

On the Cover: The number of seeds per spike is an important trait targeted to optimize yield in barley. The spike of barley forms a triple spikelet meristem with one central spikelet meristem and two lateral spikelet meristems. In two-rowed barley cultivars, only the central spikelet develops and forms a seed, while in the six-rowed barley cultivars, all three spikelets develop into grains. In addition, *intermedium* mutants are characterized by a partial development of lateral spikelets resulting in varying two- and six-rowed spike morphology. In this issue, Van Esse et al. (pp. 2397–2408) used RNA sequencing of allelic *six-rowed spike3* (*vr3*) mutants with an intermedium spike phenotype for gene identification and functional analysis. The causal gene was identified as a putative histone Lys demethylase with a conserved zinc finger and Jumonji C and N domain. Comparative transcriptional profiling of *vr3* and mutants of the known row-type regulators VRS1 (Hv.HOMEBOX1), VRS4 (Hv.RAMOSIA2), and INTERMEDIUM-C (INT-C; Hv.TEOSINTE BRANCHED1) demonstrated that VRS3 acts as transcriptional activator of both VRS1 and INT-C. The genetic dissection of regulatory networks that control lateral spikelet development provides the basis for targeted improvement of seed number in barley. The image shows barley spikes of cv Bowman (left) and two introgression lines of allelic *vr3* mutants in cv Bowman (middle and right), which exhibit a partial development of the lateral spikelets. The awns are removed from the spike to visualize the difference between cv Bowman and the *vr3* introgression lines. Photo by Wilma van Esse.

ON THE INSIDE

Peter V. Minorsky

1990

LETTER TO THE EDITOR

Does C₄ Photosynthesis Occur in Wheat Seeds? Robert J. Henry, Parimalan Rangan, Agnelo Furtado, Florian A. Busch, and Graham D. Farquhar

1992

UPDATE

^[OPEN]Leaf Hydraulic Architecture and Stomatal Conductance: A Functional Perspective. Fulton E. Rockwell and N. Michele Holbrook

Mechanistic modeling of water transport from petiole to stomata provides new perspectives on optimality in vascular and mesophyll transport properties.

1996

BREAKTHROUGH TECHNOLOGIES

^[OPEN]A High-Throughput, Field-Based Phenotyping Technology for Tall Biomass Crops. Maria G. Salas Fernandez, Yin Bao, Lie Tang, and Patrick S. Schnable

A ground-based platform enables high-throughput, image-based data and analysis to characterize plant architecture of a tall biomass crop species.

2008

Generation of a Collection of Mutant Tomato Lines Using Pooled CRISPR Libraries. Thomas B. Jacobs, Ning Zhang, Dhruv Patel, and Gregory B. Martin

Plant transformation with pooled CRISPR libraries enables the rapid production of mutant lines for functional screens.

2023

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[^{OPEN}] Analysis of the ZAR1 Immune Complex Reveals Determinants for Immunity and Molecular Interactions. *Maël Baudin, Jana A. Hassan, Karl J. Schreiber, and Jennifer D. Lewis*

Deciphering the molecular interactions within the ZAR1-ZED1 immune complex that lead to the induction of plant immunity.

2038

RESEARCH REPORT

[^{OPEN}] Optical Measurement of Stem Xylem Vulnerability. *Timothy J. Brodribb, Marc Carriqui, Sylvain Delzon, and Christopher Lucani*

An optical method is shown to accurately measure the vulnerability of stem xylem to cavitation during water stress.

2054

Monophyletic Origin and Evolution of the Largest Crucifer Genomes. *Terezie Mandáková, Petra Hloušková, Dmitry A. German, and Martin A. Lysak*

The largest Brassicaceae genomes, forming the well-supported Hesperis clade, have descended from a common ancestor with seven chromosomes and exhibit considerable karyotype and chromosome number stasis.

2062

RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

[^{OPEN}] Hydroxystilbenes Are Monomers in Palm Fruit Endocarp Lignins. *José Carlos del Río, Jorge Rencoret, Ana Gutiérrez, Hoon Kim, and John Ralph*

Lignin polymers in the tough outer skin (endocarp) of palm fruits are produced, in part, from a new class of monomers, hydroxystilbenes, including the valuable resveratrol and piceatannol.

2072

[^{CC-BY}] Two Glycerol-3-Phosphate Dehydrogenases from *Chlamydomonas* Have Distinct Roles in Lipid Metabolism. *Thomas Driver, Drupad K. Trivedi, Owen A. McIntosh, Andrew P. Dean, Royston Goodacre, and Jon K. Pittman*

*Two glycerol-3-phosphate dehydrogenases from *C. reinhardtii* are required for storage lipid accumulation in response to nutrient stress but have distinct metabolic functions.*

2083

[^{OPEN}] The Pseudoenzyme PDX1.2 Sustains Vitamin B₆ Biosynthesis as a Function of Heat Stress. *Elisa Dell'Aglio, Svetlana Boycheva, and Teresa B. Fitzpatrick*

Expression of PDX1.2 is regulated by the HSF1 transcription factor family and is an important abiotic stress tolerance strategy in most eudicots that is not utilized by monocots such as grasses.

