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Molecular chaperones: providing a safe place to weather a midlife protein-folding crisis

Nature Structural & Molecular Biology 23, 621–623 (2016)

Patricia L Clark & Adrian H Elcock

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Contrary to conventional wisdom that molecular chaperones rely on hydrophobic interactions to bind a wide variety of client proteins in danger of misfolding, three recent studies reveal that the ATP-independent chaperone Spy exploits electrostatic interactions to bind its clients quickly, yet loosely enough to enable folding of the client while it is chaperone bound.

Heat Shock Factor 1: From Fire Chief to Crowd-Control Specialist

Molecular Cell, Volume 63, Issue 1, 7 July 2016, Pages 1–2

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HSF1 is the supposed master regulator of the heat shock response. In this issue of Molecular Cell, Solís et al. reveal that it has a much narrower job description: organizing a small team of molecular chaperones that keep the proteome moving.

In vivo aspects of protein folding and quality control

Science 01 Jul 2016: Vol. 353, Issue 6294, DOI: 10.1126/science.aac4354

David Balchin, Manajit Hayer-Hartl, F. Ulrich Hartl*

Department of Cellular Biochemistry, Max Planck Institute of Biochemistry, Am Klopferspitz 18,
82152 Martinsried, Germany.

Most proteins must fold into unique three-dimensional structures to perform their biological functions. In the crowded cellular environment, newly synthesized proteins are at risk of misfolding and forming toxic aggregate species. To ensure efficient folding, different classes of molecular chaperones receive the nascent protein chain emerging from the ribosome and guide it along a productive folding pathway. Because proteins are structurally dynamic, constant surveillance of the proteome by an integrated network of chaperones and protein degradation machineries is required to maintain protein homeostasis (proteostasis). The capacity of this proteostasis network declines during aging, facilitating neurodegeneration and other chronic diseases associated with protein aggregation. Understanding the proteostasis network holds the promise of identifying targets for pharmacological intervention in these pathologies.

Crosstalk between cellular compartments protects against proteotoxicity and extends lifespan.

Sci Rep. 2016 Jun 27;6:28751. doi: 10.1038/srep28751.

Perić M[1], Dib PB[2], Dennerlein S[2], Musa M[1], Rudan M[1], Lovrić A[1], Nikolić A[1], Šarić A[3], Sobočanec S[3], Mačak Ž[3], Raimundo N[2], Kriško A[1].

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[2]Universitätsmedizin Göttingen, Institut für Zellbiochemie, Humboldtallee 23, D-37073 Göttingen, Germany.
[3]Division of Molecular Medicine, Ruđer Bošković Institute, Bijenička 54, 10000 Zagreb, Croatia.

In cells living under optimal conditions, protein folding defects are usually prevented by the action of chaperones. Here, we investigate the cell-wide consequences of loss of chaperone function in cytosol, mitochondria or the endoplasmic reticulum (ER) in budding yeast. We find that the decline in chaperone activity in each compartment results in loss of respiration, demonstrating the dependence of mitochondrial activity on cell-wide proteostasis. Furthermore, each chaperone deficiency triggers a response, presumably via the communication among the folding environments of distinct cellular compartments, termed here the cross-organelle stress response (CORE). The proposed CORE pathway encompasses activation of protein conformational maintenance machineries, antioxidant enzymes, and metabolic changes simultaneously in the cytosol, mitochondria, and the ER. CORE induction extends replicative and chronological lifespan in budding yeast, highlighting its protective role against moderate proteotoxicity and its consequences such as the decline in respiration. Our findings accentuate that organelles do not function in isolation, but are integrated in a

functional crosstalk, while also highlighting the importance of organelle communication in aging and age-related diseases.

