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Coleus forskohlii Root Cork Cells: Location of
Forskolin Biosynthesis

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On the Cover: The labdane diterpene forskolin has long been recognized for its pharmaceutical properties. Most important, forskolin increases intracellular cAMP levels which then assist in the relaxation of human blood and respiratory vessels. In nature, forskolin is produced in the roots of the plant *Coleus forskohlii*, but until now the precise site of forskolin biosynthesis and accumulation has remained unknown. In this issue, Pateraki et al. (pp. 1222–1236) show that forskolin accumulates in specialized cells harboring intracellular oil body structures within the root cork. Chemical analysis of these root oil bodies revealed that they have the capacity to store an array of terpenoids, including forskolin and its biosynthetic precursor, manoyl oxide. Pateraki et al. identified and characterized two diterpene synthases: enzymes responsible for the synthesis of manoyl oxide, and the first steps of forskolin biosynthesis. Expression of these enzymes was highest in the root cork. These findings provide an important insight into the nature of forskolin biosynthesis and will assist in future discoveries of the remaining biosynthetic components, thus potentially leading to sustainable forskolin production through biotechnological applications. The cover shows a cross section of *Coleus forskohlii* root with thick fissured cork. Cover image credits: Irini Pateraki and Helle Juel Martens.

ON THE INSIDE

Peter V. Minorsky

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BREAKTHROUGH TECHNOLOGIES

^[W]A Data Integration and Visualization Resource for the Metabolic Network of *Synechocystis* sp. PCC 6803. *Timo R. Maarleveld, Joost Boele, Frank J. Bruggeman, and Bas Teusink*

Development of an interactive graphical map of metabolism is illustrated with the model cyanobacterium Synechocystis sp. PCC 6803.

1111

^{[W][OPEN]}A Generic Tool for Transcription Factor Target Gene Discovery in Arabidopsis Cell Suspension Cultures Based on Tandem Chromatin Affinity Purification. *Aurine Verkest, Thomas Abeel, Ken S. Heyndrickx, Jelle Van Leene, Christa Lanz, Eveline Van De Slijke, Nancy De Winne, Dominique Eeckhout, Geert Persiau, Frank Van Breusegem, Dirk Inzé, Klaas Vandepoele, and Geert De Jaeger*

Tandem chromatin affinity purification in Arabidopsis cell suspension cultures omits the need for specific antibodies and improves DNA enrichment efficiency of transcription factor location experiments.

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SCIENTIFIC CORRESPONDENCE

^[C]Rapid Decline in Nuclear COSTITUTIVE PHOTOMORPHOGENESIS1 Abundance Anticipates the Stabilization of Its Target ELONGATED HYPOCOTYL5 in the Light. *Manuel Pacín, Martina Legris, and Jorge José Casal*

The classic view is challenged that the migration of the repressor of photomorphogenesis COP1 from the nucleus to the cytoplasm is too slow to participate in light-mediated developmental events.

1134

RESEARCH ARTICLES

BIOCHEMISTRY AND METABOLISM

^{[C][W][OPEN]}Lignin Modification Leads to Increased Nodule Numbers in Alfalfa. *Lina Gallego-Giraldo, Kishor Bhattarai, Catalina I. Pislariu, Jin Nakashima, Yusuke Jikumaru, Yuji Kamiya, Michael K. Udvardi, Maria J. Monteros, and Richard A. Dixon*

Reducing lignin content in stems and roots of alfalfa results in an increased nodule number phenotype.

