

On the Cover: The cover image shows *Alopecurus myosuroides* (black-grass) that has been transiently transformed with GREEN FLUORESCENT PROTEIN (GFP) using virus-mediated overexpression (VOX) driven by *Foxtail mosaic virus* (FoMV). These FoMV:GFP treated black-grass were photographed with a long pass filter and illuminated with blue light, which shows fluorescence from GFP in green and the plants' autofluorescence in red. This is the first time gain-of-function mutations have been induced in an agriculturally important weed species. Alongside VOX, we have also used virus-induced gene silencing (VIGS) to induce transient loss-of-function mutations in black-grass. VIGS and VOX are capable of generating mutations that change the herbicide resistance profiles of the transformed black-grass. The application of these virus-mediated gene modification techniques to black-grass establishes the ability to do reverse genetics in a species that poses a real threat to food security. Cover image credits: Macarena Mellado-Sánchez and Dana MacGregor, Rothamsted Research, Harpenden, UK.

ON THE INSIDE

Peter V. Minorsky

1

EDITORIAL

Plant Physiology Is Recruiting Assistant Features Editors for 2021. Mike Blatt and Mary Williams

3

NEWS AND VIEWS

True Blue: How Cry1 Inhibits Phototropism in Green Seedlings. Kasper van Gelderen

4

The Photobiology Paradox Resolved: Photoreceptors Drive Photosynthesis and Vice Versa. Charlotte Gommers

6

Terpenes in Cannabis: Solving the Puzzle of How to Predict Taste and Smell. Marc-Sven Roell

8

Keeping a Lid on Shoot Regeneration: SIZ1 Suppresses Wound-Induced Developmental Reprogramming.

Michael J. Skelly

10

Maize RNA Polymerase III Subunit NRPC2: New Kid on the Kernel Development Block. Dhineshkumar Thiruppathi

12

Post-Transcriptional Regulation of Nutrient Transporters. Stefanie Wege

14

Cryptochromes Go Toe to Toe with TOEs Too. Scott Hayes

16

LETTERS

^[OPEN]Common Components of the Strigolactone and Karrikin Signaling Pathways Suppress Root Branching in Arabidopsis. Stéphanie M. Swarbreck, Amirah Mohammad-Sidik, and Julia M. Davies

Adventitious and lateral root development is regulated by elements involved in both the strigolactone and karrikin perception pathways.

18

^[OPEN]The BAHD Acyltransferase BIA1 Uses Acetyl-CoA for Catabolic Inactivation of Brassinosteroids. Sufu Gan, Wilfried Rozhon, Elisabeth Varga, Simon Josef Unterholzner, Franz Berthiller, and Brigitte Poppenberger

Previous research complemented with results on BIA1 enzymatic activities shows that the enzyme regulates brassinosteroid homeostasis via mono- and diacetylation of castasterone.

23

UPDATES

^[OPEN]Plant Cyclic Nucleotide-Gated Channels: New Insights on Their Functions and Regulation. Petra Dietrich, Wolfgang Moeder, and Keiko Yoshioka

Recent advances of plant cyclic nucleotide-gated channels give new insight into their molecular functions focusing on regulation, subunit assembly, and phosphorylation.

27

Continued on next page

TOPICAL REVIEW

[OPEN] Plant Secondary Metabolites as Defenses, Regulators, and Primary Metabolites: The Blurred Functional Trichotomy. *Matthias Erb and Daniel J. Kliebenstein*

Plant chemicals known to mediate plant environment interactions also function as hormone-like regulators and precursors of primary metabolites.

39

BREAKTHROUGH TECHNOLOGIES, TOOLS, AND RESOURCES

[OPEN] Computational Tools for Serial Block Electron Microscopy Reveal Plasmodesmata Distributions and Wall Environments. *Andrea Paterlini, Ilya Belevich, Eija Jokitalo, and Yrjö Helariutta*

Computational tools for serial block electron microscopy data sets can extract information on the cell wall environment and spatial distribution of plasmodesmata over an entire cellular interface.

