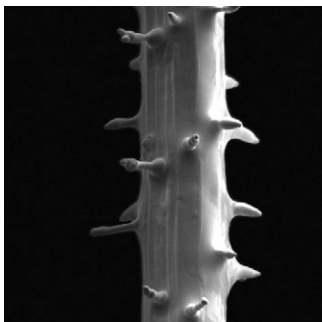


T H E  
**PLANT**  
C E L L

Volume 26 Number 4 April 2014

The electronic form of this issue, available at [www.plantcell.org](http://www.plantcell.org), is the journal of record.

**ON THE COVER**



Cells must sense and regulate their internal  $\text{NH}_4^+$  levels to modulate nitrogen levels and avoid  $\text{NH}_4^+$  toxicity. Bai et al. (pages 1497–1511) identify an *Arabidopsis*  $[\text{Ca}^{2+}]_{\text{cyt}}$ -associated protein kinase (CAP1), a receptor-like kinase that mediates  $\text{NH}_4^+$  homeostasis. CAP1 also regulates the polar growth of root hairs by maintaining tip-focused cytoplasmic  $\text{Ca}^{2+}$  gradients. The *cap1-1* mutation specifically affects root hair tip elongation and the morphology of root hairs on Murashige and Skoog medium and produces elevated levels of cytoplasmic  $\text{NH}_4^+$ . Ammonium depletion from the medium reestablished the  $\text{Ca}^{2+}$  gradient necessary for normal root hair tip growth in the mutant. The image shows abnormal root hairs in a *cap1-1* mutant grown on Murashige and Skoog medium.

**IN BRIEF**

- Nitrogen-Sparing Mechanisms in *Chlamydomonas*: Reduce, Reuse, Recycle, and Reallocate** 1379  
Nancy A. Eckardt
- Orange Carotenoid Protein Quenches Excess Energy and Singlet Oxygen** 1380  
Jennifer Mach
- Marked for Destruction: MANNOSIDASE4 and 5 Process *N*-Linked Glycans into ER-Associated Degradation Tags** 1381  
Nancy Hofmann

**LARGE-SCALE BIOLOGY ARTICLES**

- Efficient Genome-Wide Detection and Cataloging of EMS-Induced Mutations Using Exome Capture and Next-Generation Sequencing** [C](#)[W](#)[O](#)[P](#)[E](#)[N](#) 1382  
Isabelle M. Henry, Ugrappa Nagalakshmi, Meric C. Lieberman, Kathie J. Ngo, Ksenia V. Krasileva, Hans Vasquez-Gross, Alina Akhunova, Eduard Akhunov, Jorge Dubcovsky, Thomas H. Tai, and Luca Comai
- High-Throughput Genotyping of Green Algal Mutants Reveals Random Distribution of Mutagenic Insertion Sites and Endonucleolytic Cleavage of Transforming DNA** [W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1398  
Ru Zhang, Weronika Patena, Ute Armbruster, Spencer S. Gang, Sean R. Blum, and Martin C. Jonikas
- Nitrogen-Sparing Mechanisms in *Chlamydomonas* Affect the Transcriptome, the Proteome, and Photosynthetic Metabolism** [W](#) 1410  
Stefan Schmollinger, Timo Mühlhaus, Nanette R. Boyle, Ian K. Blaby, David Casero, Tabea Mettler, Jeffrey L. Moseley, Janette Kropat, Frederik Sommer, Daniela Strenkert, Dorothea Hemme, Matteo Pellegrini, Arthur R. Grossman, Mark Stitt, Michael Schroda, and Sabeeha S. Merchant

**RESEARCH ARTICLES**

- Boom-Bust Turnovers of Megabase-Sized Centromeric DNA in *Solanum* Species: Rapid Evolution of DNA Sequences Associated with Centromeres** [C](#)[W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1436  
Haiqin Zhang, Andrea Kobližková, Kai Wang, Zhiyun Gong, Ludmila Oliveira, Giovana A. Torres, Yufeng Wu, Wenli Zhang, Petr Novák, C. Robin Buell, Jiří Macas, and Jiming Jiang

