



# **Editor-in-Chief**

# Lee Sweetlove

Department of Plant Sciences, University of Oxford, South Parks Road. Oxford OX1 3RB, UK Tel: +44 (0) 1865 275137 Email: lee.sweetlove@plants.

# Research Interests:

Central metabolism; Metabolic flux; Metabolic modeling; Metabolic engineering; Metabolons and metabolite channelling

Previous Editors-in-Chief Dianna Bowles (Founding EiC), 1990-2001 Harry Klee, 2002-2009 Christoph Benning, 2009-2017

# **Editorial Office**

The Plant Journal Editorial Office, Wiley Blackwell. 9600 Garsington Road, Oxford, OX4 2DQ, UK E-mail: tpj-general@wiley.com

Jim Ruddock Managing Editor E-mail: tpj-editor@wilev.com

Lauren Dawson Editorial Assistant E-mail: tpj-submissions@wiley.com, tpj-manuscripts@wiley.com

# **Production Office**

# Rajalakshmi Sundararamanujam

Production Editor E-mail: tpi@wilev.com

# **Senior Editors**

Federica Brandizzi Michigan State University, Plant Research Michigan State University, Plant Resear Laboratory, East Lansing, MI 48824, USA Tel: (517) 353-7872; Fax: (517) 353-9168 Email: fb@msu.edu

Research Interests
Cell biology; Plant endomembranes;
Endoplasmic reticulum stress; Fluorescent protein technology; Protein trafficking

# Alisdair R. Fernie

Alisdair R. Fernie Molecular Physiology, Max-Planck Institute for Molecular Plant Physiology, Golm 14476, Germany Tel: +49 331 567 8211 Email: fernie@mpimp-golm.mpg.de Research Interests Carbohydrate metabolism; Metabolomics; Primary metabolism

# Lyza Maron (Research highlights Editor)

BoyceThompson Institute, USDA/ARS Robert W. Holley Center for Agriculture & Health, Ithaca, NY 14853, USA

Research Interests
Abiotic stress responses; Root biology; Natural variation; Gene expression regulation

Sheila McCormick (Consultant Editor) Plant and Microbial Biology, 111 Koshland Hall, UC-Berkeley, Berkeley, CA 94720, USA Email: sheilamc@berkeley.edu

Research Interests
Pollen development, Plant gametes (sperm, egg, central cell); Pollen tube growth; Pollen-pistil interactions; Receptor kinase signaling (ligands); Genetics; Genomics

## Asaph Aharoni

Weizmann Institute of Science, Department of Plant Sciences, PO.B 26, Rehovot 76100, Israel Tel: +972 8 934 3643; Fax: +972 8 934 4181 Email: asaph.aharoni@weizmann.ac.il

Research Interests
Fruit metabolism and ripening control,
The plant surface (epidermis and the cuticle),
Secondary metabolism, Functional genomics and
metabolomics, Metabolic engineering,
Metabolism – development interface

# Jose Alonso Department of Genetics

Department of Genetics, North Carolina State University, 2548 Gardner Hall, Box 7614, Raleigh, North Carolina, 27695-7614, USA Tel: +1 919 515-5729; Fax: +1 919 515-3355 Email: jmalonso@unity.ncsu.edu

Research Interests
Ethylene signaling and response pathway; Hormone interactions and signal integration; Arabidopsis functional genomics and tool development; Auxin biosynthesis; Post-transcriptional control of hormonal responses

Bonnie Bartel
Department of Biosciences, Rice University, 6100 Main Street,
MS-140, Houston, Texas 77005, USA
Tel: +1 713 348 5602; Fax: +1 713 348 5154
Email:bartel@rice.edu

Research Interests
Cell biology; Peroxisome biology; Autophagy;
Protein trafficking; Arabidopsis genetics

Protein trafficking; Arabidopsis genetics

Jörg Bohlmann

Michael Smith Laboratories, University of British Columbia,
321-2185 East Mall, Vancouver V61 T24

British Columbia, Canada
Tel: +1 604 822 0282; Fax: +1 604 822 2114

Email: bohlmann@interchange.ubc.ca

Research Interests
Secondary metabolism; Terpenoid synthases, cytochrome P450;
Plant-herbivore interactions; Chemical ecology;
Conifers, Poplar, Grapevine