53

[OPEN] *pssRNAit*: A Web Server for Designing Effective and Specific Plant siRNAs with Genome-Wide Off-Target Assessment. *Firoz Ahmed, Muthappa Senthil-Kumar, Xinbin Dai, Vemanna S. Ramu, Seonghee Lee, Kirankumar S. Mysore, and Patrick Xuechun Zhao*

The pssRNAit web server designs functional small interfering RNAs for precise gene silencing in plants and provides a path to effectively study gene functions and phenotypes in plants.

65

RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

Plastidic $\Delta 6$ Fatty-Acid Desaturases with Distinctive Substrate Specificity Regulate the Pool of C18-PUFAs in the Ancestral Picoalga *Ostreococcus tauri*. *Charlotte Degraeve-Guilbault, Rodrigo E. Gomez, Cécile Lemoigne, Nattiwong Pankansem, Soizic Morin, Karine Tiphile, Jérôme Joubès, Juliette Jouhet, Julien Gronnier, Iwane Suzuki, Denis Coulon, Frédéric Domergue, and Florence Corellou*

Ostreococcus tauri plastidic lipid C18-PUFA remodeling involves two plastid-located cytochrome-b5 fused $\Delta 6$ -desaturases with distinct preferences for both head-group and acyl-chain.

82

[OPEN] Complete Biosynthesis of the Anti-Diabetic Plant Metabolite Montbretin A. *Sandra Irmisch, Sharon Jancsik, Macaire Man Saint Yuen, Lufiani L. Madilao, and Joerg Bohlmann*

Discovery of the final two genes and enzymes for the biosynthesis of an antidiabetic compound from montbretia enables its metabolic engineering in heterologous hosts.

97

[OPEN] Autocatalytic Processing and Substrate Specificity of Arabidopsis Chloroplast Glutamyl Peptidase. *Nazmul H. Bhuiyan, Elden Rowland, Giulia Friso, Lalit Ponnala, Elena J. S. Michel, and Klaas J. van Wijk*

Chloroplast glutamate peptidase has physiological exo- and endo-glutamyl peptidase activity, and autocatalytic removal of its C-terminal prosequence increases substrate size limitation.

110

[OPEN] Terpene Synthases and Terpene Variation in *Cannabis sativa*. *Judith K. Booth, Macaire M.S. Yuen, Sharon Jancsik, Lufiani L. Madilao, Jonathan E. Page, and Jörg Bohlmann*

The terpene synthase gene family contributes to variations in cannabis metabolite profiles.

130

[OPEN] Mitochondrial CLPP2 Assists Coordination and Homeostasis of Respiratory Complexes. *Jakob Petereit, Owen Duncan, Monika W. Murcha, Ricarda Fenske, Emilia Cincu, Jonathan Cahn, Adriana Pružinská, Aneta Ivanova, Laxmikanth Kollipara, Stefanie Wortelkamp, Albert Sickmann, Jiwon Lee, Ryan Lister, A. Harvey Millar, and Shaobai Huang*

Caseinolytic protease contributes to the mitochondrial protein degradation network through supporting coordination and homeostasis of protein complexes encoded across mitochondrial and nuclear genomes.

148

CELL BIOLOGY

[OPEN] The CDK Inhibitor SIAMESE Targets Both CDKA;1 and CDKB1 Complexes to Establish Endoreplication in Trichomes. Kai Wang, Ruth W. Ndathe, Narender Kumar, Elizabeth A. Zeringue, Naohiro Kato, and John C. Larkin

The cyclin-dependent kinase inhibitor SIAMESE (SIM) targets both CDKA;1 and CDKB1 complexes, leading to establishment of endoreplication, and SIM interacts with the cyclin CYCA2;3 via SIM motif A.

165

GLABRA2 Regulates Actin Bundling Protein VILLIN1 in Root Hair Growth in Response to Osmotic Stress. Xianling Wang, Shuangtian Bi, Lu Wang, Hongpeng Li, Bi-ao Gao, Shanjin Huang, Xiaolu Qu, Jianing Cheng, Shucai Wang, Caiyuan Liu, Yikuo Jiang, Bing Zhang, Xiaoyu Liu, Shaobin Zhang, Ying Fu, Zhihong Zhang, and Che Wang

VLN1, required for bundling actin filaments in root hair growth and transcriptionally regulated by GL2, negatively regulates osmotic stress-induced root hair growth.

