On the Cover: Turgor-driven valves on the plant epidermis, stomata, are essential for the growth and survival of land plants and of far-reaching importance to our global environment as well as food security. A series of cartoons show stereotypical steps of stomatal differentiation in dicots, such as Arabidopsis, emphasizing the roles of ion transport for proper stomatal movement, allowing carbon dioxide uptake while releasing oxygen and promoting transpiration. Background images emphasize the impact of stomata on atmospheric environment (top left), successful land plants colonization (top middle), and crop production (top right). Images at the bottoms highlight the conserved nature of key stomatal regulatory genes in the basal land plant Physcomitrella patens (bottom left) and the loss of regulation of one such gene product, SCREAM, conferring an epidermis solely composed of stomata (bottom right). Cover art by Haruko Hirukawa, The photo of Physomitrella is provided by Mitsuyasu Hasebe, and a confocal microscopy image of Arabidopsis scrm-D epidermis is provided by Keiko Torii.

FOCUS ISSUE ON STOMATA

EDITORIAL
Small Pores with a Big Impact. Michael R. Blatt, Tim J. Brodribb, and Keiko U. Torii

LETTER TO THE EDITOR
A Celebration of Fred David Sack. Dominique Bergmann, Dian Clare, Lacey Samuels, and John Z. Kiss

SCIENTIFIC CORRESPONDENCE

Generation of carbon skeletons for amino acid synthesis in some C₃ plants resembles fluxes needed for CAM-type photosynthesis.


A simple model combining leaf hydraulics and abscisic acid sensitivity can predict stomatal dynamics to short-term changes in plant water status in a conifer.

TOPICAL REVIEW

While guard cells have come to represent the premier model for ion transport, the coordination of transport in driving stomatal movements continues to challenge an intuitive understanding.

Continued on next page
Recent research on vacuolar ion channels, transporters, and pumps of Arabidopsis highlight their function and roles in stomatal opening and closure.

Recent progress of the blue light signaling pathway in guard cells highlights its regulation of $H^+$-ATPase activity.

The pathway and timing of starch turnover in guard cells differs from mesophyll cells and is linked to stomatal opening in the light.

Recent advances in the stomatal biology of CAM plants are reviewed, and key opportunities for future progress are identified.

A decade has passed since the discovery of stomatal defense, and the field has expanded considerably with significant understanding of the basic mechanisms underlying the process.

Recent advances have improved our ability to model stomatal conductance using process- or optimality-based models, and continuing research should focus on how stomata sense leaf turgor and on how to quantify the direct carbon costs of low leaf water potential.

Simulating global fluxes of water, carbon, and energy at the land surface requires accurate and versatile models of stomatal conductance, currently represented by structurally similar and interchangeable forms that share weaknesses at environmental extremes.

An analysis of stomatal behavior reveals the importance of modeling slow stomatal responses and the impacts on photosynthesis under dynamic light environments.

Stomatal behavior varies both spatially and temporally, with implications for carbon assimilation and water loss.
Origins and Evolution of Stomatal Development. Caspar C. C. Chater, Robert S. Caine, Andrew J. Fleming, and Julie E. Gray

Molecular-genetic comparisons and manipulations of regulators of stomatal development raise the possibility of a single origin for stomata early in land plant evolution. 624

Evolution of the Stomatal Regulation of Plant Water Content. Timothy J. Brodribb and Scott A. M. McAdam

Changes in the function of stomata from the earliest bryophytes to derived angiosperms are examined. 639

Paleoecology, Ploidy, Paleoatmospheric Composition, and Developmental Biology: A Review of the Multiple Uses of Fossil Stomata. Jennifer C. McElwain and Margret Steinthorsdottir

Fossil plant stomata reveal insights into the evolution of atmospheric composition, trends in plant genome size, and the biology of the living plant prior to fossilization. 650

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The Role of ENHANCED RESPONSES TO ABA1 (ERA1) in Arabidopsis Stomatal Responses Is Beyond ABA Signaling. Pirko Jalakas, Yi-Chun Huang, Yu-Hung Yeh, Laurent Zimmerli, Ebe Merilo, Hannes Kollist, and Mikael Brosché