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Molecular Cell: Alert 2 July-8 July
Ubiquilins Chaperone and Triage Mitochondrial Membrane Proteins for Degradation   Original Research Article
Pages 21-33
Eisuke Itakura, Eszter Zavodszky, Sichen Shao, Matthew L. Wohlever, Robert J. Keenan, Ramanujan S. Hegde
We investigated how mitochondrial membrane proteins remain soluble in the cytosol until their delivery to mitochondria or degradation at the proteasome. We show that Ubiquilin family proteins bind transmembrane domains in the cytosol to prevent aggregation and temporarily allow opportunities for membrane targeting. Over time, Ubiquilins recruit an E3 ligase to ubiquitinate bound clients. The attached ubiquitin engages Ubiquilin's UBA domain, normally bound to an intramolecular UBL domain, and stabilizes the Ubiquilin-client complex. This conformational change precludes additional chances at membrane targeting for the client, while simultaneously freeing Ubiquilin's UBL domain for targeting to the proteasome. Loss of Ubiquilins by genetic ablation or sequestration in polyglutamine aggregates leads to accumulation of non-inserted mitochondrial membrane protein precursors. These findings define Ubiquilins as a family of chaperones for cytosolically exposed transmembrane domains and explain how they use ubiquitin to triage clients for degradation via coordinated intra- and intermolecular interactions.

Defining the Essential Function of Yeast Hsf1 Reveals a Compact Transcriptional Program for Maintaining Eukaryotic Proteostasis   Original Research Article   *Pages 60-71*
Eric J. Solís, Jai P. Pandey, Xu Zheng, Dexter X. Jin, Piyush B. Gupta, Edoardo M. Airoldi, David Pincus, Vladimir Denic

Despite its eponymous association with the heat shock response, yeast heat shock factor 1 (Hsf1) is essential even at low temperatures. Here we show that engineered nuclear export of Hsf1 results in cytotoxicity associated with massive protein aggregation. Genome-wide analysis revealed that Hsf1 nuclear export immediately decreased basal transcription and mRNA expression of 18 genes, which predominately encode chaperones. Strikingly, rescuing basal expression of Hsp70 and Hsp90 chaperones enabled robust cell growth in the complete absence of Hsf1. With the exception of chaperone gene induction, the vast majority of the heat shock response was Hsf1 independent. By comparative analysis of mammalian cell lines, we found that only heat shock-induced but not basal expression of chaperones is dependent on the mammalian Hsf1 homolog (HSF1). Our work reveals that yeast chaperone gene expression is an essential housekeeping mechanism and provides a roadmap for defining the function of HSF1 as a driver of oncogenesis.

Sequence Determinants of Intracellular Phase Separation by Complex Coacervation of a Disordered Protein   Original Research Article *Pages 72-85*

Chi W. Pak, Martyna Kosno, Alex S. Holehouse, Shae B. Padrick, Anuradha Mittal, Rustam Ali, Ali A. Yunus, David R. Liu, Rohit V. Pappu, Michael K. Rosen

Liquid-liquid phase separation, driven by collective interactions among multivalent and intrinsically disordered proteins, is thought to mediate the formation of membrane-less organelles in cells. Using parallel cellular and in vitro assays, we show that the Nephrin intracellular domain (NICD), a disordered protein, drives intracellular phase separation via complex coacervation, whereby the negatively charged NICD co-assembles with positively charged partners to form protein-rich dense liquid droplets. Mutagenesis reveals that the driving force for phase separation depends on the overall amino acid composition and not the precise sequence of NICD. Instead, phase separation is promoted by one or more regions of high negative charge density and aromatic/hydrophobic residues that are distributed across the protein. Many disordered proteins share similar sequence characteristics with NICD, suggesting that complex coacervation may be a widely used mechanism to promote intracellular phase separation.

Crosstalk between chloroplast thioredoxin systems in regulation of photosynthesis (pages 1691–1705)

Lauri Nikkanen, Jouni Toivola and Eevi Rintamäki

Version of Record online: 6 APR 2016 | DOI: 10.1111/pce.12718

Thioredoxins (TRXs) are ubiquitous protein oxidoreductases that regulate biochemical reactions in cells. Plants are distinguished from other organisms by having highly versatile thioredoxin systems. In this paper, we have investigated the redundancy and dynamics between the ferredoxin-dependent (FTR) and NADPH-dependent (NTRC) thioredoxin systems in photosynthesis *in vivo*. We show that the two chloroplast TRX systems form an interconnected functional redox network that can dynamically respond to changing light conditions and thus improve plant fitness. It is also demonstrated that an elevated chloroplast thiol redox state through NTRC overexpression improves leaf photosynthetic activity and that in addition to FTR, NTRC system participates in regulation of primary photosynthetic reactions and is particularly important in conditions where light limits photosynthesis.

