Plant Physiology®

January 2016 ● Vol. 170 ● No. 1

On the Cover: Cellulose is the major structural component of plant cell walls and has great potential as a renewable source of energy. The plant cellulose synthesis complex (CSC), also called a 'rosette' because of its hexameric appearance in transmission electron microscope (TEM) images, is a large multi-subunit transmembrane protein complex responsible for synthesis of cellulose chains and their assembly into microfibrils. Despite the importance of cellulose, fundamental properties of the CSC remain unclear. The number of cellulose synthase (CESA) proteins in the CSC and the number of cellulose chains in a microfibril have been debated for years. Vandavasi et al report a solution structure of the catalytic domain of CESA1 from *Arabidopsis thaliana* determined by small-angle scattering that provides experimental evidence for the self-assembly of CESA into a stable trimer. This study strongly supports the 'hexamer of trimers' model for the rosette CSC that synthesizes an 18-chain cellulose microfibril as its primary product. The cover shows *ab initio* structures of CESA trimers calculated from small-angle scattering data represented by semi-transparent grey surface envelopes, superposed with the computational atomic models in orange. The trimer models are arranged in a hexameric configuration consistent with the rosette shape observed in TEM images. The view is from the cytosolic side of the membrane. Cellulose microfibrils are visible in the apoplastic space. Cover image credits: Thomas Splettstoesser, scistyle.com, Berlin, Germany.

THANK YOU TO REVIEWERS

An acknowledgment of *Plant Physiology* reviewers. viii

ON THE INSIDE

Peter V. Minorsky 1

FOUNDERS REVIEW

The Cytoskeleton and Its Regulation by Calcium and Protons. *Peter K. Hepler*

Calcium and protons exert control over the formation and activity of the cytoskeleton, usually by modulating an associated motor protein or one that affects the structural organization of the polymer. 3

SCIENTIFIC CORRESPONDENCE

Inhibition of Cell Expansion by Rapid ABP1-Mediated Auxin Effect on Microtubules? A Critical Comment. *Peter Schopfer and Klaus Palme*

Critical analysis of a recent article raises questions regarding the inhibition of cell expansion by rapid ABP1-mediated auxin effect on microtubules. 23

RESEARCH REPORTS

Rj4, a Gene Controlling Nodulation Specificity in Soybeans, Encodes a Thaumatin-Like Protein But Not the One Previously Reported. *Fang Tang, Shengming Yang, Jinge Liu, and Hongyan Zhu*

A thaumatin-like protein regulates gene-for-gene interaction with specific rhizobial strains and controls nodulation specificity in soybeans. 26

[CC-BY]An Optimal Frequency in Ca^{2+} Oscillations for Stomatal Closure Is an Emergent Property of Ion Transport in Guard Cells. *Carla Minguet-Parramona, Yizhou Wang, Adrian Hills, Silvere Vialet-Chabrand, Howard Griffiths, Simon Rogers, Tracy Lawson, Virgilio L. Lew, and Michael R. Blatt*

Rapid closure of stomata occurs at an optimum frequency in Ca^{2+} and voltage oscillations, but this optimum emerges in simulations as a by-product of the transport that drives closure rather than as a signal that regulates it. 33

Continued on next page

Continued from preceding page

RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

[OPEN]Regulation of Primary Metabolism in Response to Low Oxygen Availability as Revealed by Carbon and Nitrogen Isotope Redistribution. *Carla António, Carola Päpke, Marcio Rocha, Houssein Diab, Anis M. Limami, Toshihiro Obata, Alisdair R. Fernie, and Joost T. van Dongen*

During low-oxygen stress, activation of Ala and GABA metabolism and bifurcation of the tricarboxylic acid cycle explains the down-regulation of respiratory oxygen consumption. 43

[OPEN]C_4 Photosynthesis in the Rice Paddy: Insights from the Noxious Weed *Echinochloa glabrescens*. *Sarah Covshoff, Marek Szecowka, Thomas E. Hughes, Richard Smith-Unna, Steven Kelly, Karen J. Bailey, Tammy L. Sage, Justin A. Pachebat, Richard Leegood, and Julian M. Hibberd*

Transcriptomic profiling of the paddy weed Echinochloa glabrescens identifies its C_4 molecular signature and genes important for paddy growth. 57

[OPEN]Redox-Dependent Modulation of Anthocyanin Biosynthesis by the TCP Transcription Factor TCP15 during Exposure to High Light Intensity Conditions in Arabidopsis. *Ivana L. Viola, Alejandra Camoirano, and Daniel H. Gonzalez*