Analysis of single and double mutants shows an ABA-independent role for ERA1 in stomatal opening. 665

Fern Stomatal Responses to ABA and CO2 Depend on Species and Growth Conditions. Hanna Hörak, Hannes Kollist, and Ebe Merilo

Growth conditions and species affect fern stomatal responsiveness to ABA and CO2. 672


Incorporating global sensitivity analysis to mechanistic models of stomatal guard cells highlights previously unexpected interactions in transport driving stomatal aperture. 680

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Formation of the Stomatal Outer Cuticular Ledge Requires a Guard Cell Wall Proline-Rich Protein. Lee Hunt, Samuel Amsbury, Alice Baillie, Mahsa Movahedi, Alice Mitchell, Mana Afsharifar, Kamal Swarup, Thomas Denyer, Jamie K. Hobbs, Ranjan Swarup, Andrew J. Fleming, and Julie E. Gray

Plants lacking the guard cell-expressed, proline-rich secreted protein FOCL1 are drought tolerant because they fail to form a stomatal cuticular ledge and produce stomatal pores that are covered by a continuous cuticle. 689

Immunity at Cauliflower Hydathodes Controls Systemic Infection by Xanthomonas campestris pv campestris. Aude Cerutti, Alain Jauzeau, Marie-Christine Auriac, Emmanuelle Lauber, Yves Martinez, Serge Chiarenza, Nathalie Leonhardt, Richard Berthomé, and Laurent D. Noël

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The RopGEF2-ROP7/ROP2 Pathway Activated by phyB Suppresses Red Light-Induced Stomatal Opening.
Wei Wang, Zhao Liu, Li-fuan Bao, Sha-Sha Zhang, Chun-Guang Zhang, Xin Li, Hai-Xia Li, Xiao-Lu Zhang,
Atle Magnar Bones, Zhen-Biao Yang, and Yu-Ling Chen

Guanine nucleotide exchange factor RopGEF2, which is directly activated by phytochrome phyB, suppresses red light-induced stomatal opening by activating ROP7 and ROP2. 717

Evolutionary Conservation of ABA Signaling for Stomatal Closure.  Shengguan Cai, Guang Chen,
Yuanyuan Wang, Yuqing Huang, D. Blaine Marchant, Yizhou Wang, Qian Yang, Fei Dai, Adrian Hills,
Peter J. Franks, Eviatar Nevo, Douglas E. Soltis, Pamela S. Soltis, Emily Sessa, Paul G. Wolf, Dawei Xue,
Guoping Zhang, Barry J. Pogson, Michael R. Blatt, and Zhong-Hua Chen

New evidence for ABA-induced stomatal closure in fern and known evidence in earlier diverging lineages does not support the hypothesis that stomatal responsiveness to ABA evolved first in seed plants. 732

PECTIN METHYLESTERASE34 Contributes to Heat Tolerance through Its Role in Promoting Stomatal Movement.  Ya-Chen Huang, Hui-Chen Wu, Yin-Da Wang, Chi-Hung Liu, Ching-Chih Lin, 
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Stomatal Closure, Basal Leaf Embolism, and Shedding Protect the Hydraulic Integrity of Grape Stems.  Uri Hochberg, Carol W. Windt, Alexandre Ponomarenko, Yong-Jiang Zhang,
Jessica Gersony, Fulton E. Rockwell, and N. Michele Holbrook

Grape stomata close before xylem cavitation, and if the plant continues to dehydrate, basal leaf embolism and shedding protect the hydraulic integrity of younger leaves and the stem. 764

Reducing Stomatal Density in Barley Improves Drought Tolerance without Impacting on Yield.  Jon Hughes, Christopher Hepworth, Chris Dutton, Jessica A. Dunn, Lee Hunt, Jennifer Stephens, Robbie Waugh, 
Duncan D. Cameron, and Julie E. Gray

Manipulation of a gene involved in the suppression of stomatal development in barley can reduce stomatal density, leading to improved drought tolerance without deleterious effects on yield. 776