Comparison of D1´- and D1-containing PS II reaction centre complexes under different environmental conditions in *Synechocystis* sp. PCC 6803 (pages 1715–1726)

Tim S. Crawford, Kyrin R. Hanning, Jocelyn P.S. Chua, Julian J. Eaton-Rye and Tina C. Summerfield

Version of Record online: 12 MAY 2016 | DOI: 10.1111/pce.12738

In oxygenic photosynthesis, the D1 protein of Photosystem II is the primary target of photodamage and environmental stress can accelerate this process. Cyanobacterial response to stress includes transcriptional regulation of genes encoding D1, including low-oxygen-induction of *psbA1* encoding the D1´ protein in *Synechocystis* sp. PCC 6803. We found that a D1´-PS II strain was outperformed by a D1-PS II strain when centres were produced under aerobic conditions; however, a strain containing low-oxygen-induced D1´-PS II centres was more resilient under high light than an equivalent D1 strain. Our results indicate that D1´-PS II centres are important in the reconfiguration of thylakoid electron transport in response to high light and low oxygen.

Altitudinal and climatic associations of seed dormancy and flowering traits evidence adaptation of annual life cycle timing in *Arabidopsis thaliana* (pages 1737–1748)
Deborah S. Vidigal, Alexandre C. S. S. Marques, Leo A. J. Willems, Gonda Buijs, Belén Méndez-Vigo, Henk W. M. Hilhorst, Leónie Bentsink, F. Xavier Picó and Carlos Alonso-Blanco
Version of Record online: 4 MAY 2016 | DOI: 10.1111/pce.12734

The diversity of annual life cycles is determined by genetic variation for the timing of germination, which is controlled by the level of seed dormancy and by the timing of flowering initiation. Despite the recent progress in understanding the genetic and molecular mechanisms underlying both life history traits in *Arabidopsis thaliana*, the environmental factors that contribute to maintain life cycle variation remain mostly unknown. In this study we find significant and strong correlations between seed dormancy, flowering time and multiple climatic factors, indicating that both traits have coevolved to adapt annual life cycles to climate.

Curr. Biol. 10.1016/j.cub.2016.04.036 (2016).

Essentially all organic material derives from photosynthesis. The most numerous photosynthetic organisms are marine picocyanobacteria, which synthesize about 10% of Earth's organic compounds. Even more numerous marine viruses prey on picocyanobacteria. Putty *et al.* show that the infecting viruses subvert the metabolism of their picocyanobacteria hosts, boosting the energy-producing reactions of photosynthesis to support viral infection. At the same time, they inhibit the ability of picocyanobacteria to fix CO_2 and synthesize organic material, therefore having a potentially substantial effect on global amounts of organic compounds.

Science 7/8/16

The Genome Project -Write

The Human Genome Project ("HGP-read"), nominally completed in 2004, aimed to sequence the human genome and to improve the technology, cost, and quality of DNA sequencing (*1*, *2*). It was biology's first genome-scale project and at the time was considered controversial by some. Now, it is recognized as one of the great feats of exploration, one that has revolutionized science and medicine.

Although sequencing, analyzing, and editing DNA continue to advance at a breakneck pace, the capability for constructing DNA sequences in cells is mostly limited to a small number of short segments, which restricts the ability to manipulate and understand biological systems. Further understanding of genetic blueprints could come from construction of large, gigabase (Gb)-sized animal and plant genomes, including the human genome, which would, in turn, drive development of tools and methods to facilitate large-scale synthesis and editing of genomes. To this end, we propose the Human Genome Project-Write (HGP-write), named to honor HGP-read but embracing synthesis of all large genomes.

because DNA synthesis, like sequencing and computation, is foundational technology, HGP-write could also facilitate biological engineering of many organisms, accelerating research and development (R&D) across a broad spectrum of life sciences and supporting basic R&D of new bio-based therapies, vaccines, materials, energy sources, disease vector control, and nutrition.

S-Acylation of the cellulose synthase complex is essential for its plasma membrane localization
By Manoj Kumar, Raymond Wightman, Ivan Atanassov, Anjali Gupta, Charlotte H. Hurst, Piers A. Hemsley, Simon Turner
*Science*08 Jul 2016 : 166-169

The large, multisubunit complex that makes cellulose fibers alters its own membrane environment to keep it in the correct location.

Cellulose synthase is a large, multisubunit machine that “swims” along the plant cell membrane as it spins out cellulose fibers. Kumar *et al.* show that the cellulose synthase complex is heavily modified through S-acylation. Subsets of the acylation sites were required for the complex to integrate into the plasma membrane. A single functional complex could bear as many as 100 modification sites, potentially changing its biophysical characteristics and helping it to associate with the membrane.