Federica Randizzi

Federica Randizzi

Federica Brandizzi Michigan State University, Plant Research Laboratory, East Lansing, MI 48824, USA Tel: +1517 353-7872; Fax: +1 517 353-9168 Email: fb@msu.edu

Research Interests
Cell biology; Protein trafficking; Plant endomembranes;
Endoplasmic reticulum stress; Fluorescent protein technology

Faculty of Agronomy, University of Buenos Aires, Av. San Martin 4453, 1417-Buenos Aires, Argentina Tel: +5411 4524 8070/71; Fax: +5411 4514 8730 Email: casal@ifeva.edu.ar

Research Interests
Light signaling circuitry, its architecture and functional
implications; Functional genomics, transcriptome patterns
during plant development; Photomorphogenesis in crops

John Cushman
University of Nevada, Department of Biochemistry,
Mail Stop 330, 1664 N. Virginia St., Reno89557-0330, USA
Email: joushman@unr.edu

Research Interests
Abiotic stress responses; Metabolic adaptation to stress;
Crassulacean acid metabolism; Biosystem engineering

Brendan Davies Centre for Plant Sciences, University of Leeds, Leeds LS2 9JT, UK. Tel: +44 113 343 3123; Fax: +44 113 343 3144 Email: b.h.davies@leeds.ac.uk

Research Interests
Plant development; Reproduction; Transcription factors;
Nonsense-mediated mRNA decay

Katherine Denby
University of York, Department of Biology York, YO 10 5DD, UK
Tel: +44 1904 328 670 Research Interests
Plant systems biology; Plant pathogen interaction; Functional genomics; Gene regulation; Gene regulatory networks; Crop breeding

Alisdair R. Fernie Molecular Physiology, Max-Planck Institute for Molecular Plant Physiology, Golm 14476, Germany Tel: +49 331 567 8211

Email:fernie@mpimp-golm.mpg.de

Research Interests
Carbohydrate metabolism; Metabolomics; Primary metabolism

Jaume Flexas Universitat de les Illes Balears, Biologia, Carretera de Valldemossa Km 75, Palma de Mallorca, 07122, Spain Tel: +34 971 172365; Fax: +34 971 173184 Email: jaume.flexas@uib.es

Research Interests Photosynthesis; Ecophysiology; Abiotic stress; Mesophyll conductance; Drought

Crisanto Gutierrez
Centro de Biologia Molecular Severo Ochoa, Consejo Superior
de Investigaciones Científicas, Nicolas Cabrera 1, Cantoblanco,
Madrid, 28049, Spain
Tel: +34 91196438; Fax: +34 911964420
Email: cgutierrez@cbm.uam.es

Research Interests
Cell cycle regulation, DNA replication/endoreplication,
Chromatin/Gene expression, Retinoblastoma/E2F, Cell fate, cell
differentiation – Meristems, cell proliferation in organs

Jose Gutierrez-Marcos
Life Sciences, University of Warwick, Coventry, CV4 7AL, UK
Tel: +44 247 6 57 5077
Email: j.f.gutierrez-marcos@warwick.ac.uk

Research Interests Epigenetics; Seed development

Epigenetics; Seed development
Scott Jackson
Institute for Plant Breeding, Genetics and Genomics,
University of Georgia , 111 Riverbend Rd, Athens, Georgia,
GA 30602, USA
Tel: +1 706.242.4021; Fax: +1 706-583-8120
Email: sjackson@uga.edu

Research Interests Genomics; Cytogenetics; Evolutionary genomics; Legumes; Polyploidy

rotyploidy

Kerstin Kaufmann

Humboldt-Universität zu Berlin, Chair for Plant Cell and

Molecular Biology, Philippstr. 13, 10115 Berlin, Germany
Tel: +49(0)30209349741; Fax: +49(0)30209349741

Email: kerstin.kaufmann@hu-berlin.de

Research Interests
Gene regulatory networks; Flower development;
Plant transcription factors; Epigenetics;
Transcriptional regulation; Flowering