Hornwort Stomata: Architecture and Fate Shared with 400-Million-Year-Old Fossil Plants without Leaves.  Karen S. Renzaglia, Juan Carlos Villarreal, Bryan T. Piatkowski, Jessica R. Lucas, and Amelia Merced

Guard cells in hornwort develop wall thickenings, open, die, and collapse, similar to the oldest fossil plants, and in synchrony with sporogenesis, drying of internal fluids, and sporophyte maturation. 788

Drought-Enhanced Xylem Sap Sulfate Closes Stomata by Affecting ALMT12 and Guard Cell ABA Synthesis.  Frosina Malcheska, Altaf Ahmad, Sundas Batoöl, Heike M. Müller, Jutta Ludwig-Müller, 
Jürgen Kreuzwieser, Dörte Randewig, Robert Hänsch, Ralf R. Mendel, Rüdiger Hell, Markus Wirtz, 
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Reduced unloading and enhanced loading of sulfate increased xylem sap sulfate during early drought, which affects the opening of the ALMT12 channel and induces guard cell expression of the key step in ABA synthesis, NCED3. 798

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Reconstitution of Abscisic Acid Signaling from the Receptor to DNA via bHLH Transcription Factors. Yohei Takahashi, Yuta Ebisu, and Ken-ichiro Shimazaki

Signaling from ABA receptor to its target DNA is reconstituted using basic helix-loop-helix (bHLH) transcriptional activator AKSI in vitro.

A Mutation in the bHLH Domain of the SPCH Transcription Factor Uncovers a BR-Dependent Mechanism for Stomatal Development. Alberto de Marcos, Anaxi Houbaert, Magdalena Triviño, Dolores Delgado, Mar Martín-Trillo, Eugenia Riessinova, Carmen Fenoll, and Montaña Mena

The hypomorphic mutant speechless-5 reveals a brassinosteroid-dependent mechanism for stomata formation and the involvement of the bHLH domain of SPEECHLESS in proper expression of some target genes.

REGULAR ISSUE

ON THE INSIDE

Peter V. Minorsky

UPDATE

The Multiple Signals That Control Tuber Formation. David J. Hannapel, Pooja Sharma, Tian Lin, and Anjan K. Banerjee

The three critical switches that regulate the onset of tuber formation in potato interact in a dynamic signaling pathway.

BREAKTHROUGH TECHNOLOGIES

Modeling of Dolichol Mass Spectra Isotopic Envelopes as a Tool to Monitor Isoprenoid Biosynthesis. Adam Jozwiak, Agata Lipko, Magdalena Kania, Witold Danikiewicz, Liliana Surnacz, Agnieszka Witek, Jacek Wojcik, Konrad Zdanowski, Cezary Pańczkowski, Tadeusz Chojnicki, Jarosław Poznanski, and Ewa Swiezewska

A new method enables quantitative analysis of the contributions of the MVA and MEP pathways to generating isoprenoids.

A Virus-Induced Assay for Functional Dissection and Analysis of Monocot and Dicot Flowering Time Genes. Cheng Qin, Weiwei Chen, Jiajia Shen, Linning Cheng, Femi Akande, Ke Zhang, Chen Yuan, Chunyang Li, Pengcheng Zhang, Nongnong Shi, Qi Cheng, Yule Liu, Stephen Jackson, and Yiguo Hong

A PVX-based virus-induced functional assay was designed in order to identify amino acids in the FT protein that are essential for flowering and to examine floral induction by mono- and dicotyledonous FT genes.

A Motif and Amino Acid Bias Bioinformatics Pipeline to Identify Hydroxyproline-Rich Glycoproteins. Kim L. Johnson, Andrew M. Cassin, Andrew Lonsdale, Antony Bacic, Monika S. Doblin, and Carolyn J. Schultz

An innovative bioinformatics pipeline to identify and classify a plant-specific superfamily of cell wall hydroxyproline-rich glycoproteins provides evolutionary insight from algae to flowering plants.