Plant cellulose microfibrils are synthesized by a process that propels the cellulose synthase complex (CSC) through the plane of the plasma membrane. How interactions between membranes and the CSC are regulated is currently unknown. Here, we demonstrate that all catalytic subunits of the CSC, known as cellulose synthase A (CESA) proteins, are S-acylated. Analysis of *Arabidopsis* CESA7 reveals four cysteines in variable region 2 (VR2) and two cysteines at the carboxy terminus (CT) as S-acylation sites. Mutating both the VR2 and CT cysteines permits CSC assembly and trafficking to the Golgi but prevents localization to the plasma membrane. Estimates suggest that a single CSC contains more than 100 S-acyl groups, which greatly increase the hydrophobic nature of the CSC and likely influence its immediate membrane environment.

Nature Structural & Molecular Biology Contents: 2016 Volume #23 pp 619-697

Molecular chaperones: providing a safe place to weather a midlife protein-folding crisis - pp621 - 623
Patricia L Clark & Adrian H Elcock
doi:10.1038/nsmb.3255

Technical Report

Visualizing chaperone-assisted protein folding - pp691 - 697
Contrary to conventional wisdom that molecular chaperones rely on hydrophobic interactions to bind a wide variety of client proteins in danger of misfolding, three recent studies reveal that the ATP-independent chaperone Spy exploits electrostatic interactions to bind its clients quickly, yet loosely enough to enable folding of the client while it is chaperone

Journal of Agronomy and Crop Scienc... Content Alert: 202, 4 (August 2016)

Acquired Thermo-Tolerance and Trans-Generational Heat Stress Response at Flowering in Rice (pages 309–319)
W. Shi, L. M. F. Lawas, B. R. Raju and S. V. K. Jagadish
Version of Record online: 15 DEC 2015 | DOI: 10.1111/jac.12157

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Mitochondrial unfolded protein response controls matrix pre-RNA processing and translation.
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Ubiquilins Chaperone and Triage Mitochondrial Membrane Proteins for Degradation.
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Zhu Y, Liao W, Niu L, Wang M, Ma Z.
Nitric oxide is involved in hydrogen gas-induced cell cycle activation during adventitious root formation in cucumber.
BMC Plant Biol. 2016 Jun 28;16(1):146. PMID: 27352869 [PubMed - in process]

PLOS Genetics Volume 12(6) June 2016
Mapping the Hsp90 Genetic Network Reveals Ergosterol Biosynthesis and Phosphatidylinositol-4-Kinase Signaling as Core Circuitry Governing Cellular Stress
Teresa R. O’Meara, Amanda O. Veri, Elizabeth J. Polvi, Xinliu Li, Seyedeh Fereshteh Valaei, Stephanie Diezmann, Leah E. Cowen

The EMBO Journal Table of Contents for 1 July 2016; Vol. 35, No. 13

Mitochondria just wanna have FUN(DC1) Alexander M van der Bliek
Published online 09.06.2016
http://EMBOJ.embopress.org/content/35/13/1365?etoc

Mitochondrial dynamics and mitophagy are altered upon hypoxia. New work shows that the mitochondrial outer protein FUNDC1 coordinates mitochondrial fission at the ER–mitochondria interface with hypoxia-induced mitophagy.

FUNDC1 regulates mitochondrial dynamics at the ER–mitochondrial contact site under hypoxic conditions
Wenxian Wu, Chunxia Lin, Keng Wu, Lei Jiang, Xiaojing Wang, Wen Li, Haixia Zhuang, Xingliang Zhang, Hao Chen, Shupeng Li, Yue Yang, Yue Lu, Jingjing Wang, Runzhi Zhu, Liangqing Zhang, Senfang Sui, Ning Tan, Bin Zhao, Jingjing Zhang, Longxuan Li, and Du Feng
Published online 04.05.2016
http://EMBOJ.embopress.org/content/35/13/1368?etoc

In response to hypoxia, mitophagy receptor FUNDC1 associates with ER-resident protein calnexin and thereby accumulates at the ER–mitochondrial contact site; this allows for DRP-1 recruitment and thus mitochondrial fission.

