Publications - Stress and Develop Biology

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Dietz, S.; Herz, K.; Gorzolka, K.; Jandt, U.; Bruelheide, H.; Scheel, D.; Root exudate composition of grass and forb species in natural grasslands *Sci. Rep.* **10**, 10691, (2020) DOI: 10.1038/s41598-019-54309-5

Abstract
RIS
BibTeX

Plants exude a diverse cocktail of metabolites into the soil as response to exogenous and endogenous factors. So far, root exudates have mainly been studied under artificial conditions due to methodological difficulties. In this study, each five perennial grass and forb species were investigated for polar and semi-polar metabolites in exudates under field conditions. Metabolite collection and untargeted profiling approaches combined with a novel classification method allowed the designation of 182 metabolites. The composition of exuded polar metabolites depended mainly on the local environment, especially soil conditions, whereas the pattern of semi-polar metabolites was primarily affected by the species identity. The profiles of both polar and semi-polar metabolites differed between growth forms, with grass species being generally more similar to each other and more responsive to the abiotic environment than forb species. This study demonstrated the feasibility of investigating exudates under field conditions and to identify the driving factors of exudate composition.

Bassal, M.; Abukhalaf, M.; Majovsky, P.; Thieme, D.; Herr, T.; Ayash, M.; Tabassum, N.; Al Shweiki, M. R.; Proksch, C.; Hmedat, A.; Ziegler, J.; Lee, J.; Neumann, S.; Hoehenwarter, W.; Reshaping of the Arabidopsis thaliana Proteome Landscape and Co-regulation of Proteins in Development and Immunity *Mol. Plant* **13**, 1709-1732, (2020) DOI: 10.1016/j.molp.2020.09.024

Abstract
RIS
BibTeX

Proteome remodeling is a fundamental adaptive response, and proteins in complexes and functionally related proteins are often co-expressed. Using a deep sampling strategy we define core proteomes of Arabidopsis thaliana tissues with around 10 000 proteins per tissue, and absolutely quantify (copy numbers per cell) nearly 16 000 proteins throughout the plant lifecycle. A proteome-wide survey of global post-translational modification revealed amino acid exchanges pointing to potential conservation of translational infidelity in eukaryotes. Correlation analysis of protein abundance uncovered potentially new tissue- and age-specific roles of entire signaling modules regulating transcription in photosynthesis, seed development, and senescence and abscission. Among others, the data suggest a potential function of RD26 and other NAC transcription factors in seed development related to desiccation tolerance as well as a possible function of cysteine-rich receptor-like kinases (CRKs) as ROS sensors in senescence. All of the components of ribosome

biogenesis factor (RBF) complexes were found to be co-expressed in a tissue- and age-specific manner, indicating functional promiscuity in the assembly of these less-studied protein complexes in Arabidopsis. Furthermore, we characterized detailed proteome remodeling in basal immunity by treating Arabidopsis seeldings with flg22. Through simultaneously monitoring phytohormone and transcript changes upon flg22 treatment, we obtained strong evidence of suppression of jasmonate (JA) and JA-isoleucine (JA-Ile) levels by deconjugation and hydroxylation by IAA-ALA RESISTANT3 (IAR3) and JASMONATE-INDUCED OXYGENASE 2 (JOX2), respectively, under the control of JASMONATE INSENSITIVE 1 (MYC2), suggesting an unrecognized role of a new JA regulatory switch in pattern-triggered immunity. Taken together, the datasets generated in this study present extensive coverage of the Arabidopsis proteome in various biological scenarios, providing a rich resource available to the whole plant science community.

Wirthmueller, L.; Romeis, T.; Sp(l)icing up PepR signalling *Nat. Plants* **6**, 912-913, (2020) DOI: 10.1038/s41477-020-0708-1

Abstract
RIS
BibTeX

Alternative splicing provides a fundamental and ubiquitous mechanism of gene regulation. Stimuli-induced retention of introns introduces novel proteoforms with altered signalling output: full-length CPK28 blocks immune signalling, while a truncated variant, lacking calcium responsiveness, promotes it.