2098

[^{OPEN}] Analysis of Posttranslational Activation of Alternative Oxidase Isoforms. *Jennifer Selinski, Andreas Hartmann, Adrian Kordes, Gabriele Deckers-Hebestreit, James Whelan, and Renate Scheibe*

*The multiple alternative oxidase isoforms from *Arabidopsis* are differentially activated by various metabolites, suggesting isoform-specific functions.*

2113

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The Enzyme Activity and Substrate Specificity of Two Major Cinnamyl Alcohol Dehydrogenases in Sorghum (*Sorghum bicolor*), SbCAD2 and SbCAD4. *Se-Young Jun, Alexander M. Walker, Hoon Kim, John Ralph, Wilfred Vermerris, Scott E. Sattler, and ChulHee Kang*

Substrate catalysis by cinnamyl alcohol dehydrogenases from Sorghum bicolor deduced from crystal structures, site-directed mutagenesis, and kinetics.

2128

[OPEN] Identification and Metabolite Profiling of Chemical Activators of Lipid Accumulation in Green Algae. *Nishikant Wase, Boqiang Tu, James W. Allen, Paul N. Black, and Concetta C. DiRusso*

Small compound activators of lipid accumulation in algae are distinguished by differential effects on lipid and polar metabolite profiles.

2146

[OPEN] A Novel Mechanism, Linked to Cell Density, Largely Controls Cell Division in *Synechocystis*. *Alberto A. Esteves-Ferreira, Masami Inaba, Toshihiro Obata, Antoine Fort, Gerard T.A. Fleming, Wagner L. Araújo, Alisdair R. Fernie, and Ronan Sulpice*

Nutrient limitation, self-shading, and quorum sensing are not major limiting factors for the growth of Synechocystis in batch cultures.

2166

Monogalactosyldiacylglycerol Facilitates Synthesis of Photoactive Protochlorophyllide in Etioplasts. *Sho Fujii, Koichi Kobayashi, Noriko Nagata, Tatsuru Masuda, and Hajime Wada*

Monogalactosyldiacylglycerol is required for membrane-associated processes of the protochlorophyllide synthesis pathway and the formation of protochlorophyllide-enzyme complexes in Arabidopsis etioplasts.

2183

[OPEN] Leaf Starch Turnover Occurs in Long Days and in Falling Light at the End of the Day.

Olivier Fernandez, Hirofumi Ishihara, Gavin M. George, Virginie Mengin, Anna Flis, Dean Sumner, Stéphanie Arrivault, Regina Feil, John E. Lunn, Samuel C. Zeeman, Alison M. Smith, and Mark Stitt

Starch in Arabidopsis leaves is increasingly liable to degradation with time after dawn, so that accumulation slows and turnover in response to falling light accelerates as the day proceeds.

2199

Identification and Characterization of Daurichromenic Acid Synthase Active in Anti-HIV Biosynthesis. *Miu Iijima, Ryosuke Munakata, Hironobu Takahashi, Hiromichi Kenmoku, Ryuichi Nakagawa, Takeshi Kodama, Yoshinori Asakawa, Ikuro Abe, Kazufumi Yazaki, Fumiya Kurosaki, and Futoshi Taura*

Daurichromenic acid, an anti-HIV meroterpenoid, is biosynthesized by a novel flavoprotein oxidase localized in the specialized epidermal organ, the glandular scales of Rhododendron dauricum.

2213

CELL BIOLOGY

[OPEN] The PEX1 ATPase Stabilizes PEX6 and Plays Essential Roles in Peroxisome Biology. *Mauro A. Rinaldi, Wendell A. Fleming, Kim L. Gonzalez, Jaeseok Park, Meredith J. Ventura, Ashish B. Patel, and Bonnie Bartel*

Novel missense alleles of the Arabidopsis PEX1 ATPase reveal essential peroxisomal roles that impact embryogenesis and plant growth.

2231

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[OPEN] Unique Motifs and Length of Hairpin in Oleosin Target the Cytosolic Side of Endoplasmic Reticulum and Budding Lipid Droplet. *Chien-Yu Huang and Anthony H.C. Huang*

The mechanism of oleosin targeting endoplasmic reticulum-lipid droplets and extracting LDs to the cytosol or ER lumen is delineated.

