gutsche, Sandeep Kumar, John A. Lindbo, Luis Maas, Gregory D. May, Miguel E. Vega-Sanchez, Robert M. Stupar, and Peter L. Morrell*

*With well-designed protocols and guide RNAs, off-target changes induced by site-directed nucleases are negligible with fewer genetic differences than from standing variation or induced mutagenesis.*

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## BREAKTHROUGH TECHNOLOGIES, TOOLS, AND RESOURCES

[OPEN] Bioimaging Techniques Reveal Foliar Phosphate Uptake Pathways and Leaf Phosphorus Status. *Maja Arsic, Stine Le Tougaard, Daniel Pergament Persson, Helle Juel Martens, Casey L. Doolette, Enzo Lombi, Jan Kofod Schjoerring, and Søren Husted*

*Bioimaging techniques trace foliar phosphate uptake pathways and visualize whole-leaf photosynthetic restoration processes in phosphorus-deficient barley.*

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[OPEN] Relationship between Cell Cycle and Diel Transcriptomic Changes in Metabolism in a Unicellular Red Alga. *Takayuki Fujiwara, Shunsuke Hirooka, Ryudo Ohbayashi, Ryo Onuma, and Shin-ya Miyagishima*

*A data set of diel and cell-cycle-dependent transcriptomic changes in a eukaryotic alga with a minimal set of genes clarifies the relationship between metabolism and the cell cycle.*

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## RESEARCH ARTICLES

### BIOCHEMISTRY AND METABOLISM

[OPEN] NAA50 Is an Enzymatically Active N<sup>α</sup>-Acetyltransferase That Is Crucial for Development and Regulation of Stress Responses. *Laura Armbruster, Eric Linster, Jean-Baptiste Boyer, Annika Brünje, Jürgen Eirich, Iwona Stephan, Willy V. Bienvenut, Jonas Weidenhausen, Thierry Meinel, Ruediger Hell, Irmgard Sinning, Iris Finkemeier, Carmela Giglione, and Markus Wirtz*

*Knockout of an N-acetyltransferase, AtNAA50, causes arrest of growth in the model plant *Arabidopsis* but does not affect the activity of the essential NatA complex.*

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### CELL BIOLOGY

[OPEN] The SUN Domain Proteins OsSUN1 and OsSUN2 Play Critical but Partially Redundant Roles in Meiosis. *Fanfan Zhang, Lijun Ma, Chao Zhang, Guijie Du, Yi Shen, Ding Tang, Yafei Li, Hengxiu Yu, Bojun Ma, and Zhukuan Cheng*

*Two SUN domain proteins have partially redundant functions in the regulation of telomere clustering, homologous pairing, and crossover formation during rice meiosis.*

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[OPEN] Chloroplast Autophagy and Ubiquitination Combine to Manage Oxidative Damage and Starvation Responses. *Yuta Kikuchi, Sakuya Nakamura, Jesse D. Woodson, Hiroyuki Ishida, Qihua Ling, Jun Hidema, R. Paul Jarvis, Shinya Hagihara, and Masanori Izumi*

*Chloroplast autophagy and chloroplast-associated ubiquitination independently contribute to chloroplast degradation, the management of ROS damage, and the adaptation to starvation.*

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[CC-BY] *MutS* homologue 4 and *MutS* homologue 5 Maintain the Obligate Crossover in Wheat Despite Stepwise Gene Loss following Polyploidization. *Stuart D. Desjardins, Daisy E. Ogle, Mohammad A. Ayoub, Stefan Heckmann, Ian R. Henderson, Keith J. Edwards, and James D. Higgins*  
*MSH4 and MSH5 promote class I crossovers in wheat despite pseudogenization of MSH5B in the tetraploid and MSH5B and MSH4D in the hexaploid, which may be an adaptive response to modulate recombination.* 1545

[OPEN] Quantitative Structural Organization of Bulk Apical Membrane Traffic in Pollen Tubes. *Gleb Grebnev, Mislav Cvitkovic, Carolin Fritz, Giampiero Cai, Ana-Suncana Smith, and Benedikt Kost*  
*Massive secretion underlying pollen tube tip growth delivers proteins and lipids to the same apical plasma membrane domain and is balanced by endocytic lipid recycling in a defined subapical region.* 1559

[OPEN] Functional Analysis of the Plant Chromosomal Passenger Complex. *Shinichiro Komaki, Hidenori Takeuchi, Yuki Hamamura, Maren Heese, Takashi Hashimoto, and Arp Schnittger*  
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*Cell-wall thickening, rather than starch accumulation, leads to a decrease in mesophyll conductance after a reduction in the sink-source ratio in soybean and French bean.* 1600