The transcription factor TCP15 represses anthocyanin biosynthesis in a redox-dependent manner during high-light intensity conditions. 74

Enhanced Photosynthesis and Growth in *atquac1* Knockout Mutants Are Due to Altered Organic Acid Accumulation and an Increase in Both Stomatal and Mesophyll Conductance. *David B. Medeiros, Samuel C.V. Martins, João Henrique F. Cavalcanti, Danilo M. Daloso, Enrico Martinoia, Adriano Nunes-Nesi, Fábio M. DaMatta, Alisdair R. Fernie, and Wagner L. Araújo*

Impaired stomatal closure in a anion channel mutant is accompanied by increased mesophyll conductance, photosynthesis, and leaf area, ultimately enhancing biomass accumulation under controlled conditions. 86

[OPEN]Reversible Burst of Transcriptional Changes during Induction of Crassulacean Acid Metabolism in *Talinum triangulare*. *Dominik Brilhaus, Andrea Bräutigam, Tabea Mettler-Altmann, Klaus Winter, and Andreas P.M. Weber*

Rapid, reversible induction of Crassulacean acid metabolism (CAM) in conjunction with pronounced reconfiguration of carbon metabolism enables Talinum to survive cycles of severe drought. 102

A Structural Study of CESA1 Catalytic Domain of Arabidopsis Cellulose Synthesis Complex: Evidence for CESA Trimers. *Venu Gopal Vandavasi, Daniel K. Putnam, Qiu Zhang, Loukas Petridis, William T. Heller, B. Tracy Nixon, Candace H. Haigler, Udaya Kalluri, Leighton Coates, Paul Langan, Jeremy C. Smith, Jens Meiler, and Hugh O'Neill*

Assembly into stable trimers provides strong evidence for 18 protein subunits to assemble in a cellulose synthesis complex that synthesizes an 18-chain cellulose microfibril. 123

[OPEN]Combining Quantitative Genetics Approaches with Regulatory Network Analysis to Dissect the Complex Metabolism of the Maize Kernel. *Weiwei Wen, Haijun Liu, Yang Zhou, Min Jin, Ning Yang, Dong Li, Jie Luo, Yingjie Xiao, Qingchun Pan, Takayuki Tohge, Alisdair R. Fernie, and Jianbing Yan*

A metabolic quantitative trait loci study combined with a regulatory network unraveled the genetic architecture of the natural variation of 155 metabolites in mature maize kernels. 136

Continued on next page

Continued from preceding page

[OPEN]Functional Analysis of the Hsp93/ClpC Chaperone at the Chloroplast Envelope. *Úrsula Flores-Pérez, Jocelyn Bédard, Noriaki Tanabe, Panagiotis Lymperopoulos, Adrian K. Clarke, and Paul Jarvis*

Chloroplast chaperone Hsp93 associates with the inner envelope membrane via interaction with the Tic110 translocon and likely functions in quality control but not in import propulsion of translocating preproteins. 147

[OPEN]Identification of Arabidopsis *GPAT9* (At5g60620) as an Essential Gene Involved in Triacylglycerol Biosynthesis. *Jay Shockey, Anushobha Regmi, Kimberly Cotton, Neil Adhikari, John Browse, and Philip D. Bates*

Arabidopsis GPAT9 is a highly conserved, single-copy, and essential glycerol-3-phosphate acyltransferase involved in seed oil biosynthesis. 163

[OPEN]The Arabidopsis ABHD11 Mutant Accumulates Polar Lipids in Leaves as a Consequence of Absent Acylhydrolase Activity. *Anitha Vijayakumar, Panneerselvam Vijayaraj, Arun Kumar Vijayakumar, and Ram Rajasekharan*

Disruption of the ABHD11 hydrolase causes polar lipids accumulation, thereby enhancing plant growth. 180

[OPEN]The bHLH Transcription Factors TSAR1 and TSAR2 Regulate Triterpene Saponin Biosynthesis in *Medicago truncatula*. *Jan Mertens, Jacob Pollier, Robin Vanden Bossche, Irene Lopez-Vidriero, José Manuel Franco-Zorrilla, and Alain Goossens*

Basic helix-loop-helix family transcription factors from subclade IVa specifically regulate the biosynthesis of the triterpene saponins in a model legume. 194