2248

ECOPHYSIOLOGY AND SUSTAINABILITY

[OPEN] Variation in Leaf Respiration Rates at Night Correlates with Carbohydrate and Amino Acid Supply. *Brendan M. O'Leary, Chun Pong Lee, Owen K. Atkin, Riyan Cheng, Tim B. Brown, and A. Harvey Millar*

Mature Arabidopsis leaves display substantial variation in nighttime respiration rates that is metabolically linked to daytime carbon and nitrogen assimilation but not to nighttime protein synthesis.

2261

The Auxin Biosynthetic TRYPTOPHAN AMINOTRANSFERASE RELATED TaTAR2.1-3A Increases Grain Yield of Wheat. *An Shao, Wenying Ma, Xueqiang Zhao, Mengyun Hu, Xue He, Wan Teng, Hui Li, and Yiping Tong*

Overexpression of the auxin biosynthesis gene TaTAR2.1-3A in wheat increases grain yield under different nitrogen nutritional conditions.

2274

[OPEN] Root Tip Shape Governs Root Elongation Rate under Increased Soil Strength. *Tino Colombi, Norbert Kirchgessner, Achim Walter, and Thomas Keller*

Root tip shape in wheat is a pivotal trait governing root tip 11 penetration stress and thus root elongation rate in soils of greater strength.

2289

[OPEN] Genetic Control of Plasticity in Root Morphology and Anatomy of Rice in Response to Water Deficit. *Niteen N. Kadam, Anandhan Tamilselvan, Lovely M.F. Lawas, Cherryl Quinones, Rajeev N. Bahuguna, Michael J. Thomson, Michael Dingkuhn, Raveendran Muthurajan, Paul C. Struik, Xinyou Yin, and S.V. Krishna Jagadish*

The genetic analysis of root morphology and anatomy in a rice diversity panel resulted in identification of the genetic loci that regulates the rooting plasticity in response to water deficit.

2302

OsHAD1, a Haloacid Dehalogenase-Like APase, Enhances Phosphate Accumulation. *Bipin K. Pandey, Poonam Mehra, Lokesh Verma, Jyoti Bhadouria, and Jitender Giri*

Overexpression of OsHAD1 enhances P accumulation in rice by activation of Pi starvation responses such as ATP depletion, APase secretion, organic acid production, and induction of Pi transporters.

2316

[OPEN] Root Cortical Senescence Improves Growth under Suboptimal Availability of N, P, and K. *Hannah M. Schneider, Johannes A. Postma, Tobias Wojciechowski, Christian Kuppe, and Jonathan P. Lynch*

SimRoot, a functional-structural plant model, demonstrated how root cortical senescence in barley may have utility for soil resource capture in edaphic stress conditions.

2333

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GENES, DEVELOPMENT, AND EVOLUTION

Transcription Factor AREB2 Is Involved in Soluble Sugar Accumulation by Activating Sugar Transporter and Amylase Genes. *Qi-Jun Ma, Mei-Hong Sun, Jing Lu, Ya-Jing Liu, Da-Gang Hu, and Yu-Jin Hao*

The ABA-responsive transcription factor MdAREB2 directly activates the expression of amylase and sugar transporter genes to promote soluble sugar accumulation.

2348

[OPEN] NTL8 Regulates Trichome Formation in Arabidopsis by Directly Activating R3 MYB Genes TRY and TCL1. *Hainan Tian, Xianling Wang, Hongyan Guo, Yuxin Cheng, Chunjiang Hou, Jin-Gui Chen, and Shucai Wang*

NTL8, a membrane-associated NAC transcription factor, negatively regulates trichome formation in Arabidopsis.

2363

Ripening Transcriptomic Program in Red and White Grapevine Varieties Correlates with Berry Skin Anthocyanin Accumulation. *Mélanie Massonnet, Marianna Fasoli, Giovanni Battista Tornielli, Mario Altieri, Marco Sandri, Paola Zuccolotto, Paola Paci, Massimo Gardiman, Sara Zenoni, and Mario Pezzotti*

Grapevine berry development features both common and skin color-dependent transcriptomic changes.

2376

[OPEN] Six-Rowed Spike3 (VRS3) Is a Histone Demethylase That Controls Lateral Spikelet Development in Barley. *G. Wilma van Esse, Agatha Walla, Andreas Finke, Maarten Koornneef, Ales Pecinka, and Maria von Korff*

Six-rowed spike3 (VRS3) encodes a histone demethylase that controls lateral spikelet development by activating the expression of INTERMEDIUM C (TEOSINTE BRANCHED1) and VRS1.

2397

MEMBRANES, TRANSPORT, AND BIOENERGETICS

A Dual Role for the OsK5.2 Ion Channel in Stomatal Movements and K⁺ Loading into Xylem Sap. *Thanh Hao Nguyen, Shouguang Huang, Donaldo Meynard, Christian Chaine, Rémy Michel, M. Rob G. Roelfsema, Emmanuel Guiderdoni, Hervé Sentenac, and Anne-Aliénor Véry*

The rice K⁺ channel OsK5.2 is necessary for rapid stomatal closure and contributes to shoot K⁺ supply from the root, thus highlighting the differing functional distribution of Shaker channels compared to Arabidopsis.