Transcriptional regulation; Flowering
Tracy Lawson
University of Essex, School of Biological Siences,
Wivenhoe Park, Colchester, Essex CO4 3SQ, UK
Tel: +44 1206 873327; Fax: +44 1206 872552
Email: tlawson@essex.ac.uk
Research Interests
Pleast Publications Pleast phonotyping: Conductance

Plant physiology; Plant phenotyping; Conductance; Gas exchange; Water use efficiency

Olivier Loudet
INRA - IJPB, Route de Saint Cyr, 78000 Versailles, France
Email: olivier.loudet@versailles.inra.fr

Research Interests
Natural variation; Quantitative genetics; Abiotic stress
tolerance; High-throughput phenotyping; Arabidopsis genetics
Jianxin Ma

**Jianxin Ma** Purdue University, 915 S. University St, West Lafayette, Indiana 47907, USA Tel: 765-496-3662; Fax: 765-496-7255; Email: maj@purdue.edu

Research Interests
ROS; Comparative genomics; Genome evolution; Transposable elements; Soybean genetics; Crop domestication

Hiroshi Maeda
University of Wisconsin – Madison, Department of Botany,
410 dunicol Drive , Madison, Wisconsin 53706, USA
Tel: +1 608-262-5833; Fax: +1 608-262-7509;
Email: maeda2@wisc.edu

Research Interests
Amino acid metabolism; Specialized metabolism; Interaction of metabolism and plant development and physiology

Ron Mittler University of North Texas College of Arts and Sciences, Department of Biological Sciences, College of Science, 1155 Union Circle #305220, Denton, Texas 76203-5017, USA Tel: +1 940 293 7170; Fax: +1 940 565 3821 Email: ron.mittler@unt.edu

Research Interests ROS; Abiotic stress; Gene expression; Systems biology; Efiji Nambara University of Toronto, Cell & Systems Biology, 25 Willcocks Street, Toronto, Ontario M5S 3B2, Canada Email: eiji.nambara@utoronto.ca

Research Interests
Plant hormone; Biosynthesis; Catabolism; Abscisic acid; Seed;
Stress response

Holger Puchta
Plant Molecular Biology and Biochemistry Karlsruhe Institute
of Technology (KIT), Hertzstr. 16 Geb. 06.35, Karlsruhe D-76187,
Germany
Tel: +49 721 608 8894; Fax: +49 721 608 4874
Email: holger.puchta@kit.edu

Research Interests
DNA repair; Meiotic recombination; DNA processing enzymes;
Genome evolution; Gene technology

Dominique Roby
Laboratory of Plant Microorganism Interactions (LIPM),
UMR CNRS-INRA 2594/441, BP 52627, F-31326,
Castanet-Tolosan cedex, France
Tel: +33 05 61 28 55 11; Fax: +33 05 61 28 50 61
Email: dominique.roby@toulouse.inra.fr
Research Interests
Plant-microbe interactions; Genetic analyses of plant
disease resistance pathways; Defence regulatory proteins;
Programmed cell death and transcriptional regulators;
Pathogen effector activities; Quantitative resistance to
pathogens

lan Small
University of Western Australia,
ARC Centre of Excellence in Plant Energy Biology, 35 Stirling
Highway, Crawley, Perth, 609 Western Australia
Tei: +61 (0)8 6488 4499; Fax: +61 (0)8 6488 4401
Email: lansmalle cyllene.uwa.edu.au
Research Intelests
Organelle biogenesis; Gene expression in mitochondria
and chloroplasts; Protein and RNA targeting;
Post-transcriptional regulation of gene expression;
Energy metabolism; Functional genomics,
bioinformatics and systems biology

Edgar Spalding Department of Botany, University of Wisconsin-Madison, 430 Lincoln Drive Madison WI 53706, USA Tel: +1 608 265 529 Email: spalding @wisc.edu Research Interests Research Interests
Ion transport and electrophysiology Growth;
control by light and auxin
Phenotype platforms; computer vision-based