CELL BIOLOGY

The Adaptor Complex AP-4 Regulates Vacuolar Protein Sorting at the trans-Golgi Network by Interacting with VACUOLAR SORTING RECEPTOR1. *Kentaro Fuji, Makoto Shirakawa, Yuki Shimono, Tadashi Kunieda, Yoichiro Fukao, Yasuko Koumoto, Hideyuki Takahashi, Ikuko Hara-Nishimura, and Tomoo Shimada*

The Arabidopsis AP-4 adaptor complex functions in vacuolar sorting at a subdomain of the TGN by directly recognizing a Tyr-based motif of the receptor. 211

[OPEN]Profilin-Dependent Nucleation and Assembly of Actin Filaments Controls Cell Elongation in Arabidopsis. *Lingyan Cao, Jessica L. Henty-Ridilla, Laurent Blanchoin, and Christopher J. Staiger*

Analysis of single actin filament dynamics reveals a novel role for profilin and formins in the generation of branched filament networks in living epidermal cells. 220

[OPEN]Xyloglucan Deficiency Disrupts Microtubule Stability and Cellulose Biosynthesis in Arabidopsis, Altering Cell Growth and Morphogenesis. *Chaowen Xiao, Tian Zhang, Yunzhen Zheng, Daniel J. Cosgrove, and Charles T. Anderson*

A mutant lacking xyloglucan in its cell walls has bundled, aligned cellulose and unstable microtubules that uncover new links between cell wall and cytoskeletal integrity. 234

[OPEN]Roles of Arabidopsis PARC6 in Coordination of the Chloroplast Division Complex and Negative Regulation of FtsZ Assembly. *Min Zhang, Cheng Chen, John E. Froehlich, Allan D. TerBush, and Katherine W. Osteryoung*

A plant-specific chloroplast division protein has multiple functions in coordinating and influencing the assembly of internal and external contractile rings across the two envelope membranes. 250

Continued on next page

Continued from preceding page

[OPEN]In Vivo Quantification of Peroxisome Tethering to Chloroplasts in Tobacco Epidermal Cells Using Optical Tweezers. *Hongbo Gao, Jeremy Metz, Nick A. Teanby, Andy D. Ward, Stanley W. Botchway, Benjamin Coles, Mark R. Pollard, and Imogen Sparkes*

Optical tweezers show that peroxisomes are strongly tethered to chloroplasts and more weakly to other structures. 263

ECOPHYSIOLOGY AND SUSTAINABILITY

Noninvasive Measurement of Vulnerability to Drought-Induced Embolism by X-Ray Microtomography. *Brendan Choat, Eric Badel, Regis Burlett, Sylvain Delzon, Herve Cochard, and Steven Jansen*

X-ray computed microtomography provides a high-resolution, noninvasive method to evaluate vulnerability to drought-induced embolism in living, intact plants. 273

GENES, DEVELOPMENT AND EVOLUTION

[OPEN]AINTEGUMENTA and AINTEGUMENTA-LIKE6/PLETHORA3 Induce *LEAFY* Expression in Response to Auxin to Promote the Onset of Flower Formation in Arabidopsis. *Nobutoshi Yamaguchi, Cheol Woong Jeong, Staci Nole-Wilson, Beth A. Krizek, and Doris Wagner*

Two parallel pathways confer floral identity on developing lateral primordia downstream of auxin. 283

[OPEN]RNA Recognition Motif-Containing Protein ORRM4 Broadly Affects Mitochondrial RNA Editing and Impacts Plant Development and Flowering. *Xiaowen Shi, Arnaud Germain, Maureen R. Hanson, and Stéphane Bentolila*

Growth and development of Arabidopsis is affected by mutation of a member of the RNA recognition motif gene family that is required for RNA editing of more than 40% of the mitochondrial C targets in Arabidopsis. 294

[OPEN]Targets of the *StBEL5* Transcription Factor Include the FT Ortholog *StSP6A*. *Pooja Sharma, Tian Lin, and David J. Hannapel*

Among the targets of a BEL1-like homeodomain transcription factor are genes involved in growth and hormone metabolism as well as two key tuberization signals. 310

CONSTANS Controls Floral Repression by Up-Regulating *VERNALIZATION2* (*VRN-H2*) in Barley. *Muhammad Aman Mulki and Maria von Korff*

The functional characterization of homologs of a flowering-time transcription factor provides new insights into the control of floral repression before vernalization in barley. 325

[OPEN]Novel Vein Patterns in Arabidopsis Induced by Small Molecules. *Francine Carland, Andrew Defries, Sean Cutler, and Timothy Nelson*