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Insights into the Evolution of Hydroxyproline-Rich Glycoproteins from 1000 Plant Transcriptomes.  
Kim L. Johnson, Andrew M. Cassin, Andrew Lonsdale, Gane Ka-Shu Wong, 
Douglas E. Soltis, Nicholas W. Miles, Michael Melkonian, Barbara Melkonian, Michael K. Deyholos, 
James Leebens-Mack, Carl J. Rothfels, Dennis W. Stevenson, Sean W. Graham, Xumin Wang, 
Shuangxiu Wu, J. Chris Pires, Patrick P. Edgar, Eric J. Carpenter, Antony Bacic, Monika S. Doblin, 
and Carolyn J. Schultz

Evaluation of hydroxyproline-rich glycoproteins identified in 1KP transcriptomic data sets to gain insight into their evolutionary history from chlorophyte algae to flowering plants.

ChloroKB: A Web Application for the Integration of Knowledge Related to Chloroplast Metabolic Network.  
Pauline Gloaguen, Sylvain Bouriaux, Claude Alban, Stéphane Ravanel, Daphné Seigneurin-Berny, 
Michel Matringe, Marnanne Tardif, Marcel Kuntz, Myriam Ferro, Christophe Bruley, Norbert Rolland, 
Yves Vandenbrouck, and Gilles Curien

ChloroKB is a Web-based application that enables the user to explore the chloroplast metabolic network in Arabidopsis.

RESEARCH REPORT
CRISPR-Cas9 Targeted Mutagenesis Leads to Simultaneous Modification of Different Homoeologous Gene Copies in Polyploid Oilseed Rape (Brassica napus).  
Janina Braatz, Hans-Joachim Harloff, Martin Mascher, Nils Stein, Axel Himmelbach, and Christian Jung

A single CRISPR-Cas9 target efficiently induces heritable mutations in two rapeseed gene homologs.

RESEARCH ARTICLES
BIOCHEMISTRY AND METABOLISM
Functional Diversification of Kaurene Synthase-Like Genes in Isodon rubescens.  
Baolong Jin, Guanghong Cui, Juan Guo, Jinfu Tang, Lixin Duan, Huixin Lin, Ye Shen, Tong Chen, Huabei Zhang, 
and Luqi Huang

Numerous kaurene synthase-like cyclases have been identified in Isodon rubescens, providing new perspectives into understanding the evolution of diterpenoid chemical diversity in Lamiacea.

Cytosolic and Chloroplastic DHARs Cooperate in Oxidative Stress-Driven Activation of the Salicylic Acid Pathway.  
Marie-Sylviane Rahantaniaina, Shengchun Li, Gilles Chatel-Innocenti, Andrée Tuzet, Emmanuelle Issakidis-Bourguet, Amma Mhamdi, and Graham Noctor

Arabidopsis mutants with negligible DHAR activity can maintain wild-type ascorbate status, but decreased oxidation of glutathione alters downstream responses to intracellular H₂O₂.

Disrupting Flavone Synthase II Alters Lignin and Improves Biomass Digestibility.  
Pui Ying Lam, Yuki Tobinatsu, Yuri Takeda, Shiro Suzuki, Masaomi Yamamura, Toshiaki Umezawa, 
and Clèo Lo

Disruption of the flavone synthase II gene in rice results in an altered cell wall lignin incorporating naringenin as a novel flavonoid component and improves biomass saccharification efficiency.

The activity of LPEAT affects the growth of Arabidopsis and is essential for maintaining an adequate level of PE, LPE, and LPC in the cells.

Genomic Insights into the Evolution of the Nicotine Biosynthesis Pathway in Tobacco. Masataka Kajikawa, Nicolas Sierro, Haruhiko Kawaguchi, Nicolas Bakaher, Nikolai V. Ivanov, Takashi Hasimoto, and Tsubasa Shoji

A series of metabolic and transport genes involved in the nicotine pathway form a regulon under the control of jasmonate-responsive transcription factors in tobacco.

Regulatory Phosphorylation of Bacterial-Type PEP Carboxylase by the Ca2+-Dependent Protein Kinase RcCDPK1 in Developing Castor Oil Seeds. Sheng Ying, Allyson T. Hill, Michal Pyc, Erin M. Anderson, Wayne A. Snedden, Robert T. Mullen, Yi-Min She, and William C. Plaxton

RcCDPK1 catalyzes in vivo inhibitory phosphorylation of the bacterial-type PEP carboxylase subunits of the novel heteromeric Class-2 PEPC complex of developing castor beans.