## EDITORIAL BOARD

### Editor in Chief

Cathie Martin

### Coeeditors

Sarah M. Assmann

Jody Banks

Alice Barkan

Sebastian Bednarek

James Birchler

Ulla Bonas

Christopher Bowler

Judy Callis

XiaoFeng Cao

Vincenzo De Luca

Xing Wang Deng

Xinnian Dong

Allan Downie

Alisdair Fernie

Pascal Genschik

Jean T. Greenberg

Thomas Guilfoyle

Herman R. Höfte

David Jackson

Regine Kahmann

Martin Kater

Daniel J. Kliebenstein

William Lucas

Blake Meyers

Ortrun Mittelsten Scheid

Giles Oldroyd

Michael Palmgren

Markus Pauly

Scott C. Peck

Barry Pogson

Zhaohui Qin

Karin Schumacher

David Smyth

Chris J. Staiger

Keiko Sugimoto

### Managing Editor

Patti Lockhart

### Senior Features Editor

Nancy A. Eckardt

### Features Editor

Mary Williams

### Science Editors

Greg Bertoni

Kathleen L. Farquharson

Nancy R. Hofmann

Jennifer Lockhart

Jennifer M. Mach

### Production Manager

Susan L. Entwistle

### Manuscript Manager

Annette Kessler

### Publications Director

Nancy A. Winchester

### Publisher

American Society of

Plant Biologists

Executive Director,

Crispin Taylor

### Editorial Office

15501 Monona Drive

Rockville, Maryland 20855-2768

Telephone: 301/296-0908

Fax: 301/279-2996


http://www.aspb.org

Online at [www.plantcell.org](http://www.plantcell.org)


- Homoeologous Chromosome Sorting and Progression of Meiotic Recombination in *Brassica napus*: Ploidy Does Matter!** [W](#) 1448  
Laurie Grandont, Nieves Cuñado, Olivier Coriton, Virgine Huteau, Frédérique Eber, Anne Marie Chèvre, Mathilde Grelon, Liudmila Chelysheva, and Eric Jenczewski
- STM/BP-Like KNOX1 Is Uncoupled from ARP in the Regulation of Compound Leaf Development in *Medicago truncatula*** [C](#)[W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1464  
Chuanen Zhou, Lu Han, Guifen Li, Maofeng Chai, Chunxiang Fu, Xiaofei Cheng, Jiangqi Wen, Yuhong Tang, and Zeng-Yu Wang
- Analysis of the Root System Architecture of *Arabidopsis* Provides a Quantitative Readout of Crosstalk between Nutritional Signals** [W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1480  
Fabian Kellermeier, Patrick Armengaud, Triona J. Seditas, John Danku, David E. Salt, and Anna Amtmann
- A Receptor-Like Kinase Mediates Ammonium Homeostasis and Is Important for the Polar Growth of Root Hairs in *Arabidopsis*** [W](#) 1497  
Ling Bai, Xiaonan Ma, Guozeng Zhang, Shufei Song, Yun Zhou, Lijie Gao, Yuchen Miao, and Chun-Peng Song
- The Rice Basic Helix-Loop-Helix Transcription Factor TDR INTERACTING PROTEIN2 Is a Central Switch in Early Anther Development** [C](#)[W](#) 1512  
Zhenzhen Fu, Jing Yu, Xiaowei Cheng, Xu Zong, Jie Xu, Mingjiao Chen, Zongyun Li, Dabing Zhang, and Wanqi Liang
- The ARC1 E3 Ligase Promotes Two Different Self-Pollen Avoidance Traits in *Arabidopsis*** [C](#)[W](#) 1525  
Emily Indriolo, Darya Safavian, and Daphne R. Goring
- ABORTED MICROSPORES Acts as a Master Regulator of Pollen Wall Formation in *Arabidopsis*** [C](#)[W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1544  
Jie Xu, Zhiwen Ding, Gema Vizcay-Barrena, Jianxin Shi, Wanqi Liang, Zheng Yuan, Danièle Werck-Reichhart, Lukas Schreiber, Zoe A. Wilson, and Dabing Zhang
- EARLY FLOWERING3 Regulates Flowering in Spring Barley by Mediating Gibberellin Production and *FLOWERING LOCUS T* Expression** [C](#)[W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1557  
Scott A. Boden, David Weiss, John J. Ross, Noel W. Davies, Ben Trevaskis, Peter M. Chandler, and Steve M. Swain
- Functional Analysis of the Hydrophilic Loop in Intracellular Trafficking of *Arabidopsis* PIN-FORMED Proteins** [W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1570  
Anindya Ganguly, Minho Park, Mahipal Singh Kesawat, and Hyung-Taeg Cho
- SPX4 Negatively Regulates Phosphate Signaling and Homeostasis through Its Interaction with *PHR2* in Rice** [W](#)[I](#)[O](#)[P](#)[E](#)[N](#) 1586  
Qundan Lv, Yongjia Zhong, Yuguang Wang, Zhiye Wang, Li Zhang, Jing Shi, Zhongchang Wu, Yu Liu, Chuanzao Mao, Keke Yi, and Ping Wu
- Light-Harvesting Complex Protein LHCBM9 Is Critical for Photosystem II Activity and Hydrogen Production in *Chlamydomonas reinhardtii*** [C](#)[W](#) 1598  
Sabrina Grewe, Matteo Ballottari, Marcelo Alcocer, Cosimo D'Andrea, Olga Blifernez-Klassen, Ben Hankamer, Jan H. Mussgnug, Roberto Bassi, and Olaf Kruse
- ACTIN-RELATED PROTEIN6 Regulates Female Meiosis by Modulating Meiotic Gene Expression in *Arabidopsis*** [W](#) 1612  
Yuan Qin, Lihua Zhao, Megan I. Skaggs, Sebastien Andreuzza, Tatsuya Tsukamoto, Aneesh Panoli, Kirsten N. Wallace, Steven Smith, Imran Siddiqi, Zhenbiao Yang, Ramin Yadegari, and Ravishankar Palanivelu
- Actin-Dependent and -Independent Functions of Cortical Microtubules in the Differentiation of *Arabidopsis* Leaf Trichomes** [W](#) 1629  
Adrian Sambade, Kim Findlay, Anton R. Schäffner, Clive W. Lloyd, and Henrik Buschmann