Plant, Cell & Environment Content Alert (New Articles)

Plasma membrane proteomics in the maize primary root growth zone: novel insights into root growth adaptation to water stress

Priyamvada Voothuluru, Jeffrey C. Anderson, Robert E. Sharp and Scott C. Peck
Accepted manuscript online: 24 JUN 2016 04:45PM EST | DOI: 10.1111/pce.12778

Nature Methods

Quantitative assessment of fluorescent proteins **pp557 - 562**
Paula J Cranfill, Brittney R Sell, Michelle A Baird, John R Allen, Zeno Lavagnino *et al.*
doi:10.1038/nmeth.3891
This Analysis provides a head-to-head comparison of >40 monomeric fluorescent proteins in terms of photophysical properties, photostability and performance in fusions to help users choose the best-performing tools.

Comparison of Cas9 activators in multiple species **pp563 - 567**
Alejandro Chavez, Marcelle Tuttle, Benjamin W Pruitt, Ben Ewen-Campen, Raj Chari *et al.*
doi:10.1038/nmeth.3871
A comparison of seven dCas9-based transcriptional activators shows that VPR, SAM, and Suntag perform best in cell lines from a variety of organisms.

Plant Cell
Moss Chloroplasts are Surrounded by a Peptidoglycan Wall Containing D-Amino Acids
Takayuki Hirano, Koji Tanidokoro, Yasuhiro Shimizu, Yutaka Kawarabayasi, Toshihisa Ohshima, Momo Sato, Shinji Tadano, Hayato Ishikawa, Susumu Takio, Katsuaki Takechi, and Hiroyoshi Takano

Plant Cell 2016 tpc.16.00104; Advance Publication June 20, 2016; doi:10.1105/tpc.16.00104
OPEN
http://www.plantcell.org/content/early/2016/06/20/tpc.16.00104.abstract

Journal of Plant Physiology: Alert 9 June-15 June
The role of nitric oxide in basal and induced resistance in relation with hydrogen peroxide and antioxidant enzymes   Original Research Article
Pages 29-38
Vahid Keshavarz-Tohid, Parissa Taheri, Seyed Mohsen Taghavi, Saeed Tarighi

Ureide metabolism under abiotic stress in Arabidopsis thaliana   Original Research Article
Pages 87-95
Solmaz Irani, Christopher D Todd

Role of calcium in the mitigation of heat stress in the cyanobacterium Anabaena PCC 7120   Original Research Article
Pages 67-75
Anupam Tiwari, Priyanka Singh, Ravi Kumar Asthana

Parental epigenetic asymmetry of PRC2-mediated histone modifications in the Arabidopsis endosperm
Jordi Moreno-Romero, Hua Jiang, Juan Santos-González, and Claudia Köhler
Published online 25.04.2016
Genomewide mapping of the epigenetic state in early plant endosperm links polycomb to the maintenance of parental imprinting and explains how DNA hypomethylation of the maternal genome is maintained after fertilization.
http://EMBOJ.embopress.org/content/35/12/1298?etoc

Review Articles The FEBS Journal Content Alert (New Articles)

FREE **Ground Control to Major TOM: Mitochondria-Nucleus Communication**
Michal Eisenberg-Bord and Maya Schuldiner
Accepted manuscript online: 10 JUN 2016 02:31AM EST | DOI: 10.1111/febs.13778

Advances in Botanical Research Volume 79 , Pages 1-248, 2016
Artificial Photosynthesis   Edited by Robert Bruno

Plant, Cell & Environment Content Alert: 39, 7 (July 2016)
Growth temperature impact on leaf form and function in *Arabidopsis thaliana* ecotypes from northern and southern Europe (pages 1549–1558)
Jared J. Stewart, Barbara Demmig-Adams, Christopher M. Cohu, Coleman A. Wenzl, Onno Muller and William W. Adams III
Version of Record online: 6 APR 2016 | DOI: 10.1111/pce.12720

At low temperature, *Arabidopsis thaliana* developed thicker leaves with higher rates of photosynthesis, likely facilitated by a greater number of phloem cells per minor vein for the active loading and export of sugars, with an ecotype from Sweden exhibiting greater adjustments in these features than an ecotype from Italy. However, with global temperatures on an upward trajectory, the response of this winter annual to elevated temperature may be more important in the future. Growth under elevated temperature resulted in leaves with a higher vein density and greater number of tracheary elements per minor vein, likely facilitating higher rates of transpirational water loss and evaporative cooling, in both ecotypes. However, only the Swedish ecotype exhibited a reduction in growth as a result of exposure to higher temperature.