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- [W][OPEN]Functional Convergence of Oxylinin and Abscisic Acid Pathways Controls Stomatal Closure in Response to Drought. *Tatyana Savchenko, Venkat A. Kolla, Chang-Quan Wang, Zainab Nasafi, Derrick R. Hicks, Bpantamars Phadungchob, Wassim E. Chehab, Federica Brandizzi, John Froehlich, and Katayoon Dehesh*
- Oxylinin affects stomatal closure, functioning most effectively with ABA in response to drought.* 1151
- [C][W][OPEN]The Flavonoid Biosynthetic Enzyme Chalcone Isomerase Modulates Terpenoid Production in Glandular Trichomes of Tomato. *Jin-Ho Kang, John McRoberts, Feng Shi, Javier E. Moreno, A. Daniel Jones, and Gregg A. Howe*
- An isoform of chalcone isomerase that catalyzes flavonoid synthesis modulates terpenoid production in glandular trichomes of tomato.* 1161
- [W][OPEN]Plastidial NAD-Dependent Malate Dehydrogenase Is Critical for Embryo Development and Heterotrophic Metabolism in Arabidopsis. *Seraina Beeler, Hung-Chi Liu, Martha Stadler, Tina Schreier, Simona Eicke, Wei-Ling Lue, Elisabeth Truernit, Samuel C. Zeeman, Jychian Chen, and Oliver Kötting*
- Reduction-oxidation homeostasis of plastids is crucial for embryo development and heterotrophic metabolism in Arabidopsis.* 1175
- [W][OPEN]Novel Roles for the Polyphenol Oxidase Enzyme in Secondary Metabolism and the Regulation of Cell Death in Walnut. *Soha Araj, Theresa A. Grammer, Ross Gertzen, Stephen D. Anderson, Maja Mikulic-Petkovsek, Robert Veberic, My L. Phu, Anita Solar, Charles A. Leslie, Abhaya M. Dandekar, and Matthew A. Escobar*
- The polyphenol oxidase enzyme functions in the metabolism of the amino acid tyrosine in walnut.* 1191
- [W][OPEN]Remarkable Reproducibility of Enzyme Activity Profiles in Tomato Fruits Grown under Contrasting Environments Provides a Roadmap for Studies of Fruit Metabolism. *Benoît Biais, Camille Bénard, Bertrand Beauvoit, Sophie Colombié, Duyên Prodhomme, Guillaume Ménard, Stéphane Bernillon, Bernadette Gehl, Hélène Gautier, Patricia Ballias, Jean-Pierre Mazat, Lee Sweetlove, Michel Génard, and Yves Gibon*
- Enzyme activities in central metabolism of tomato fruits are strongly influenced by developmental stage but only weakly by environment.* 1204
- [W][OPEN]Manoyl Oxide (13R), the Biosynthetic Precursor of Forskolol, Is Synthesized in Specialized Root Cork Cells in *Coleus forskohlii*. *Irini Pateraki, Johan Andersen-Ranberg, Britta Hamberger, Allison Maree Heskes, Helle Juel Martens, Philipp Zerbe, Søren Spanner Bach, Birger Lindberg Møller, Jörg Bohlmann, and Björn Hamberger*
- The first two steps of the biosynthesis of forskolin are active in Coleus forskohlii root cork cells harboring hydrophobic intracellular compartments used for terpenoid storage.* 1222
- CELL BIOLOGY**
- [W][OPEN]The Evolutionary Conserved Oil Body Associated Protein OBAP1 Participates in the Regulation of Oil Body Size. *Ignacio López-Ribera, José Luis La Paz, Carlos Repiso, Nora García, Mercè Miquel, María Luisa Hernández, José Manuel Martínez-Rivas, and Carlos M. Vicent*
- A new family of oil body associated proteins present in plants, fungi, and bacteria are involved in determining oil body size and shape.* 1237
- [W][OPEN]Golgi- and Trans-Golgi Network-Mediated Vesicle Trafficking Is Required for Wax Secretion from Epidermal Cells. *Heather E. McFarlane, Yoichiro Watanabe, Weili Yang, Yan Huang, John Ohlrogge, and A. Lacey Samuels*
- Plant epidermal cells, which produce large amounts of protective lipids, rely on vesicle traffic to export these wax molecules to the cuticle.* 1250

[W][OPEN] Hitching a Ride on Vesicles: Cauliflower Mosaic Virus Movement Protein Trafficking in the Endomembrane System. *Anna Vittoria Carluccio, Stefania Zicca, and Livia Stavolone*

A tubule-forming viral movement protein traffics in post-Golgi compartments and requires endocytosis for tubule formation and virus movement.

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[C][W][OPEN] Multiple RNA Binding Protein Complexes Interact with the Rice Prolamine RNA Cis-Localization Zipcode Sequences. *Yongil Yang, Andrew J. Crofts, Naoko Crofts, and Thomas W. Okita*

Multiprotein complexes are assembled and remodeled for the transport and localization of prolamine RNAs to the cortical endoplasmic reticulum in developing rice endosperm.

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ECOPHYSIOLOGY AND SUSTAINABILITY

[W][OPEN] The Coordination of C₄ Photosynthesis and the CO₂-Concentrating Mechanism in Maize and *Miscanthus × giganteus* in Response to Transient Changes in Light Quality. *Wei Sun, Nerea Ubierna, Jian-Ying Ma, Berkley J. Walker, David M. Kramer, and Asaph B. Cousins*

Light quality coordinates a CO₂-concentrating mechanism during C₄ photosynthesis.

1283

[W] Sugar and Auxin Signaling Pathways Respond to High-Temperature Stress during Anther Development as Revealed by Transcript Profiling Analysis in Cotton. *Ling Min, Yaoyao Li, Qin Hu, Longfu Zhu, Wenhui Gao, Yuanlong Wu, Yuanhao Ding, Shiming Liu, Xiyang Yang, and Xianlong Zhang*

Anther indehiscence at high temperatures is coordinately regulated by sugar and auxin.