176

ECOPHYSIOLOGY AND SUSTAINABILITY

The Apple *microR171i*-SCARECROW-LIKE PROTEINS26.1 Module Enhances Drought Stress Tolerance by Integrating Ascorbic Acid Metabolism. Yantao Wang, Chen Feng, Zefeng Zhai, Xiang Peng, Yanyan Wang, Yueting Sun, Jian Li, Xiaoshuai Shen, Yuqin Xiao, Shengjiao Zhu, Xuewang Huang, and Tianhong Li

Deep sequencing identified small non-coding RNAs involved in drought stress tolerance and a microRNA-target module that enhances drought stress tolerance in Malus sieversii.

194

[OPEN] Xylem Embolism Spreads by Single-Conduit Events in Three Dry Forest Angiosperm Stems. Kate M. Johnson, Craig Brodersen, Madeline R. Carins-Murphy, Brendan Choat, and Timothy J. Brodribb

Drought-induced failure of the plant water transport system occurs largely by air bubble formation in single, discrete conduits in the stems of three angiosperm tree species.

212

GENES, DEVELOPMENT AND EVOLUTION

[OPEN] ATP-Binding Cassette G Transporters SGE1 and MtABCG13 Control Stigma Exsertion. Butuo Zhu, Hui Li, Xiuzhi Xia, Yingying Meng, Na Wang, LuLu Li, Jianxin Shi, Yanxi Pei, Min Lin, Lifang Niu, and Hao Lin

Two ABCG transporters in Medicago truncatula collaboratively regulate flower cuticle secretion and control stigma exsertion by affecting physical contact between floral organs.

223

Spatial Divergence of *PHR*-*PHT1* Modules Maintains Phosphorus Homeostasis in Soybean Nodules. Mingyang Lu, Zhiyuan Cheng, Xiao-Mei Zhang, Penghui Huang, Chengming Fan, Guolong Yu, Fulu Chen, Kun Xu, Qingshan Chen, Yuchen Miao, Yuzhen Han, Xianzhong Feng, Liangyu Liu, and Yong-Fu Fu

Tissue-specific differentiation of phosphorus transporters coordinated with their regulators confers phosphorus homeostasis, regulating nodule development.

236

MORE FLORET1 Encodes a MYB Transcription Factor That Regulates Spikelet Development in Rice. Deyong Ren, Yuchun Rao, Haiping Yu, Qiankun Xu, Yuanjiang Cui, Saisai Xia, Xiaoqi Yu, He Liu, Haitao Hu, Dawei Xue, Dali Zeng, Jiang Hu, Guangheng Zhang, Zhenyu Gao, Li Zhu, Qiang Zhang, Lan Shen, Longbiao Guo, and Qian Qian

A MYB domain protein with typical ethylene response factor-associated amphiphilic repression (EAR) motifs plays an important role in the regulation of organ identity and spikelet determinacy in rice.

251

Drought-Responsive *ZmFDL1*/*MYB94* Regulates Cuticle Biosynthesis and Cuticle-Dependent Leaf Permeability. Giulia Castorina, Frédéric Domergue, Matteo Chiara, Massimo Zilio, Martina Persico, Valentina Ricciardi, David Stephen Horner, and Gabriella Consonni

The MYB transcription factor FUSED LEAVES1 regulates and abscisic acid influences cuticle biosynthesis and cuticle-mediated drought response during the juvenile phase of maize plant growth.

266

[OPEN] The OsABC17 Transporter Interacts with OsHCF222 to Stabilize the Thylakoid Membrane in Rice. Yan He, Yongfeng Shi, Xiaobo Zhang, Xia Xu, Huimei Wang, Liangjian Li, Zhihong Zhang, Huihui Shang, Zhonghao Wang, and Jian-Li Wu

The OsABC17 transporter interacts with OsHCF222 at thylakoid membranes to regulate reactive oxygen species homeostasis, thereby maintaining thylakoid membrane stability.