Defining the Diverse Cell Populations Contributing to Lignification in Arabidopsis Stems. Rebecca A. Smith, Mathias Schuetz, Steven D. Karlen, David Bird, Naohito Tokunaga, Yasushi Sato, Shawn D. Mansfield, John Ralph, and A. Lacey Samuels

Xylem vessel lignification in young Arabidopsis stems requires neighboring xylary parenchyma, but, as stems mature, fibers primarily produce their own lignin monomers.

LIL3, a Light-Harvesting Complex Protein, Links Terpenoid and Tetrapyrrole Biosynthesis in Arabidopsis thaliana. Daniel Hey, Maxi Rothbart, Josephine Herbst, Peng Wang, Jakob Müller, Daniel Wittmann, Kirsten Gruhl, and Bernhard Grimm

LIL3 associates with POR and CHLP and thus contributes to the supply of the two metabolites, chlorophyllide and phytol pyrophosphate, required for the final step in chlorophyll a synthesis in Arabidopsis.


An integrative glycobiology approach provides new insight into multiple modes of cell wall remodeling during pea border cell formation and mechanisms of their release.

Roles of Dicer-Like Proteins 2 and 4 in Intra- and Intercellular Antiviral Silencing. Cheng Qin, Bin Li, Yaya Fan, Xiao Zhang, Zhiming Yu, Eugene Ryabov, Mei Zhao, Hui Wang, Nongnong Shi, Pengcheng Zhang, Stephen Jackson, Mahmut Tör, Qi Cheng, Yule Liu, Philippe Gallusci, and Yiguo Hong

DCL4 inhibits intercellular VIGS, whereas DCL2 along with DCL2-processed/dependent siRNAs are involved in non-cell-autonomous VIRS in Nicotiana benthamiana.
ECOPHYSIOLOGY AND SUSTAINABILITY

Excess Diffuse Light Absorption in Upper Mesophyll Limits CO₂ Drawdown and Depresses Photosynthesis.  J. Mason Earles, Guillaume Théroux-Rancourt, Matthew E. Gilbert, Andrew J. McElrone, and Craig R. Brodersen

Excess absorption of diffuse versus direct light in the upper mesophyll of Helianthus annuus sun leaves leads to suboptimal photosynthesis.

GENES, DEVELOPMENT, AND EVOLUTION


LEAFY and APETALA1/CAULIFLOWER have partially antagonistic activities in the control of floral initiation.

UV-B Inhibits Leaf Growth through Changes in Growth Regulating Factors and Gibberellin Levels.  Julieta Fina, Romina Casadevall, Hamada AbdElgawad, Els Prinsen, Marios N. Markakis, Gerrit T. S. Beemster, and Paula Casati

Solar UV-B inhibits leaf growth in maize by suppressing cell proliferation, a response mediated through a decrease in GAs in the growth zone.

Small kernel2 Encodes a Glutaminase in Vitamin B₆ Biosynthesis Essential for Maize Seed Development.  Yan-Zhuo Yang, Shuo Ding, Yong Wang, Cui-Ling Li, Yun Shen, Robert Meeley, Donald R. McCarty, and Bao-Cai Tan

A small kernel mutant in maize highlights vitamin B₆ biosynthesis in embryogenesis and endosperm development.

Night-Break Experiments Shed Light on the Photoperiod1-Mediated Flowering.  Stephen Pearce, Lindsay M. Shaw, Huiqiong Lin, Jennifer D. Cotter, Chengxia Li, and Jorge Dubcovsky

Interruptions of long nights by short pulses of light (“night-break”) for several days accelerates wheat flowering, but only in the presence of the PHOTOPERIOD1 gene.

A Rice PECTATE LYASE-LIKE Gene Is Required for Plant Growth and Leaf Senescence.  Yujia Leng, Yaolong Yang, Deyong Ren, Lichao Huang, Liping Dai, Yuqiong Wang, Long Chen, Zhengjun Tu, Yihong Gao, Xueyong Li, Li Zhu, Jiang Hu, Guangheng Zhang, Zhenyu Gao, Longbiao Gao, Zhaosheng Kong, Yongjun Lin, Qian Qian, and Dali Zeng

DE1 affects rice growth and leaf senescence mediated by PECTATE LYASE-LIKE genes.