1293

[W] A Novel Protective Function for Cytokinin in the Light Stress Response Is Mediated by the ARABIDOPSIS HISTIDINE KINASE2 and ARABIDOPSIS HISTIDINE KINASE3 Receptors. *Anne Cortleven, Silvia Nitschke, Marion Klaumünzer, Hamada AbdElgawad, Han Asard, Bernhard Grimm, Michael Riefler, and Thomas Schmillig*

Cytokinin protects plants from the consequences of light stress by acting on reactive oxygen species scavenging and D1 protein levels, thereby preventing photoinhibition.

1470

GENES, DEVELOPMENT, AND EVOLUTION

[W] Genetic Dissection of Leaf Development in *Brassica rapa* Using a Genetical Genomics Approach. *Dong Xiao, Huange Wang, Ram Kumar Basnet, Jianjun Zhao, Ke Lin, Xilin Hou, and Guusje Bonnema*

Genes affecting leaf size and shape are identified by combining gene expression and phenotypic trait data.

1309

[W][OPEN] Trithorax Group Protein *Oryza sativa* Trithorax1 Controls Flowering Time in Rice via Interaction with Early heading date3. *Sang Chul Choi, Shinyoung Lee, Sung-Ryul Kim, Yang-Seok Lee, Chunyan Liu, Xiaofeng Cao, and Gynheung An*

Histone methyltransferase promotes flowering time predominantly under long-day conditions in rice.

1326

[C][W][OPEN] ECHIDNA Protein Impacts on Male Fertility in Arabidopsis by Mediating trans-Golgi Network Secretory Trafficking during Anther and Pollen Development. *Xinping Fan, Caiyun Yang, Doris Klisch, Alison Ferguson, Rishi P. Bhaellero, Xiwu Niu, and Zoe A. Wilson*

ECHIDNA-mediated trans-Golgi network trafficking is needed for full male fertility in Arabidopsis and is required for anther and pollen formation, filament elongation, and anther dehiscence in addition to pollen tube formation.

1338

[C][W][I][O][P][E][N] Differential Methylation during Maize Leaf Growth Targets Developmentally Regulated Genes. Jasper Candaele, Kirin Demuyne, Douglas Mosoti, Gerrit T.S. Beemster, Dirk Inzé, and Hilde Nelissen

The successive growth processes of cell division and cell elongation in maize leaves are characterized by differential DNA methylation that is correlated with differential expression.

1350

[C][W][I][O][P][E][N] Alterations in the Transcriptome of Soybean in Response to Enhanced Somatic Embryogenesis Promoted by Orthologs of AGAMOUS-Like15 and AGAMOUS-Like18. Qiaolin Zheng and Sharyn E. Perry

Transcriptome analysis indicates that ectopic expression of MADS domain transcription factors mimics the induction of somatic embryogenesis, providing a mechanism for its enhancement in culture.

1365

[C][W][I][O][P][E][N] Using a Viral Vector to Reveal the Role of MicroRNA159 in Disease Symptom Induction by a Severe Strain of Cucumber mosaic virus. Zhiyou Du, Aizhong Chen, Wenhui Chen, Jack H. Westwood, David C. Baulcombe, and John P. Carr

A vector based on a mild strain of Cucumber mosaic virus carrying a microRNA decoy sequence uncovered the relevance of microRNA159 to disease symptoms induced by a severe Cucumber mosaic virus strain.

1378

[C][W][I][O][P][E][N] ETHYLENE RESPONSE FACTOR070 Regulates Root Development and Phosphate Starvation-Mediated Responses. Madhuvanthi Ramaiah, Ajay Jain, and Kashchandra G. Raghohama

An ethylene response transcription factor helps in the maintenance of phosphate homeostasis by altering root and shoot growth in Arabidopsis.

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MEMBRANES, TRANSPORT, AND BIOENERGETICS

[C][W][I][O][P][E][N] An Arabidopsis Stomatin-Like Protein Affects Mitochondrial Respiratory Supercomplex Organization. Bernadette Gehl, Chun Pong Lee, Pedro Bota, Michael R. Blatt, and Lee J. Sweetlove

A mitochondrial membrane protein forms a large oligomeric complex that affects the abundance of complex I and respiratory supercomplexes.