2409

[OPEN] A Light Harvesting Complex-Like Protein in Maintenance of Photosynthetic Components in *Chlamydomonas*. *Lei Zhao, Dongmei Cheng, Xiahe Huang, Mei Chen, Luca Dall'Osto, Jiale Xing, Liyan Gao, Lingyu Li, Yale Wang, Roberto Bassi, Lianwei Peng, Yingchun Wang, Jean-David Rochaix, and Fang Huang*

Msf1 is required for the maintenance of PSI and chlorophyll-binding proteins mainly under stress conditions in Chlamydomonas.

2419

[OPEN] Wheat Vacuolar Iron Transporter TaVIT2 Transports Fe and Mn and Is Effective for Biofortification. *James M. Connorton, Eleanor R. Jones, Ildefonso Rodríguez-Ramiro, Susan Fairweather-Tait, Cristobal Uauy, and Janneke Balk*

Altering the expression of a vacuolar iron transporter doubles iron content in white wheat flour.

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SIGNALING AND RESPONSE

[OPEN]ROOT DETERMINED NODULATION1 Is Required for *M. truncatula* CLE12, But Not CLE13, Peptide Signaling through the SUNN Receptor Kinase. Tessema Kassaw, Stephen Nowak, Elise Schnabel, and Julia Frugoli

Genetic analysis of the autoregulation of nodulation pathway in M. truncatula reveals diversity in how CLE peptides that signal through the SUNN receptor kinase may be modified in the root. 2445

Autophosphorylation Affects Substrate-Binding Affinity of Tobacco Ca²⁺-Dependent Protein Kinase1. Takeshi Ito, Sarahmi Ishida, Shota Oe, Jutarou Fukazawa, and Yohsuke Takahashi

Autophosphorylation could prevent the excessive phosphorylation of substrates and alter the substrate preference of Ca²⁺-dependent protein kinases. 2457

[OPEN]The MicroRNA390/TAS3 Pathway Mediates Symbiotic Nodulation and Lateral Root Growth. Karen Vanesa Hobecker, Mauricio Alberto Reynoso, Pilar Bustos-Sanmamed, Jiangqi Wen, Kirankumar S. Mysore, Martín Crespi, Flavio Antonio Blanco, and María Eugenia Zanetti

miR390/TAS3 affect rhizobial infection, nodule proliferation, and the maintenance of a single-nodule meristem in addition to lateral root growth in Medicago truncatula. 2469

[OPEN]A PIF1/PIF3-HY5-BBX23 Transcription Factor Cascade Affects Photomorphogenesis. Xinyu Zhang, Junling Huai, Fangfang Shang, Gang Xu, Weijiang Tang, Yanjun Jing, and Rongcheng Lin

Two PIF transcription factors activate the expression of HY5 and BBX23, the proteins of which interact to affect downstream gene expression in photomorphogenesis. 2487

A Lectin Receptor-Like Kinase Mediates Pattern-Triggered Salicylic Acid Signaling. Xuming Luo, Ning Xu, Junkai Huang, Feng Gao, Huasong Zou, Marie Boudsoq, Gitta Coaker, and Jun Liu

The Arabidopsis L-type lectin receptor-like kinase LecRK-IX.2 recruits calcium dependent protein kinases (CPKs) to phosphorylate NADPH oxidase RbohD to activate H₂O₂-SA circuit. 2501

SYSTEMS AND SYNTHETIC BIOLOGY

AtAIRP2 E3 Ligase Affects ABA and High-Salinity Responses by Stimulating Its ATP1/SDIRIP1 Substrate Turnover. Tae Rin Oh, Jong Hum Kim, Seok Keun Cho, Moon Young Ryu, Seong Wook Yang, and Woo Taek Kim

AtAIRP2 and SDIR1 RING E3 Ub ligases play combinatory roles in response to ABA and high-salinity stress during germination growth via the UPS-dependent down-regulation of ATP1/SDIRIP1 in Arabidopsis. 2515

[OPEN]Spatial Mapping and Profiling of Metabolite Distributions during Germination. Adam D. Feenstra, Liza E. Alexander, Zhihong Song, Andrew R. Korte, Marna D. Yandean-Nelson, Basil J. Nikolau, and Young Jin Lee

A combination of metabolomics and mass spectrometry imaging provides new insights in metabolic processes during the germination of maize seeds. 2532

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CORRECTION

Sensitivity to Flg22 Is Modulated by Ligand-Induced Degradation and de Novo Synthesis of the Endogenous Flagellin-Receptor FLAGELLIN-SENSING2. *Smith J.M., Salamango D.J., Leslie M.E., Collins C.A., and Heese A.*

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