Dorothea Tholl
Department of Biological Sciences, Virginia Polytechnic
Institute and State University, 408 Latham Hall, Agquad
Lane, Blacksburg, VA 24061, USA
Tel: +1 540 231 4567; Fax: +1 540 231 3347
Email: tholl@vt.edu

Research Interests Isoprenoid biochemistry, Secondary metabolism, Chemical diversity, Plant volatiles, Plant chemical interactions, Root biology, Metabolic pathways, Evolution, Engineering

Michael F. Thomashow Michigan State University, MSU-DDE Plant Research Laboratory, Plant Biology Building, 312 Wilson Rd, East Lansing, MI 48824, USA Tel: 1 517 355 2299; Fax: 1 517 353 9168 Email: thomash6@msu.edu

# Research Interests Abiotic stress; Biotic stress

Vess Van de Peer
Department of Plant Biotechnology and Genetics,
University of Gent, Technologiepark 927,
9052 Zwijnaarde, Belgium
Tel: +09 331 38 07; Fax: +09 331 38 09
Email: vess.vandepeer@ugent.be
Research Interests
Compartative genomics, systems biology, evolutionary
analysis, genome evolution, gene and genome
duplication

Saskia van Wees Utrecht University, Biology, Padualaan 8, Utrecht, 3584 CH, Netherlands Tel: +31-302536861; Fax: +31-302532837; Email:s.vanwees@uu.nl

Research Interests
Plant-microbe interactions; Plant-insect interactions;
Defenses to pathogens and insects; Gene expression
profiling; Gene expression regulation; Hormonal regulation
of plant immunity

Daoxin Xie School of Life Sciences, Tsinghua University, Beijing 100084, China Email: daoxinlab@tsinghua.edu.cn Research Interests
Hormone perception; Jasmonate signal transduction;
Strigolactone signaling; Hormonal crosstalk

Bin Yu Center for Plant Science Innovation, & School of Biological Sciences, University of Nebraska, Lincoln, 1901, Unive St, Lincoln, NE, USA Tel: 402-472-2125; 191: 402-472-725; Email: byu3@unl.edu Research Interests Small RNA metabolism; Epigenetics; RNA silencing; Non-coding RNAs; Arabidopsis genetics

# **Subscription information**

The Plant Journal is published semi-monthly (four volumes per annum), with two issues published each month. Subscription prices for 2019 are: Online only: US\$7274 (The Americas), US\$8488 (Rest of World), €4996 (Europe); £3936 (UK). Prices are exclusive of tax. Asia-Pacific GST, Canadian GST and European VAT will be applied at the appropriate rates. For more information on current tax rates, please go to www. wileyonlinelibrary.com/tax-vat. The price includes online access to the current and all online back files to January 1st 2015, where available. For other pricing options, including access information and terms and conditions, please visit www.wileyonlinelibrary.com/access.

# **Back issues**

Single issues from current and prior year are available at the single issue price from cs-journals@wiley.com. Earlier issues may be obtained from the Periodicals Service Company, 11 Main Street, Germantown, NY 12526, USA. Tel: +1 518 537 4700, Fax: +1 518 537 5899, Email: psc@periodicals.com.

# **Publisher**

The Plant Journal is published by John Wiley & Sons Ltd, 9600 Garsington Road, Oxford OX4 2DQ. Tel: +44 (0)1865 776868; Fax: +44 (0)1865 714591.

# **Journal Customer Services**

For ordering information, claims and any enquiry concerning your journal subscription please go to www.wiley customerhelp.com/ask or contact your nearest office:

Americas: Email: cs-journals@wiley.com; Tel: +1 781 388 8598 or 1 800 835 6770 (Toll free in the USA & Canada). Europe, Middle East and Africa: E-mail: cs-journals@wiley.

com; Tel: +44 (0) 1865 778315

Asia Pacific: E-mail: cs-journals@wiley.com; Tel: +65 6511 8000

**Japan:** For Japanese speaking support, e-mail: cs-japan@ wiley.com

**Visit our Online Customer Help** available in 7 languages at www.wileycustomerhelp.com.

# Despatch

THE PLANT JOURNAL, (ISSN 0960-7412), is published semi-monthly (four volumes per annum). US mailing agent: Mercury Media Processing, LLC 1850 Elizabeth Avenue, Suite #C, Rahway, NJ 07065, USA. Periodical postage paid at Rahway, NJ.