[OPEN] Leaf Carbon Export and Nonstructural Carbohydrates in Relation to Diurnal Water Dynamics in Mature Oak Trees. *Jess T. Gersony, Uri Hochberg, Fulton E. Rockwell, Maria Park, Paul P. G. Gauthier, and N. Michele Holbrook*  
*Leaves of red oak trees maintain carbon export throughout the day despite midday water loss while also accumulating sugars in their leaves that account for 50% of the diurnal osmotic adjustment.* 1612

[OPEN] Cutinsomes and CUTIN SYNTHASE1 Function Sequentially in Tomato Fruit Cutin Deposition. *Patricia Segado, José Alejandro Heredia-Guerrero, Antonio Heredia, and Eva Domínguez*  
*In tomato fruit development, cutinsomes participate in procuticle deposition and CUTIN SYNTHASE1 in cutin synthesis during the later cell expansion period.* 1622

Drought-Induced Mortality: Branch Diameter Variation Reveals a Point of No Recovery in Lavender Species. *Lia Lamacque, Guillaume Charrier, Fernanda dos Santos Farnese, Benjamin Lemaire, Thierry Améglio, and Stéphane Herbette*  
*Under extreme drought, death of lavender plants occurs when the water storage of the elastic compartment of the branch is exhausted.* 1638

## GENES, DEVELOPMENT AND EVOLUTION

[OPEN] Calmodulin HvCaM1 Negatively Regulates Salt Tolerance via Modulation of HvHKT1s and HvCAMTA4. *Qiufang Shen, Liangbo Fu, Tingting Su, Lingzhen Ye, Lu Huang, Liuhui Kuang, Liyuan Wu, Dezhi Wu, Zhong-Hua Chen, and Guoping Zhang*  
*Barley calmodulin HvCaM1 regulates salt tolerance by mediating the expression of Na<sup>+</sup> transport-related HKT1 genes and the transcriptional regulation by a CaM-binding transcription activator, HvCAMTA4.* 1650

[OPEN] Genes of the RAV Family Control Heading Date and Carpel Development in Rice. *Michela Osnato, Luis Matias-Hernandez, Andrea Elizabeth Aguilar-Jaramillo, Martin M. Kater, and Soraya Pelaz*  
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The miR399-CsUBC24 Module Regulates Reproductive Development and Male Fertility in Citrus. *Rong Wang, Yan-Ni Fang, Xiao-Meng Wu, Mei Qing, Chao-Chao Li, Kai-Dong Xie, Xiu-Xin Deng, and Wen-Wu Guo*  
*The functions of a microRNA in flower development and pollen sterility are related to its regulation of Pi homeostasis and interactions of that target with floral development regulators.* 1681

- The Kernel Size-Related Quantitative Trait Locus *qKW9* Encodes a Pentatricopeptide Repeat Protein That Affects Photosynthesis and Grain Filling. Juan Huang, Gang Lu, Lei Liu, Mohammad Sharif Raihan, Jieting Xu, Liumei Jian, Lingxiao Zhao, Thu M. Tran, Qinghua Zhang, Jie Liu, Wenqiang Li, Cunxu Wei, David M. Braun, Qing Li, Alisdair R. Fernie, David Jackson, and Jianbing Yan  
*A pentatricopeptide repeat protein exerts a quantitative effect on maize kernel weight and size by affecting photosynthesis and grain filling.* 1696
- The N<sup>1</sup>-Methyladenosine Methylome of Petunia mRNA. Weiyuan Yang, Jie Meng, Juanxu Liu, Beibei Ding, Tao Tan, Qian Wei, and Yixun Yu  
*Silencing of petunia tRNA-specific methyltransferase 61A decreases mRNA m<sup>1</sup>A levels, leading to abnormal leaf development.* 1710
- MEMBRANES, TRANSPORT AND BIOENERGETICS**
- Characterization of a Giant PSI Supercomplex in the Symbiotic Dinoflagellate Symbiodiniaceae. Hiroki Kato, Ryutaro Tokutsu, Hisako Kubota-Kawai, Raymond N. Burton-Smith, Eunuchul Kim, and Jun Minagawa  
*The Symbiodiniaceae symbiotic dinoflagellate Breviolum minutum has a giant PSI supercomplex that harbors photoprotective pigments.* 1725
- [OPEN] A Chlorophyte Alga Utilizes Alternative Electron Transport for Primary Photoprotection. Maxwell A. Ware, Darcy Hunstiger, Michael Cantrell, and Graham Peers  
*Constitutive small antennae, alternative electron transport, and an efficient PSII turnover capacity enable *Desmodesmus armatus* to photosynthesize efficiently.* 1735
- [OPEN] Regulation of Light Harvesting in *Chlamydomonas reinhardtii* Two Protein Phosphatases Are Involved in State Transitions. Federica Cariti, Marie Chazaux, Linnka Lefebvre-Legendre, Paolo Longoni, Bart Ghysels, Xenie Johnson, and Michel Goldschmidt-Clermont  
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- SIGNALLING AND RESPONSE**
- [OPEN] Ectopic Expression of a Self-Incompatibility Module Triggers Growth Arrest and Cell Death in Vegetative Cells. Zongcheng Lin, Fei Xie, Marina Triviño, Mansour Karimi, Maurice Bosch, Veronica E. Franklin-Tong, and Moritz K. Nowack  
**Papaver rhoeas* S-determinants, which specify self-incompatibility and rejection of self-pollen, trigger growth arrest and programmed cell death in vegetative *Arabidopsis* tissues when expressed ectopically.* 1765
- [OPEN] Low Blue Light Enhances Phototropism by Releasing Cryptochrome1-Mediated Inhibition of PIF4 Expression. Alessandra Boccaccini, Martina Legris, Johanna Kraemer, Laure Allenbach-Petrolati, Anupama Goyal, Carlos Galvan-Ampudia, Teva Vernoux, Elizabeth Karayekov, Jorge J. Casal, and Christian Fankhauser  
*Persistent low blue light in natural canopy shade relieves the inhibitory effect of cryptochrome1 on PHYTOCHROME INTERACTING FACTOR4, enhancing phototropism in de-etiolated *Arabidopsis* seedlings.* 1780
- [OPEN] CYCLIC NUCLEOTIDE-GATED ION CHANNELS 14 and 16 Promote Tolerance to Heat and Chilling in Rice. Yongmei Cui, Shan Lu, Zhan Li, Jiawen Cheng, Peng Hu, Tianquan Zhu, Xiang Wang, Mei Jin, Xinxue Wang, Luqi Li, Shuying Huang, Baohong Zou, and Jian Hua  
*Cyclic nucleotide-gated ion channels in rice promote tolerance to both heat and chilling and affect the calcium response to temperature stresses.* 1794
- [OPEN] Analysis of Global Methylome and Gene Expression during Carbon Reserve Mobilization in Stems under Soil Drying. Guanqun Wang, Haoxuan Li, Shuan Meng, Jianchang Yang, Nenghui Ye, and Jianhua Zhang  
*DNA methylation and gene expression in carbon reserve mobilization of rice stems occurs during grain filling under moderate soil drying.* 1809

