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Liese, A.; Eichstädt, B.; Lederer, S.; Schulz, P.; Oehlschläger, J.; Matschi, S.; Feijó, J. A.; Schulze, W. X.; Konrad, K. R.; Romeis, T.; Imaging of plant calcium-sensor

kinase conformation monitors real time calcium-dependent decoding in planta *Plant Cell* **36**, 276-296, (2024) DOI: 10.1093/plcell/koad196

Abstract
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Changes in cytosolic calcium (Ca2+) concentration are among the earliest reactions to a multitude of stress cues. While a plethora of Ca2+-permeable channels may generate distinct Ca2+ signatures and contribute to response specificities, the mechanisms by which Ca2+ signatures are decoded are poorly understood. Here we developed a genetically encoded FRET (Förster resonance energy transfer)-based reporter that visualizes the conformational changes in Ca2+-dependent protein kinases (CDPKs/CPKs). We focused on two CDPKs with distinct Ca2+-sensitivities, highly Ca2+-sensitive Arabidopsis (Arabidopsis thaliana) AtCPK21 and rather Ca2+-insensitive AtCPK23, to report conformational changes accompanying kinase activation. In tobacco (Nicotiana tabacum) pollen tubes, which naturally display coordinated spatial and temporal Ca2+ fluctuations, CPK21-FRET, but not CPK23-FRET, reported oscillatory emission ratio changes mirroring cytosolic Ca2+ changes, pointing to the isoform-specific Ca2+-sensitivity and reversibility of the conformational change. In Arabidopsis guard cells, CPK21-FRET-monitored conformational dynamics suggest that CPK21 serves as a decoder of signal-specific Ca2+ signatures in response to abscisic acid and the flagellin peptide flg22. Based on these data, CDPK-FRET is a powerful approach for tackling real-time live-cell Ca2+ decoding in a multitude of plant developmental and stress responses.

Vainonen, J. P.; Gossens, R.; Krasensky-Wrzaczek, J.; De Masi, R.; Danciu, I.; Puukko, T.; Battchikova, N.; Jonak, C.; Wirthmueller, L.; Wrzaczek, M.; Shapiguzov, A.; Kangasjärvi, J.; Poly(ADP-ribose)-binding protein RCD1 is a plant PARylation reader regulated by Photoregulatory Protein Kinases *Commun. Biol.* **6**, 429, (2023) DOI: 10.1038/s42003-023-04794-2

Abstract
Internet
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Poly(ADP-ribosyl)ation (PARylation) is a reversible post-translational protein modification that has profound regulatory functions in metabolism, development and immunity, and is conserved throughout the eukaryotic lineage. Contrary to metazoa, many components and mechanistic details of PARylation have remained unidentified in plants. Here we present the transcriptional co-regulator RADICAL-INDUCED CELL DEATH1 (RCD1) as a plant PAR-reader. RCD1 is a multidomain protein with intrinsically disordered regions (IDRs) separating its domains. We have reported earlier that RCD1 regulates plant development and stress-tolerance by interacting with numerous transcription factors (TFs) through its C-terminal RST domain. This study suggests that the N-terminal WWE and PARP-like domains, as well as the connecting IDR play an important regulatory role for RCD1 function. We show that RCD1 binds PAR in vitro via its WWE domain and that PAR-binding determines RCD1 localization to nuclear bodies (NBs) in vivo. Additionally, we found that RCD1 function and stability is controlled by Photoregulatory Protein Kinases (PPKs). PPKs localize with RCD1

in NBs and phosphorylate RCD1 at multiple sites affecting its stability. This work proposes a mechanism for negative transcriptional regulation in plants, in which RCD1 localizes to NBs, binds TFs with its RST domain and is degraded after phosphorylation by PPKs.