Postmaster: Send all address changes to THE PLANT JOURNAL, John Wiley & Sons Inc., C/OThe Sheridan Press, PO Box 465, Hanover, PA 17331.

# Copyright and Copying

Copyright © 2019 John Wiley & Sons Ltd and the Society for Experimental Biology. All rights reserved. No part of this publication may be reproduced, stored or transmitted in any form or by any means without the prior permission in writing from the copyright holder. Authorization to copy items for internal and personal use is granted by the copyright holder for libraries and other users registered with their local Reproduction Rights Organisation (RRO), e.g. Copyright Clearance Center (CCC), 222 Rosewood Drive, Danvers, MA 01923, USA (www.copyright.com), provided the appropriate fee is paid directly to the RRO. This consent does not extend to other kinds of copying, such as copying for general distribution,

for advertising and promotional purposes, for creating new collective works or for resale. Special requests should be addressed to: permissions@wiley.com.

# **Online Open**

OnlineOpen is available to authors of primary research articles who wish to make their article available to nonsubscribers on publication, or whose funding agency requires grantees to archive the final version of their article. With OnlineOpen, the author, the author's funding agency, or the author's institution pays a fee to ensure that the article is made available to non-subscribers upon publication via Wiley Online Library, as well as deposited in the funding agency's preferred archive. For the full list of terms and conditions, see http://wileyonlinelibrary.com/onlineOpen\_Terms.

Any authors wishing to send their paper OnlineOpen will be required to complete the payment form available from our website at: https://authorservices.wiley.com/bauthor/onlineopen\_order.asp.

Prior to acceptance there is no requirement to inform an Editorial Office that you intend to publish your paper OnlineOpen if you do not wish to. All OnlineOpen articles are treated in the same way as any other article. They go through the journal's standard peer-review process and will be accepted or rejected based on their own merit.

The Journal is indexed by Current Contents/Life Sciences, Science Citation Index, Index Medicus, MEDLINE and BIOBASE/Current Awareness in Biological Sciences.

Access to this journal is available free online within institutions in the developing world through the AGORA initiative with the FAO, the HINARI initiative with the WHO and the OARE initiative with UNEP. For information, visit www.aginternet.org, www.healthinternetwork.org, www.oarescience.org.

Published by John Wiley & Sons Ltd, in association with the Society for Experimental Biology. Information on this journal can be accessed at http://www.theplantjournal.com. This journal is available online at Wiley Online Library. Visit wileyonlinelibrary.com to search the articles and register for Table of Contents email alerts.

Wiley's Corporate Citizenship initiative seeks to address the environmental, social, economic, and ethical challenges faced in our business and which are important to our diverse stakeholder groups. We have made a long-term commitment to standardize and improve our efforts around the world to reduce our carbon footprint. Follow our progress at www.wiley.com/go/citizenship.

# Disclaimer

The Publisher, the Society for Experimental Biology and Editors cannot be held responsible for errors or any consequences arising from the use of information contained in this journal; the views and opinions expressed do not necessarily reflect those of the Publisher, the Society for Experimental Biology and editors, neither does the publication of advertisements constitute any endorsement by the Publisher, the Society for Experimental Biology and the Editors of the products advertised.

# **Editorial correspondence**

Correspondence relating to editorial matters should be directed to *The Plant Journal* Editorial Office, John Wiley & Sons Ltd, 9600 Garsington Road, Oxford, OX4 2DQ, UK (E-mail: tpj-general@wiley.com).