Numerous compounds inducing leaf vein pattern defects target auxin biology. 338

The MTL1 Pentatricopeptide Repeat Protein Is Required for Both Translation and Splicing of the Mitochondrial *NADH DEHYDROGENASE SUBUNIT7* mRNA in Arabidopsis. *Nawel Haïli, Noelya Planchard, Nadège Arnal, Martine Quadrado, Nathalie Vrielynck, Jennifer Dahan, Catherine Colas des Francs-Small, and Hakim Mireau*

A mitochondria-targeted pentatricopeptide repeat protein specifically facilitates the translation of a respiratory chain transcript without inducing any cleavage in its upstream noncoding region. 354

Continued on next page

Continued from preceding page

MEMBRANES, TRANSPORT AND BIOENERGETICS

Revisiting Plant Plasma Membrane Lipids in Tobacco: A Focus on Sphingolipids. *Jean-Luc Cacas, Corinne Buré, Kevin Grosjean, Patricia Gerbeau-Pissot, Jeannine Lherminier, Yoann Rombouts, Emmanuel Maes, Claire Bossard, Julien Gronnier, Fabienne Furt, Laetitia Fouillen, Véronique Germain, Emmanuelle Bayer, Stéphanie Cluzet, Franck Robert, Jean-Marie Schmitter, Magali Deleu, Laurence Lins, Françoise Simon-Plas, and Sébastien Mongrand*

Glycosyl-Inositol-Phosphoryl-Ceramides are major lipids of the plasma membrane and form rafts in the outer leaflet, yet extend into the inner leaflet of the membrane through very long-chain fatty acids to interdigitate across the membrane. 367

[OPEN]The EXS Domain of PHO1 Participates in the Response of Shoots to Phosphate Deficiency via a Root-to-Shoot Signal. *Stefanie Wege, Ghazanfar Abbas Khan, Ji-Yul Jung, Evangelia Vogiatzaki, Sylvain Pradervand, Isabel Aller, Andreas J. Meyer, and Yves Poirier*

A key hydrophobic domain of the PHO1 phosphate exporter plays an important role in the response of shoots to phosphate deficiency. 385

[OPEN]Constitutive and Companion Cell-Specific Overexpression of *AVP1*, Encoding a Proton-Pumping Pyrophosphatase, Enhances Biomass Accumulation, Phloem Loading, and Long-Distance Transport. *Aswad S. Khadilkar, Umesh P. Yadav, Carolina Salazar, Vladimir Shulaev, Julio Paez-Valencia, Gaston A. Pizzio, Roberto A. Gaxiola, and Brian G. Ayre*

H^+-pumping pyrophosphatases appear to function in companion cells to increase phloem loading and long-distance transport, leading to more robust plants with enhanced growth. 401

SIGNALING AND RESPONSE

[OPEN]Protein *S*-Acyltransferase 14: A Specific Role for Palmitoylation in Leaf Senescence in Arabidopsis. *Yaxiao Li, Rod Scott, James Doughty, Murray Grant, and Baoxiu Qi*

A protein S-acyltransferase is involved in leaf senescence via modulating salicylic acid metabolism and perception. 415

The RING Finger Ubiquitin E3 Ligase OsHTAS Enhances Heat Tolerance by Promoting H_2O_2-Induced Stomatal Closure in Rice. *Jianping Liu, Cuicui Zhang, Chuchu Wei, Xin Liu, Mugui Wang, Feifei Yu, Qi Xie, and Jumin Tu*

A RING finger ubiquitin ligase functions enhances heat tolerance through the modulation of H_2O_2-induced stomatal closure. 429

The Synthetic Elicitor 2-(5-Bromo-2-Hydroxy-Phenyl)-Thiazolidine-4-Carboxylic Acid Links Plant Immunity to Hormesis. *Melinda Rodriguez-Salus, Yasemin Bektas, Mercedes Schroeder, Colleen Knoth, Trang Vu, Philip Roberts, Isgouhi Kaloshian, and Thomas Eulgem*

Immunity triggered by high doses a and hormetic growth enhancement triggered by low doses of a synthetic elicitor doses are associated with distinct transcriptional profiles. 444

[OPEN]Phytochrome A and B Function Antagonistically to Regulate Cold Tolerance via Abscisic Acid-Dependent Jasmonate Signaling. *Feng Wang, Zhixin Guo, Huizi Li, Mengmeng Wang, Eugen Onac, Jie Zhou, Xiaojian Xia, Kai Shi, Jingquan Yu, and Yanhong Zhou*