Prautsch, J.; Erickson, J.; Özyürek, S.; Gormanns, R.; Franke, L.; Lu, Y.; Marx, J.; Niemeyer, F.; Parker, J. E.; Stuttmann, J.; Schattat, M. H.; Effector XopQ-induced stromule formation in Nicotiana benthamiana depends on ETI signaling components ADR1 and NRG1 *Plant Physiol.* **191**, 161-176, (2023) DOI: 10.1093/plphys/kiac481

Abstract
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In Nicotiana benthamiana, the expression of the Xanthomonas effector XANTHOMONAS OUTER PROTEIN Q (XopQ) triggers RECOGNITION OF XOPQ1 (ROQ1)-dependent effector-triggered immunity (ETI) responses accompanied by the accumulation of plastids around the nucleus and the formation of stromules. Both plastid clustering and stromules were proposed to contribute to ETI-related hypersensitive cell death and thereby to plant immunity. Whether these reactions are directly connected to ETI signaling events has not been tested. Here, we utilized transient expression experiments to determine whether XopQ-triggered plastid reactions are a result of XopQ perception by the immune receptor ROQ1 or a consequence of XopQ virulence activity. We found that N. benthamiana mutants lacking ROQ1, ENHANCED DISEASE SUSCEPTIBILITY 1, or the helper NUCLEOTIDE-BINDING LEUCINE-RICH REPEAT IMMUNE RECEPTORS (NLRs) N-REQUIRED GENE 1 (NRG1) and ACTIVATED DISEASE RESISTANCE GENE 1 (ADR1), fail to elicit XopQ-dependent host cell death and stromule formation. Mutants lacking only NRG1 lost XopQ-dependent cell death but retained some stromule induction that was abolished in the nrg1_adr1 double mutant. This analysis aligns XopQ-triggered stromules with the ETI signaling cascade but not to host programmed cell death. Furthermore, data reveal that XopQ-triggered plastid clustering is not strictly linked to stromule formation during ETI. Our data suggest that stromule formation, in contrast to chloroplast perinuclear dynamics, is an integral part of the N. benthamiana ETI response and that both NRG1 and ADR1 hNLRs play a role in this ETI response.

Ortmann, S.; Marx, J.; Lampe, C.; Handrick, V.; Ehnert, T.-M.; Zinecker, S.; Reimers, M.; Bonas, U.; Erickson, J.; A conserved microtubule-binding region in Xanthomonas XopL is indispensable for induced plant cell death reactions *PLOS Pathog.* **19**, e1011263, (2023) DOI: 10.1371/journal.ppat.1011263

Abstract
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Pathogenic Xanthomonas bacteria cause disease on more than 400 plant species. These Gram-negative bacteria utilize the type III secretion system to inject type III effector proteins (T3Es) directly into the plant

cell cytosol where they can manipulate plant pathways to promote virulence. The host range of a given Xanthomonas species is limited, and T3E repertoires are specialized during interactions with specific plant species. Some effectors, however, are retained across most strains, such as Xanthomonas Outer Protein L (XopL). As an 'ancestral' effector, XopL contributes to the virulence of multiple xanthomonads, infecting diverse plant species. XopL homologs harbor a combination of a leucine-rich-repeat (LRR) domain and an XL-box which has E3 ligase activity. Despite similar domain structure there is evidence to suggest that XopL function has diverged, exemplified by the finding that XopLs expressed in plants often display bacterial species-dependent differences in their sub-cellular localization and plant cell death reactions. We found that XopL from X. euvesicatoria (XopLXe) directly associates with plant microtubules (MTs) and causes strong cell death in agroinfection assays in N. benthamiana. Localization of XopLXe homologs from three additional Xanthomonas species, of diverse infection strategy and plant host, revealed that the distantly related X. campestris pv. campestris harbors a XopL (XopLXcc) that fails to localize to MTs and to cause plant cell death. Comparative sequence analyses of MT-binding XopLs and XopLXcc identified a proline-rich-region (PRR)/α-helical region important for MT localization. Functional analyses of XopLXe truncations and amino acid exchanges within the PRR suggest that MT-localized XopL activity is required for plant cell death reactions. This study exemplifies how the study of a T3E within the context of a genus rather than a single species can shed light on how effector localization is linked to biochemical activity.