GmILPA1, Encoding an APC8-like Protein, Controls Leaf Petiole Angle in Soybean.  Jinshan Gao, Sixin Yang, Wen Cheng, Yongfu Fu, Jiuntian Leng, Xiaohui Yuan, Ning Jiang, Jianxin Ma, and Xianzhong Feng

An APC8-like protein regulates leaf petiole angle by modulating establishment of pulvinus in soybean.
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[OPEN] Functional Conservation and Divergence among Homoeologs of TaSPL20 and TaSPL21, Two SBP-Box Genes Governing Yield-Related Traits in Hexaploid Wheat. Bin Zhang, Weina Xu, Xia Liu, Xinguo Mao, Ang Li, Jingyi Wang, Xiaoping Chang, Xueyong Zhang, and Ruilian Jing

The triplicated homoeologs of two paralogous TaSPL loci display diverse functions in governing yield-related traits in hexaploid wheat.


FIS2 and MEA have diverged in concert after simultaneous gene duplication, resulting in functional divergence of the PRC2 complexes in Brassicaceae, which is a novel fate for duplicated genes whose products act in complexes.

[OPEN] SDG2-Mediated H3K4me3 Is Crucial for Chromatin Condensation and Mitotic Division during Male Gametogenesis in Arabidopsis. Violaine Pinon, Xiaozhen Yao, Aiwu Dong, and Wen-Hui Shen

Active H3K4me3 deposition is essential for gametophyte chromatin landscape, playing critical roles in gamete mitotic cell cycle progression and pollen vegetative cell function.

SIGNALING AND RESPONSE


mRNAs coding for ribosomal proteins are preferentially stored during heat shock and released during recovery phase to enhance ribosome production in an HSP101-dependent manner.

[CC-BY] MAP Kinase PrMPK9-1 Contributes to the Self-Incompatibility Response. Lijun Chai, Richard L. Tudor, Natalie S. Poulter, Katie A. Wilkins, Deborah J. Eaves, F. Christopher H. Franklin, and Veronica E. Franklin-Tong

A TDY-class MAPK is functionally involved in mediating self-incompatibility in Papaver.

Constitutively Active Arabidopsis MAP Kinase 3 Triggers Defense Responses Involving Salicylic Acid and SUMM2 Resistance Protein. Baptiste Genot, Julien Lang, Souha Berriri, Marie Garmier, Françoise Gilard, Stéphanie Paleyron, Katrien Haustaeet, Dominique Van Der Streuten, Heribert Hirt, and Jean Colcombet

The stress-activated MPK3 and the SUPPRESSOR OF MKK1 MKK2 1/2 module control a similar set of responses, which include accumulation of salicylic acid, reactive oxygen species, and phytoalexins and modulation of defense genes.


GA regulates SL biosynthesis through the GA receptor GID1 and F-box protein GID2.
Brassinosteroid Biosynthesis Is Modulated via a Transcription Factor Cascade of COG1, PIF4, and PIF5.
Zhuoyun Wei, Tong Yuan, Danuše Tarkowská, Jeongsik Kim, Hong Gil Nam, Ondřej Novák, Kai He,
Xiaoping Gou, and Jia Li

Transcriptional control of brassinosteroid biosynthesis genes engages a transcription factor cascade in Arabidopsis.

Tetrahydrofolate Modulates Floral Transition through Epigenetic Silencing.
Lei Wang, Dongdong Kong,
Qiang Lv, Guoqi Niu, Tingting Han, Xuanchao Zhao, Shulin Meng, Qian Cheng, Shouchun Guo, Jing Du,
Zili Wu, Jinzheng Wang, Fang Bao, Yong Hu, Xiaojun Pan, Jinchan Xia, Dong Yuan, Lida Han, Tong Lian,
Chunyi Zhang, Haiyang Wang, Xin-jian He, and Yi-kun He

Folate regulates DNA methylation to affect Arabidopsis flowering time.

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