[OPEN]Molecular Characterization of Differences between the Tomato Immune Receptors Flagellin Sensing 3 and Flagellin Sensing 2. *Robyn Roberts, Alexander E. Liu, Lingwei Wan, Annie M. Geiger, Sarah R. Hind, Hernan G. Rosli, and Gregory B. Martin*

*Differences in outputs between Fls3 and Fls2immunity receptors suggest they use distinct mechanisms to activate immunity in tomato.*

1825

[OPEN]Loss of the Acetyltransferase NAA50 Induces Endoplasmic Reticulum Stress and Immune Responses and Suppresses Growth. *Matthew Neubauer and Roger W. Innes*

*Knockout of the broadly conserved N-terminal acetyltransferase NAA50 in Arabidopsis thaliana induces endoplasmic reticulum stress, leading to severe dwarfism and induction of defense responses.*

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[OPEN]Light Signaling-Dependent Regulation of PSII Biogenesis and Functional Maintenance. *Xue Li, Hong-Bin Wang, and Hong-Lei Jin*

*The photoreceptors phytochrome and cryptochrome regulate PSII biogenesis, assembly, and repair mediated by regulation of gene expression by ELONGATED HYPOCOTYL5 (HY5).*

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[OPEN]Tomato Wall-Associated Kinase SIWak1 Depends on Fls2/Fls3 to Promote Apoplastic Immune Responses to *Pseudomonas syringae*. *Ning Zhang, Marina A. Pombo, Hernan G. Rosli, and Gregory B. Martin*

*The wall-associated kinase Wak1 acts in a complex with the pattern recognition receptors Fls2/Fls3 and is important during later stages of pattern-triggered immunity in the apoplast.*

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## SYSTEMS AND SYNTHETIC BIOLOGY

[OPEN]METHYLTRANSFERASE1 and Ripening Modulate Vivipary during Tomato Fruit Development. *Mengqin Yao, Weiwei Chen, Junhua Kong, Xinlian Zhang, Nongnong Shi, Silin Zhong, Ping Ma, Philippe Gallusci, Stephen Jackson, Yule Liu, and Yiguo Hong*

*Analysis of a unique tomato epiallele reveals an epigenetic pathway that, along with the ripening process, modulates vivipary in tomato fruits.*

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[OPEN]Increased Power and Accuracy of Causal Locus Identification in Time Series Genome-wide Association in Sorghum. *Chenyong Miao, Yuhang Xu, Sanzhen Liu, Patrick S. Schnable, and James C. Schnable*

*Applying functional principal component analyses to time series genome-wide association studies increases the power and accuracy of gene identification in a sorghum association panel.*

1898

## CORRECTION

Modulation of Auxin Signaling and Development by Polyadenylation Machinery. *Zeng W., Dai X., Sun J., Hou Y., Ma X., Cao X., Zhao Y., and Cheng Y*

1910

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