Wang, W.; Liu, N.; Gao, C.; Cai, H.; Romeis, T.; Tang, D.; The Arabidopsis exocyst subunits EXO70B1 and EXO70B2 regulate FLS2 homeostasis at the plasma membrane *New Phytol.* **227**, 529-544, (2020) DOI: 10.1111/nph.16515

Abstract
RIS
BibTeX

The plasma membrane (PM)-localized receptor kinase FLAGELLIN SENSING 2 (FLS2) recognizes bacterial flagellin or its immunogenic epitope flg22, and initiates microbe-associated molecular pattern-triggered immunity, which inhibits infection by bacterial pathogens. The localization, abundance and activity of FLS2 are under dynamic control.Here, we demonstrate that Arabidopsis thaliana EXO70B1, a subunit of the exocyst complex, plays a critical role in FLS2 signaling that is independent of the truncated Toll/interleukin-1 receptor-nucleotide binding sequence protein TIR-NBS2 (TN2). In the exo70B1-3 mutant, the abundance of FLS2 protein at the PM is diminished, consistent with the impaired flg22 response of this mutant. EXO70B1-GFP plants showed increased FLS2 accumulation at the PM and therefore enhanced FLS2 signaling.The EXO70B1-mediated trafficking of FLS2 to the PM is partially independent of the PENETRATION 1 (PEN1)-containing secretory pathway. In addition, EXO70B1 interacts with EXO70B2, a close homolog of EXO70B1, and both proteins associate with FLS2 and contribute to the accumulation of FLS2 at the PM.Taken together, our data suggest that the exocyst complex subunits EXO70B1 and EXO70B2 regulate the trafficking of FLS2 to the PM, which represents a new layer of regulation of FLS2 function in plant immunity.

Trempel, F.; Eschen-Lippold, L.; Bauer, N.; Ranf, S.; Westphal, L.; Scheel, D.; Lee, J.; A mutation in Asparagine-

Linked Glycosylation 12 (ALG12) leads to receptor misglycosylation and attenuated responses to multiple microbial elicitors *FEBS Lett.* **594**, 2440-2451, (2020) DOI: 10.1002/1873-3468.13850

Abstract
RIS
BibTeX

Changes in cellular calcium levels are one of the earliest signalling events in plants exposed to pathogens or other exogenous factors. In a genetic screen, we identified an Arabidopsis thaliana 'changed calcium elevation 1 ' (cce1) mutant with attenuated calcium response to the bacterial flagellin flg22 peptide and several other elicitors. Whole genome re-sequencing revealed a mutation in ALG12 (Asparagine-Linked Glycosylation 12) that encodes the mannosyltransferase responsible for adding the eighth mannose residue in an α-1,6 linkage to the dolichol-PP-oligosaccharide N -glycosylation glycan tree precursors. While properly targeted to the plasma membrane, misglycosylation of several receptors in the cce1 background suggests that N -glycosylation is required for proper functioning of client proteins.

Tabassum, N.; Eschen-Lippold, L.; Athmer, B.; Baruah, M.; Brode, M.; Maldonado-Bonilla, L. D.; Hoehenwarter, W.; Hause, G.; Scheel, D.; Lee, J.; Phosphorylation-dependent control of an RNA granule-localized protein that fine-tunes defence gene expression at a post-transcriptional level *Plant J.* **101**, 1023-1039, (2020) DOI: 10.1111/tpj.14573

Abstract
RIS
BibTeX

Mitogen-activated protein kinase (MAPK) cascades are key signalling modules of plant defence responses to pathogen-associated molecular patterns (PAMPs, e.g. bacterial flg22 peptide). The Tandem Zinc Finger Protein 9 (TZF9) is an RNA-binding protein that is phosphorylated by two PAMP-responsive MAPKs, MPK3 and MPK6. We mapped the major phosphosites in TZF9 and showed their importance for controlling in vitro RNA-binding activity, in vivo flg22-induced rapid disappearance of TZF9-labelled processing body-like structures and TZF9 protein turnover. Microarray analysis showed a strong discordance between transcriptome (total mRNA) and translatome (polysome-associated mRNA) in the tzf9 mutant, with more mRNAs associated to ribosomes in the absence of TZF9. This suggests that TZF9 may sequester and inhibit translation of subsets of mRNAs. Fittingly, TZF9 physically interacts with poly(A)-binding protein 2 (PAB2), a hallmark constituent of stress granules – a site for stress-induced translational stalling/arrest. TZF9 even promotes stress granule assembly in the absence of stress. Hence, MAPKs may control defence gene expression post-transcriptionally through release from translation arrest within TZF9-PAB2-containing RNA granules or perturbing PAB2 functions in translation control (e.g. in the mRNA closed-loop model of translation).