CONTENTS OF VOL. 98, NO. 5, JUNE 2019

# RESEARCH HIGHLIGHT

765 Progress for the pea of prosperity. L. Maron (Research Highlights Editor)

### RESOURCE

767 **The genome of cowpea (Vigna unguiculata [L.] Walp.).** S. Lonardi, M. Muñoz-Amatriaín, Q. Liang, S. Shu, S. I. Wanamaker, S. Lo, J. Tanskanen, A. H. Schulman, T. Zhu, M.-C. Luo, H. Alhakami, R. Ounit, A. M. Hasan, J. Verdier, P. A. Roberts, J. R. P. Santos, A. Ndeve, J. Doležel, J. Vrána, S. A. Hokin, A. D. Farmer, S. B. Cannon and T. J. Close

# **ORIGINAL ARTICLES**

- 783 The hypersensitive induced reaction 3 (HIR3) gene contributes to plant basal resistance via an EDS1 and salicylic aciddependent pathway. S. Li, J. Zhao, Y. Zhai, Q. Yuan, H. Zhang, X. Wu, Y. Lu, J. Peng, Z. Sun, L. Lin, H. Zheng, J. Chen and F. Yan
- 798 Hetero-oligomeric CPN60 resembles highly symmetric group-I chaperonin structure revealed by Cryo-EM. Q. Zhao, X. Zhang, F. Sommer, N. Ta, N. Wang, M. Schroda, Y. Cong and C. Liu
- 813 ABA inhibits myristoylation and induces shuttling of the RGLG1 E3 ligase to promote nuclear degradation of PP2CA.

  B. Belda-Palazon, J. Julian, A. Coego, Q. Wu, X. Zhang, O. Batistic, S. A. Alquraishi, J. Kudla, C. An and P. L. Rodriguez
- 826 In situ transcriptomic and metabolomic study of the loss of photosynthesis in the leaves of mixotrophic plants exploiting fungi. F. Lallemand, M.-L. Martin-Magniette, F. Gilard, B. Gakière, A. Launay-Avon, É. Delannoy and M.-A. Selosse
- 842 The Mediator kinase module serves as a positive regulator of salicylic acid accumulation and systemic acquired resistance.

  J. Huang, Y. Sun, A. R. Orduna, R. Jetter and X. Li
- 853 Leveraging GWAS data to identify metabolic pathways and networks involved in maize lipid biosynthesis. H. Li, A. Thrash, J. D. Tang, L. He, J. Yan and M. L. Warburton
- 864 Transcriptional signatures modulating shoot apical meristem morphometric and plant architectural traits enhance yield and productivity in chickpea. L. Narnoliya, U. Basu, D. Bajaj, N. Malik, V. Thakro, A. Daware, A. Sharma, S. Tripathi, V. S. Hegde, H. D. Upadhyaya, A. K. Singh, A. K. Tyagi and S. K. Parida
- 884 A Nck-associated protein 1-like protein affects drought sensitivity by its involvement in leaf epidermal development and stomatal closure in rice. L. Huang, L. Chen, L. Wang, Y. Yang, Y. Rao, D. Ren, L. Dai, Y. Gao, W. Zou, X. Lu, G. Zhang, L. Zhu, J. Hu, G. Chen, L. Shen, G. Dong, Z. Gao, L. Guo, Q. Qian and D. Zeng
- 898 Light-induced stabilization of ACS contributes to hypocotyl elongation during the dark-to-light transition in Arabidopsis seedlings. D. H. Seo and G. M. Yoon

# RESOURCE

912 Evolutionary dynamics of lincRNA transcription in nine citrus species. L. Ke, Z. Zhou, X.-W. Xu, X. Wang, Y. Liu, Y. Xu, Y. Huang, S. Wang, X. Deng, L.-L. Chen and Q. Xu

# TECHNICAL ADVANCE

- 928 Optimized small-molecule pull-downs define MLBP1 as an acyl-lipid-binding protein. Y. Sterlin, O. Pri-Tal, G. Zimran, S.-Y. Park, J. Ben-Ari, J. Kourelis, I. Verstraeten, M. Gal, S. R. Cutler and A. Mosquna
- 942 Direct analysis of pollen fitness by flow cytometry: implications for pollen response to stress. G. Luria, N. Rutley, I. Lazar, J. F. Harper and G. Miller
- 953 Correction



**Front cover**: The cover image shows Cowpea plants with maturing pods in an experimental field at UC Riverside's Coachella Valley Agricultural Research Station in Thermal, California, 17 November 2016. Photo:TJ Close. For details, see article by Lonardi, S. *et al.* (pp.767–782).