Ribosomal P3 protein AtP3B of Arabidopsis acts as both protein and RNA chaperone to increase tolerance of heat and cold stresses (pages 1631–1642)
Chang Ho Kang, Young Mee Lee, Joung Hun Park, Ganesh M. Nawkar, Hun Taek Oh, Min Gab Kim, Soo In Lee, Woe Yeon Kim, Dae-Jin Yun and Sang Yeol Lee
Version of Record online: 5 MAY 2016 | DOI: 10.1111/pce.12742

In a screen for components of heat-stable high-molecular weight (HMW) complexes, the plant specific P3 protein AtP3B was isolated from heat-treated *Arabidopsis* suspension cultures. Based on our results, the expression of *AtP3B* was increased in response to both high- and low-temperature stresses, and AtP3B protein was stably retained in HMW complexes following heat shock. The recombinant AtP3B protein exhibited both protein and RNA chaperone activities; furthermore, knockdown of *AtP3B* by RNAi made plants sensitive to both high- and low-temperature stresses, whereas overexpression of *AtP3B* increased tolerance of both conditions, suggesting that AtP3B protects cells against both high- and low-temperature stresses. These findings provide novel insight into the molecular functions and *in vivo* roles of acidic ribosomal P-proteins, thereby expanding our knowledge of the protein production machinery.

Plant Cell Table of Contents for May 2016; Vol. 28, No. 5
The Role of LORELEI in Pollen Tube Reception at the Interface of the Synergid Cell and Pollen Tube Requires the Modified Eight-Cysteine Motif and the Receptor-Like Kinase FERONIA
Xunliang Liu, Claudia Castro, Yanbing Wang, Jennifer Noble, Nathaniel Ponvert, Mark Bundy, Chelsea Hoel, Elena Shpak, and Ravishankar Palanivelu
Plant Cell 2016 28: 1035-1052. First Published on April 14, 2016; doi:10.1105/tpc.15.00703
http://www.plantcell.org/content/28/5/1035.abstract
Structure-function analysis reveals domains in LORELEI critical for its role in pollen tube reception at the synergid surface, which it performs in conjunction with the receptor-like kinase FERONIA.

Dual and Opposing Roles of Xanthine Dehydrogenase in Defense-Associated Reactive Oxygen Species Metabolism in Arabidopsis
Xianfeng Ma, Wenming Wang, Florian Bittner, Nadine Schmidt, Robert Berkey, Lingli Zhang, Harlan King, Yi Zhang, Jiayue Feng, Yinqiang Wen, Liqiang Tan, Yue Li, Qiong Zhang, Ziniu Deng, Xingyao Xiong, and Shunyuan Xiao
Plant Cell 2016 28: 1108-1126. First Published on May 5, 2016; doi:10.1105/tpc.15.00880
http://www.plantcell.org/content/28/5/1108.abstract
Plant xanthine dehydrogenase contributes to H_2O_2 accumulation for pathogen defense in epidermal cells and also generates uric acid to remove H_2O_2 in chloroplasts, protecting mesophyll cells from oxidative stress.

The Plant Journal Content Alert: 86, 3 (May 2016)

Transcriptome dynamics of Arabidopsis during sequential biotic and abiotic stresses (pages 249–267)

Silvia Coolen, Silvia Proietti, Richard Hickman, Nelson H. Davila Olivas, Ping-Ping Huang, Marcel C. Van Verk, Johan A. Van Pelt, Alexander H.J. Wittenberg, Martin De Vos, Marcel Prins, Joop J.A. Van Loon, Mark G.M. Aarts, Marcel Dicke, Corné M.J. Pieterse and Saskia C.M. Van Wees

Version of Record online: 10 JUN 2016 | DOI: 10.1111/tpj.13167

Significance Statement

Plants have to cope simultaneously with diverse and often interacting stresses. Here we analyzed the dynamics of whole genome transcriptome profiles of Arabidopsis plants in response to six combinations of sequential biotic and abiotic stresses. We found that the transcriptome profile of sequentially stressed plants is largely determined by the last stress encountered. First-stress signatures in the second stress transcriptome provide leads to identify molecular players with decisive roles in positive or negative interactions between stress pathways.