Seybold, H.; Bortlik, J.; Conrads, B.; Hoehenwarter, W.; Romeis, T.; Prioritization of abiotic and biotic stress responses by direct linkage of ABI1 phosphatase and CPK5 calcium-dependent protein kinase *bioRxiv* (2019) DOI: 10.1101/839662

Abstract
RIS
BibTeX

In nature plants are constantly challenged by simultaneous abiotic and biotic stresses, and under conflicting stress scenarios prioritization of stress responses is required for plant survival. Calcium-dependent protein kinase CPK5 is a central hub in local and distal immune signaling, required upstream of hormone salicylic acid (SA)-dependent systemic acquired resistance (SAR). Here we show that CPK5 signaling-dependent immune responses are effectively blocked and pathogen resistance is reverted either upon treatment of plants with abscisic acid (ABA) or in genetic mutant backgrounds lacking PP2C phosphatase activities including abi1-2. Consistently, enhanced immune responses occur upon co-expression of CPK5 kinase with active variants of ABI1 phosphatase ABI1G180S and ABI1G181A. Biochemical studies and mass spectrometry-based phosphosite analysis reveal a direct ABI1 phosphatase-catalyzed de-phosphorylation of CPK5 at T98, a CPK5 auto-phosphorylation site. CPK5T98A, mimicking continuous de-phosphorylation through ABI1, correlates with an increase in kinase activity and CPK5 function in ROS production. CPK5T98D, mimicking a CPK5 auto-phosphorylated status under ABA-induced phosphatase inhibition, leads to inactivated CPK5 causative to an immediate stop of immune responses.Our work reveals an elegant mechanism for plant stress prioritization, where the ABA-dependent phosphatase ABI1, negative regulator of abiotic responses, functions as positive regulator of biotic stress responses, stabilizing CPK5-dependent immune responses in the absence of ABA. This mechanism allows continuous immune signaling during pathogen survey in environmentally non-challenging conditions. Under severe abiotic stress, immune signaling is discontinued via a direct biochemical intersection through a phosphatase/kinase pair recruiting two key regulatory enzymes of these antagonistic signaling pathways.

Jiang, X.; Hoehenwarter, W.; Scheel, D.; Lee, J.;
Phosphorylation of the CAMTA3 transcription factor triggers its destabilization and nuclear export *bioRxiv* (2019) DOI: 10.1101/825323

Abstract
RIS
BibTeX

The calmodulin-binding transcription activator 3 (CAMTA3) is a repressor of immunity-related genes but an activator of cold-induced genes in plants. Post-transcriptional or -translational mechanisms have been proposed to control CAMTA3's role in the crosstalk between immune and chilling responses. Here, we show that treatment with the bacterial flg22 elicitor, but not cold stress, induces a phospho-mobility shift of CAMTA3 proteins. Correspondingly, CAMTA3 is directly phosphorylated by two flg22-responsive mitogen-activated protein kinases (MAPKs), MPK3 and MPK6, which triggers CAMTA3 nuclear export and destabilization. SR1IP1, a substrate E3 ubiquitin ligase adaptor required for pathogen-induced CAMTA3 degradation, is shown here to be likely plasma-membrane-localized and therefore cannot physically interact with the nuclear CAMTA3. Despite the flg22-inducible re-localization of CAMTA3 to the cytoplasm, we failed to detect CAMTA3-SR1IP1 complexes. Hence, the role of SR1IP1 for CAMTA3 degradation needs to be re-evaluated. Surprisingly, flg22 elicitation can still induce nuclear export and phospho-mobility shift of a phospho-null CAMTA3 that cannot be phosphorylated by MAPKs, suggesting the participation of additional flg22-responsive kinase(s). A constitutively-active calcium-dependent protein kinase, CPK5, can stimulate a

phospho-mobility shift in CAMTA3 similar to that induced by flg22. Although CPK5 can interact with CAMTA3, it did not directly phosphorylate CAMTA3, suggesting the requirement of a still unidentified downstream kinase or additional components. Overall, at least two flg22-responsive kinase pathways target CAMTA3 to induce degradation that presumably serves to remove CAMTA3 from target promoters and de-repress expression of defence genes.