- Choreography of Transcriptomes and Lipidomes of *Nannochloropsis* Reveals the Mechanisms of Oil Synthesis in Microalgae** [W|OPEN](#) 1645  
Jing Li, Danxiang Han, Dongmei Wang, Kang Ning, Jing Jia, Li Wei, Xiaoyan Jing, Shi Huang, Jie Chen, Yantao Li, Qiang Hu, and Jian Xu
- Arabidopsis* Cuticular Wax Biosynthesis Is Negatively Regulated by the DEWAX Gene Encoding an AP2/ERF-Type Transcription Factor** [W|OPEN](#) 1666  
Young Sam Go, Hyojin Kim, Hae Jin Kim, and Mi Chung Suh
- Methylcrotonyl-CoA Carboxylase Regulates Triacylglycerol Accumulation in the Model Diatom *Phaeodactylum tricorutum*** [C|W|OPEN](#) 1681  
Feng Ge, Weichao Huang, Zhuo Chen, Chunye Zhang, Qian Xiong, Chris Bowler, Juan Yang, Jin Xu, and Hanhua Hu
- Plasma Membranes Are Subcompartmentalized into a Plethora of Coexisting and Diverse Microdomains in *Arabidopsis* and *Nicotiana benthamiana*** [C|W](#) 1698  
Iris K. Jarsch, Sebastian S.A. Konrad, Thomas F. Stratil, Susan L. Urbanus, Witold Szymanski, Pascal Braun, Karl-Heinz Braun, and Thomas Ott
- Arabidopsis* Class I  $\alpha$ -Mannosidases MNS4 and MNS5 Are Involved in Endoplasmic Reticulum-Associated Degradation of Misfolded Glycoproteins** [C|W|OPEN](#) 1712  
Silvia Hüttner, Christiane Veit, Ulrike Vavra, Jennifer Schoberer, Eva Liebming, Daniel Maresch, Josephine Grass, Friedrich Altmann, Lukas Mach, and Richard Strasser
- Clathrin and Membrane Microdomains Cooperatively Regulate RbohD Dynamics and Activity in *Arabidopsis*** [C|W](#) 1729  
Huaiqing Hao, Lusheng Fan, Tong Chen, Ruili Li, Xiaojuan Li, Qihua He, Miguel A. Botella, and Jinxing Lin
- The Enzyme-Like Domain of *Arabidopsis* Nuclear  $\beta$ -Amylases Is Critical for DNA Sequence Recognition and Transcriptional Activation** [C|W|OPEN](#) 1746  
Sebastian Soyk, Klára Šimková, Evelyne Zürcher, Leonie Luginbühl, Luise H. Brand, Cara K. Vaughan, Dierk Wanke, and Samuel C. Zeeman
- HEAT-INDUCED *TAS1 TARGET1* Mediates Thermotolerance via HEAT STRESS TRANSCRIPTION FACTOR A1a-Directed Pathways in *Arabidopsis*** [C|W](#) 1764  
Shuxia Li, Jinxin Liu, Zhongyuan Liu, Xiaorong Li, Feijie Wu, and Yuke He
- The Cyanobacterial Photoactive Orange Carotenoid Protein Is an Excellent Singlet Oxygen Quencher** [C|W](#) 1781  
Arezki Sedoud, Rocío López-Igual, Ateeq ur Rehman, Adjélé Wilson, François Perreau, Clémence Boulay, Imre Vass, Anja Krieger-Liszkay, and Diana Kirilovsky
- Arabidopsis* *miR156* Regulates Tolerance to Recurring Environmental Stress through *SPL* Transcription Factors** [C|W](#) 1792  
Anna Stief, Simone Altmann, Karen Hoffmann, Bikram Datt Pant, Wolf-Rüdiger Scheible, and Isabel Bäurle
- The H<sup>+</sup>-ATPase HA1 of *Medicago truncatula* Is Essential for Phosphate Transport and Plant Growth during Arbuscular Mycorrhizal Symbiosis** [C|W|OPEN](#) 1808  
Franziska Krajinski, Pierre-Emmanuel Courty, Daniela Sieh, Philipp Franken, Haoqiang Zhang, Marcel Bucher, Nina Gerlach, Igor Kryvoruchko, Daniela Zoeller, Michael Udvardi, and Bettina Hause