283

Continued on next page

- [OPEN]Variation in Maize Chlorophyll Biosynthesis Alters Plant Architecture. *Rajdeep S. Khangura, Gurmukh S. Johal, and Brian P. Dilkes*
Chlorophyll reduction in maize suppresses branching in classical tillering mutants and high-tillering natural variants, reduces stem girth, and shortens plants, but the effect on height is nonlinear. 300
- The Intrinsically Disordered Protein CARP9 Bridges HYL1 to AGO1 in the Nucleus to Promote MicroRNA Activity. *Ariel H. Tomassi, Delfina A. Re, Facundo Romani, Damian A. Cambiagno, Lucía Gonzalo, Javier E. Moreno, Agustin L. Arce, and Pablo A. Manavella*
An intrinsically disordered protein interacts with HYPONASTIC LEAVES1 and ARGONAUTE1 in a post-miRNA processing complex to promote ARGONAUTE1 stability and miRNA activity. 316
- [OPEN]The SUMO E3 Ligase SIZ1 Negatively Regulates Shoot Regeneration. *Duncan Coleman, Ayako Kawamura, Momoko Ikeuchi, David S. Favero, Alice Lambalez, Bart Rymen, Akira Iwase, Takamasa Suzuki, and Keiko Sugimoto*
SAP AND MIZ1 DOMAIN-CONTAINING LIGASE1 (SIZ1) negatively regulates in vitro shoot regeneration by suppressing transcriptional activation of reprogramming regulators. 330
- NGATHA-LIKEs Control Leaf Margin Development by Repressing CUP-SHAPED COTYLEDON2 Transcription. *Jingxia Shao, Jingjing Meng, Feng Wang, Bidong Shou, Yu Chen, Hui Xue, Jun Zhao, Yafei Qi, Lijun An, Fei Yu, and Xiayan Liu*
Arabidopsis NGATHA-LIKE transcription factors repress the transcription of CUP-SHAPED COTYLEDON2 gene and inhibit the formation of serrations along the leaf margin. 345
- [OPEN]Loss of Function of an RNA Polymerase III Subunit Leads to Impaired Maize Kernel Development. *Hailiang Zhao, Yao Qin, Ziyi Xiao, Qi Li, Ning Yang, Zhenyuan Pan, Dianming Gong, Qin Sun, Fang Yang, Zuxin Zhang, Yongrui Wu, Cao Xu, and Fazhan Qiu*
ZmNRPC2 affects RNAPIII activity and regulates the expression of genes involved in cell proliferation and endoreduplication to control maize kernel development. 359
- ZmCCD10a Encodes a Distinct Type of Carotenoid Cleavage Dioxygenase and Enhances Plant Tolerance to Low Phosphate. *Yanting Zhong, Xiaoying Pan, Ruifeng Wang, Jiuliang Xu, Jingyu Guo, Tingxue Yang, Jianyu Zhao, Faisal Nadeem, Xiaoting Liu, Hongyan Shan, Yanjun Xu, and Xuexian Li*
A unified 4-clade phylogenetic tree of CCDs highlights ZmCCD10a, a previously unknown CCD enzyme in terms of cleavage sites, that facilitates plant tolerance to phosphate limitation. 374
- [OPEN]Rice GROWTH-REGULATING FACTOR7 Modulates Plant Architecture through Regulating GA and Indole-3-Acetic Acid Metabolism. *Yunping Chen, Zhiwu Dan, Feng Gao, Pian Chen, Fengfeng Fan, and Shaoqing Li*
A transcriptional regulator maintains compact plant architecture and decreased leaf angle by regulating GA synthesis and auxin signaling pathways. 393
- MEMBRANES, TRANSPORT AND BIOENERGETICS**
- Sphingolipids Modulate Secretion of Glycosylphosphatidylinositol-Anchored Plasmodesmata Proteins and Callose Deposition. *Arya Bagus Boedi Iswanto, Jong Cheol Shon, Kwang Hyeon Liu, Minh Huy Vu, Ritesh Kumar, and Jae-Yean Kim*
Arabidopsis glucosyl sphingolipid-modulated plasmodesmal gating involves modulation of the glycosylphosphatidylinositol-anchored PdBG2 protein secretion machinery and a change in callose accumulation. 407
- [OPEN]Does the Arabidopsis proton gradient regulation5 Mutant Leak Protons from the Thylakoid Membrane? *Hiroshi Yamamoto and Toshiharu Shikanai*
*High g_{H^+} of the pgr5 mutant is restored to the wild-type level by introduction of flavodiiron protein and strong downregulation of the cytochrome *b_f* complex, counteracting proton leakage from the thylakoid membrane.* 421
- An SMU Splicing Factor Complex Within Nuclear Speckles Contributes to Magnesium Homeostasis in Arabidopsis. *Zhihang Feng, Hiroshi Nagao, Baohai Li, Naoyuki Sotta, Yusuke Shikanai, Katsushi Yamaguchi, Shuji Shigenobu, Takehiro Kamiya, and Toru Fujiwara*
Two splicing factors localized to nucleoplasm as well as nuclear speckles regulate the pre-mRNA splicing of a Mg^{2+} transporter gene, and contribute to Mg homeostasis in Arabidopsis. 428