1389

[C][W][I][O][P][E][N] The Arabidopsis Class II Sirtuin Is a Lysine Deacetylase and Interacts with Mitochondrial Energy Metabolism. Ann-Christine König, Markus Hartl, Phuong Anh Pham, Miriam Laxa, Paul J. Boersema, Anne Orwat, Ievgeniia Kalitventseva, Magdalena Plöching, Hans-Peter Braun, Dario Leister, Matthias Mann, Andreas Wachter, Alisdair R. Fernie, and Iris Finkemeier

The mitochondrial deacetylase targets protein complexes involved in energy metabolism and regulates the activity of the ATP/ADP carrier.

1401

[W] Distinct Amino Acids in the C-Linker Domain of the Arabidopsis K⁺ Channel KAT2 Determine Its Subcellular Localization and Activity at the Plasma Membrane. Manuel Nieves-Cordones, Alain Chavanieu, Linda Jeanguenin, Carine Alcon, Wojciech Szponarski, Sebastien Estaran, Isabelle Chérel, Sabine Zimmermann, Hervé Sentenac, and Isabelle Gaillard

The C-linker domain of a K⁺ channel is required for the control of channel gating via its first α -helix located just below the channel pore and for the proper folding of the channel.

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SIGNALING AND RESPONSE

[C][W][OPEN] A Nuclear Factor Y Interacting Protein of the GRAS Family is Required for Nodule Organogenesis, Infection Thread Progression, and Lateral Root Growth. *Marina Battaglia, Carolina Rípodas, Joaquín Clúa, Maël Baudin, O. Mario Aguilar, Andreas Niebel, María Eugenia Zanetti, and Flavio Antonio Blanco*

Initiation and development of nodules during legume-rhizobia symbiosis and lateral root growth are modulated by two interacting transcription factors.

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[W][OPEN] Antagonistic Regulation of Growth and Immunity by the Arabidopsis Basic Helix-Loop-Helix Transcription Factor HOMOLOG OF BRASSINOSTEROID ENHANCED EXPRESSION2 INTERACTING WITH INCREASED LEAF INCLINATION1 BINDING bHLH1. *Frederikke Gro Malinovsky, Martine Batoux, Benjamin Schwessinger, Ji Hyun Youn, Lena Stransfeld, Joe Win, Seong-Ki Kim, and Cyril Zipfel*

A basic helix-loop-helix transcription factor antagonistically regulates growth and immunity.

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[W][OPEN] Transgenic Plants That Express the Phytoplasma Effector SAP11 Show Altered Phosphate Starvation and Defense Responses. *Yen-Ting Lu, Meng-Ying Li, Kai-Tan Cheng, Choon Meng Tan, Li-Wen Su, Wei-Yi Lin, Hsien-Tzung Shih, Tzyy-Jen Chiou, and Jun-Yi Yang*

Expression of a bacterial effector alters plant responses to phosphorus nutrient and a bacterial pathogen.

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[C][W][OPEN] The Wheat Ethylene Response Factor Transcription Factor PATHOGEN-INDUCED ERF1 Mediates Host Responses to Both the Necrotrophic Pathogen *Rhizoctonia cerealis* and Freezing Stresses. *Xiuliang Zhu, Lin Qi, Xin Liu, Shibin Cai, Huijun Xu, Rongfeng Huang, Jiarui Li, Xuening Wei, and Zengyan Zhang*

*An ethylene response factor transcription factor positively affects the interactions between stress responses to the pathogen *Rhizoctonia cerealis* and freezing in wheat.*

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[C][W] Cytokinin Antagonizes Abscisic Acid-Mediated Inhibition of Cotyledon Greening by Promoting the Degradation of ABSCISIC ACID INSENSITIVE5 Protein in Arabidopsis. *Chunmei Guan, Xingchun Wang, Jian Feng, Sulei Hong, Yan Liang, Bo Ren, and Jianru Zuo*

Cytokinin represses abscisic acid signaling by promoting the degradation of the ABI5 transcription factor in Arabidopsis.

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[C][W] Revisiting the Evolutionary History and Roles of Protein Phosphatases with Kelch-Like Domains in Plants. *Gustavo A. Maselli, Claudio H. Slamovits, Javier I. Bianchi, Josep Vilarrasa-Blasi, Ana I. Caño-Delgado, and Santiago Mora-García*

A group of plant-specific protein phosphatases has a rich evolutionary history and performs essential roles in development.

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[W][OPEN] Phytochrome B Promotes Branching in Arabidopsis by Suppressing Auxin Signaling. *Srirama Krishna Reddy and Scott A. Finlayson*

Phytochrome B promotes branching in Arabidopsis by suppressing auxin signaling.

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CORRECTIONS

Regulation of Plant Disease Resistance, Stress Responses, Cell Death and Ethylene Signaling in Arabidopsis by the EDR1 Protein Kinase. *Tang D., Christiansen K.M., and Innes R.W.*

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