Low red/far-red light ratios increase cold tolerance in tomato via the activation of phytochrome A and ABA-dependent JA signaling. 459

Continued on next page

Continued from preceding page

[OPEN]Genetic Variation for Thermotolerance in Lettuce Seed Germination Is Associated with Temperature-Sensitive Regulation of *ETHYLENE RESPONSE FACTOR1* (*ERF1*). *Fei-Yian Yoong, Laurel K. O'Brien, Maria Jose Truco, Heqiang Huo, Rebecca Sideman, Ryan Hayes, Richard W. Michelmore, and Kent J. Bradford*

An allele of a gene encoding a transcription factor involved in the ethylene response pathway is associated with the ability of lettuce seeds to germinate at warm temperatures. 472

[OPEN]Profiling of the Early Nitrogen Stress Response in the Diatom *Phaeodactylum tricornutum* Reveals a Novel Family of RING-Domain Transcription Factors. *Michiel Matthijs, Michele Fabris, Stefan Broos, Wim Vyverman, and Alain Goossens*

A new family of RING-domain transcription factors associated with nitrogen stress is conserved in diatoms. 489

Arabidopsis PHL2 and PHR1 Act Redundantly as the Key Components of the Central Regulatory System Controlling Transcriptional Responses to Phosphate Starvation. *Lichao Sun, Li Song, Ye Zhang, Zai Zheng, and Dong Liu*

Two transcription factors act redundantly to regulate the transcriptional responses to phosphate starvation at genomic level. 499

[OPEN]Differential Roles of Two Homologous Cyclin-Dependent Kinase Inhibitor Genes in Regulating Cell Cycle and Innate Immunity in Arabidopsis. *Safae Hamdoun, Chong Zhang, Manroop Gill, Narender Kumar, Michelle Churchman, John C. Larkin, Ashley Kwon, and Hua Lu*

Two homologous kinase inhibitor proteins play differential roles in regulating plant cell cycle and defense. 515

[OPEN]A G-Box-Like Motif Is Necessary for Transcriptional Regulation by Circadian Pseudo-Response Regulators in Arabidopsis. *Tiffany L. Liu, Linsey Newton, Ming-Jung Liu, Shin-Han Shiu, and Eva M. Farré*

Pseudo-response regulators associate with overlapping sets of putative target genes and require G-box-like cis-regulatory elements for transcriptional activity. 528

[OPEN]ZINC FINGER OF ARABIDOPSIS THALIANA12 (ZAT12) Interacts with FER-LIKE IRON DEFICIENCY-INDUCED TRANSCRIPTION FACTOR (FIT) Linking Iron Deficiency and Oxidative Stress Responses. *Cham Thi Tuyet Le, Tzvetina Brumbarova, Rumen Ivanov, Claudia Stoof, Eva Weber, Julia Mohrbacher, Claudia Fink-Straube, and Petra Bauer*

Two transcription factors interact and negatively regulate the plant response to prolonged iron deficiency. 540

[OPEN]Putrescine Alleviates Iron Deficiency via NO-Dependent Reutilization of Root Cell-Wall Fe in Arabidopsis. *Xiao Fang Zhu, Bin Wang, Wen Feng Song, Shao Jian Zheng, and Ren Fang Shen*

Putrescine enhances Fe deficiency-induced accumulation of nitric oxide which ultimately leads to the reutilization of cell wall Fe under Fe-deficient conditions. 558

SYSTEMS AND SYNTHETIC BIOLOGY

A Systems Genetics Approach Identifies Gene Regulatory Networks Associated with Fatty Acid Composition in *Brassica rapa* Seed. *Ram Kumar Basnet, Dunia Pino Del Carpio, Dong Xiao, Johan Bucher, Mina Jin, Kerry Boyle, Pierre Fobert, Richard G.F. Visser, Chris Maliepaard, and Guusje Bonnema*

A systems genetics approach identifies gene regulatory networks associated with fatty acid composition in Brassica rapa seed. 568

Continued on next page

Continued from preceding page

[OPEN]Genome-Wide Analysis of Alternative Splicing during Development and Drought Stress in *Zea mays*. *Shawn R. Thatcher, Olga N. Danilevskaya, Xin Meng, Mary Beatty, Gina Zastrow-Hayes, Charlotte Harris, Brandon Van Allen, Jeffrey Habben, and Bailin Li*

Alternative splicing is common during development and drought, with a high degree of tissue specificity even among related tissue types. 586