SIGNALLING AND RESPONSE

- [OPEN] **The GIGANTEA-ENHANCED EM LEVEL Complex Enhances Drought Tolerance via Regulation of Abscisic Acid Synthesis.** Dongwon Baek, Woe-Yeon Kim, Joon-Yung Cha, Hee Jin Park, Gilok Shin, Junghoon Park, Chae Jin Lim, Hyun Jin Chun, Ning Li, Doh Hoon Kim, Sang Yeol Lee, Jose M. Pardo, Min Chul Kim, and Dae-Jin Yun
The GIGANTEA-ENHANCED EM LEVEL complex enhances plant tolerance to drought by modulating the diurnal transcription of a gene encoding a rate-limiting enzyme in abscisic acid biosynthesis. 443
- [OPEN] **Seedling Chloroplast Responses Induced by N-Linolenylethanolamine Require Intact G-Protein Complexes.** Chengshi Yan, Ashley E. Cannon, Justin Watkins, Jantana Keereetaweep, Bibi Rafeiza Khan, Alan M. Jones, Elison B. Blancaflor, Rajeev K. Azad, and Kent D. Chapman
Lack of intact G-protein complexes strongly attenuates N-linolenylethanolamine-induced degreening of cotyledons through transcriptional regulation of chlorophyll processes. 459
- [OPEN] **The Class III Gibberellin 2-Oxidases AtGA2ox9 and AtGA2ox10 Contribute to Cold Stress Tolerance and Fertility.** Theo Lange, Carolin Krämer, and Maria João Pimenta Lange
Two multifunctional class III gibberellin 2-oxidases contribute to freezing tolerance and to the regulation of seed production. 478
- Photoexcited Cryptochrome2 Interacts Directly with TOE1 and TOE2 in Flowering Regulation.** Sha-Sha Du, Ling Li, Li Li, Xuxu Wei, Feng Xu, Pengbo Xu, Wenxiu Wang, Peng Xu, Xiaoli Cao, Langxi Miao, Tongtong Guo, Sheng Wang, Zhilei Mao, and Hong-Quan Yang
Cryptochrome2 interacts with transcription factors TOE1 and TOE2 in a blue-light-dependent manner, thereby regulating CO and FT activity and photoperiodic flowering. 487
- [OPEN] **PHYTOCHROME-INTERACTING FACTOR-LIKE14 and SLENDER RICE1 Interaction Controls Seedling Growth under Salt Stress.** Weiping Mo, Weijiang Tang, Yanxin Du, Yanjun Jing, Qingyun Bu, and Rongcheng Lin
A transcriptional module integrates the light and gibberellic acid signaling pathways to precisely control rice seedling growth under salt stress. 506
- The Tomato DELLA Protein PROCERA Promotes Abscisic Acid Responses in Guard Cells by Upregulating an Abscisic Acid Transporter.** Hagai Shohat, Natanella Illouz-Eliaz, Yuri Kanno, Mitsunori Seo, and David Weiss
The tomato DELLA protein PROCERA promotes abscisic acid-induced stomatal closure and gene expression by upregulating expression of the ABA transporter ABA-IMPORTING TRANSPORTER1 in guard cells. 518
- AGAMOUS-LIKE67 Cooperates with the Histone Mark Reader EBS to Modulate Seed Germination under High Temperature.** Ping Li, Qili Zhang, Danni He, Yun Zhou, Huanhuan Ni, Dagang Tian, Guanxiao Chang, Yanjun Jing, Rongcheng Lin, Jinling Huang, and Xiangyang Hu
A MADS-box protein recruits a histone mark reader to modulate thermoinhibition of seed germination by epigenetically regulating abscisic acid and gibberellic acid metabolism. 529
- [OPEN] Articles can be viewed online without a subscription.