Westphal, L.; Strehmel, N.; Eschen-Lippold, L.; Bauer, N.; Westermann, B.; Rosahl, S.; Scheel, D.; Lee, J.; pH effects on plant calcium fluxes: lessons from acidification-mediated calcium elevation induced by the γ-glutamyl-leucine dipeptide identified from Phytophthora infestans *Sci. Rep.* **9**, 4733, (2019) DOI: 10.1038/s41598-019-41276-0

Abstract
RIS
BibTeX

Cytosolic Ca2+ ([Ca2+]cyt) elevation is an early signaling response upon exposure to pathogen-derived molecules (so-called microbe-associated molecular patterns, MAMPs) and has been successfully used as a quantitative read-out in genetic screens to identify MAMP receptors or their associated components. Here, we isolated and identified by mass spectrometry the dipeptide γ-Glu-Leu as a component of a Phytophthora infestans mycelium extract that induces [Ca2+]cyt elevation. Treatment of Arabidopsis seedlings with synthetic γ-Glu-Leu revealed stimulatory effects on defense signaling, including a weak enhancement of the expression of some MAMP-inducible genes or affecting the refractory period to a second MAMP elicitation. However, γ-Glu-Leu is not a classical MAMP since pH adjustment abolished these activities and importantly, the observed effects of γ-Glu-Leu could be recapitulated by mimicking extracellular acidification. Thus, although γ-Glu-Leu can act as a direct agonist of calcium sensing receptors in animal systems, the Ca2+-mobilizing activity in plants reported here is due to acidification. Low pH also shapes the Ca2+ signature of well-studied MAMPs (e.g. flg22) or excitatory amino acids such as glutamate. Overall, this work serves as a cautionary reminder that in defense signaling studies where Ca2+ flux measurements are concerned, it is important to monitor and consider the effects of pH.

Nietzschmann, L.; Gorzolka, K.; Smolka, U.; Matern, A.; Eschen-Lippold, L.; Scheel, D.; Rosahl, S.; Early Pep-13-induced immune responses are SERK3A/B-dependent in potato *Sci. Rep.* **9**, 18380, (2019) DOI: 10.1038/s41598-019-54944-y

Abstract
RIS
BibTeX

Potato plants treated with the pathogen-associated molecular pattern Pep-13 mount salicylic acid- and jasmonic acid-dependent defense responses, leading to enhanced resistance against Phytophthora infestans, the causal agent of late blight disease. Recognition of Pep-13 is assumed to occur by binding to a yet unknown plasma membrane-localized receptor kinase. The potato genes annotated to encode the co-receptor BAK1, StSERK3A and StSERK3B, are activated in response to Pep-13 treatment. Transgenic RNAi-potato plants with reduced expression of both SERK3A and SERK3B were generated. In response to Pep-13

treatment, the formation of reactive oxygen species and MAP kinase activation, observed in wild type plants, is highly reduced in StSERK3A/B-RNAi plants, suggesting that StSERK3A/B are required for perception of Pep-13 in potato. In contrast, defense gene expression is induced by Pep-13 in both control and StSERK3A/B-depleted plants. Altered morphology of StSERK3A/B-RNAi plants correlates with major shifts in metabolism, as determined by untargeted metabolite profiling. Enhanced levels of hydroxycinnamic acid amides, typical phytoalexins of potato, in StSERK3A/B-RNAi plants are accompanied by significantly decreased levels of flavonoids and steroidal glycoalkaloids. Thus, altered metabolism in StSERK3A/B-RNAi plants correlates with the ability of StSERK3A/B-depleted plants to mount defense, despite highly decreased early immune responses.