Ertao Wang, Nan Yu, S. Asma Bano, Chengwu Liu, Anthony J. Miller, Donna Cousins, Xiaowei Zhang, Pascal Ratet, Million Tadege, Kirankumar S. Mysore, J. Allan Downie, Jeremy D. Murray, Giles E.D. Oldroyd, and Michael Schultze

 Some figures in this article are displayed in color online but in black and white in the print edition.

 Online version contains Web-only data.

 Articles can be viewed online without a subscription.



© 2014 American Society of Plant Biologists. All rights reserved. Printed on acid-free paper effective with Volume 1, Number 1, January 1989. Printed in the United States of America.

*The Plant Cell* (ISSN 1040-4651, online ISSN 1532-298X) is published monthly (one volume per year) by the American Society of Plant Biologists, 15501 Monona Drive, Rockville, MD 20855-2768, and is produced by Dartmouth Journal Services, Waterbury, VT. The institutional price for the print and online versions is based on type of institution; contact [institution@aspb.org](mailto:institution@aspb.org). Single copies may be purchased for \$40 each, plus \$10 shipping (U.S.) or \$12 (outside U.S.). Members of the American Society of Plant Biologists may subscribe to *The Plant Cell* for \$240. Nonmember individuals may subscribe for \$500. Students may subscribe for \$165. For matters regarding subscriptions, contact Suzanne Cholwek, ASPB, 15501 Monona Drive, Rockville, MD 20855-2768; telephone 301/296-0926; fax 301/251-6740; e-mail [scholwek@aspb.org](mailto:scholwek@aspb.org). Notify ASPB in writing within 3 months (domestic) or 6 months (foreign) of issue date, and defective copies or copies lost in the mail will be replaced. Send all inquiries regarding display advertising to FASEB AdNet, 9650 Rockville Pike, Bethesda, MD 20814-3998; telephone 301/634-7791; fax 301/634-7153; e-mail [adnet@faseb.org](mailto:adnet@faseb.org). Periodicals postage paid at Rockville, MD 20850, and at additional mailing offices.

**Postmaster:** Send address changes to *The Plant Cell*, American Society of Plant Biologists, 15501 Monona Drive, Rockville, MD 20855-2768. The online version of *The Plant Cell* is available at [www.plantcell.org](http://www.plantcell.org).

**Permission to Reprint:** Permission to make digital or hard copies of part or all of a work published in *The Plant Cell* is granted without fee for personal or classroom use provided that copies are not made or distributed for profit or commercial advantage and that copies bear the full citation and the following notice on the first page: "Copyright American Society of Plant Biologists." For all other kinds of copying, request permission in writing from Nancy A. Winchester, Publications Director, ASPB headquarters.

This information is current as of February 20, 2019

<b>Permissions</b>	<a href="https://www.copyright.com/ccc/openurl.do?sid=pd_hw1532298X&amp;issn=1532298X&amp;WT.mc_id=pd_hw1532298X">https://www.copyright.com/ccc/openurl.do?sid=pd_hw1532298X&amp;issn=1532298X&amp;WT.mc_id=pd_hw1532298X</a>
<b>eTOCs</b>	Sign up for eTOCs at: <a href="http://www.plantcell.org/cgi/alerts/ctmain">http://www.plantcell.org/cgi/alerts/ctmain</a>
<b>CiteTrack Alerts</b>	Sign up for CiteTrack Alerts at: <a href="http://www.plantcell.org/cgi/alerts/ctmain">http://www.plantcell.org/cgi/alerts/ctmain</a>
<b>Subscription Information</b>	Subscription Information for <i>The Plant Cell</i> and <i>Plant Physiology</i> is available at: <a href="http://www.aspb.org/publications/subscriptions.cfm">http://www.aspb.org/publications/subscriptions.cfm</a>