Aryal, B.; Xia, J.; Hu, Z.; Stumpe, M.; Tsering, T.; Liu, J.; Huynh, J.; Fukao, Y.; Glöckner, N.; Huang, H.-Y.; Sancho-Andrés, G.; Pakula, K.; Ziegler, J.; Gorzolka, K.; Zwiewka, M.; Nodzynski, T.; Harter, K.; Sánchez-Rodríguez, C.; Jasiński, M.; Rosahl, S.; Geisler, M. M.; An LRR receptor kinase controls ABC transporter substrate preferences during plant growth-defense decisions *Curr. Biol.* **33**, 2008-2023, (2023)
DOI: 10.1016/j.cub.2023.04.029

Abstract
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The exporter of the auxin precursor indole-3-butyric acid (IBA), ABCG36/PDR8/PEN3, from the model plant Arabidopsis has recently been proposed to also function in the transport of the phytoalexin camalexin. Based on these bonafide substrates, it has been suggested that ABCG36 functions at the interface between growth and defense. Here, we provide evidence that ABCG36 catalyzes the direct, ATP-dependent export of camalexin across the plasma membrane. We identify the leucine-rich repeat receptor kinase, QIAN SHOU KINASE1 (QSK1), as a functional kinase that physically interacts with and phosphorylates ABCG36. Phosphorylation of ABCG36 by QSK1 unilaterally represses IBA export, allowing camalexin export by ABCG36 conferring pathogen resistance. As a consequence, phospho-dead mutants of ABCG36, as well as qsk1 and abcg36 alleles, are hypersensitive to infection with the root pathogen Fusarium oxysporum, caused by elevated fungal progression. Our findings indicate a direct regulatory circuit between a receptor kinase and an ABC transporter that functions to control transporter substrate preference during plant growth and defense balance decisions.

Abukhalaf, M.; Proksch, C.; Thieme, D.; Ziegler, J.; Hoehenwarter, W.; Changing turn-over rates regulate

abundance of tryptophan, GS biosynthesis, IAA transport and photosynthesis proteins in Arabidopsis growth defense transitions *BMC Biol.* **21**, 249, (2023) DOI: 10.1186/s12915-023-01739-3

Abstract
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Background Shifts in dynamic equilibria of the abundance of cellular molecules in plant-pathogen interactions need further exploration. We induced PTI in optimally growing Arabidopsis thaliana seedlings for 16 h, returning them to growth conditions for another 16 h. Methods Turn-over and abundance of 99 flg22 responding proteins were measured chronologically using a stable heavy nitrogen isotope partial labeling strategy and targeted liquid chromatography coupled to mass spectrometry (PRM LC–MS). These experiments were complemented by measurements of mRNA and phytohormone levels. Results Changes in synthesis and degradation rate constants (Ks and Kd) regulated tryptophane and glucosinolate, IAA transport, and photosynthesis-associated protein (PAP) homeostasis in growth/PTI transitions independently of mRNA levels. Ks values increased after elicitation while protein and mRNA levels became uncorrelated. mRNA returned to pre-elicitation levels, yet protein abundance remained at PTI levels even 16 h after media exchange, indicating protein levels were robust and unresponsive to transition back to growth. The abundance of 23 PAPs including FERREDOXIN-NADP(+)-OXIDOREDUCTASE (FNR1) decreased 16 h after PAMP exposure, their depletion was nearly abolished in the myc234 mutant. FNR1 Kd increased as mRNA levels decreased early in PTI, its Ks decreased in prolonged PTI. FNR1 Kd was lower in myc234, mRNA levels decreased as in wild type. Conclusions Protein Kd and Ks values change in response to flg22 exposure and constitute an additional layer of protein abundance regulation in growth defense transitions next to changes in mRNA levels. Our results suggest photosystem remodeling in PTI to direct electron flow away from the photosynthetic carbon reaction towards ROS production as an active defense mechanism controlled post-transcriptionally and by MYC2 and homologs. Target proteins accumulated later and PAP and auxin/IAA depletion was repressed in myc234 indicating a positive effect of the transcription factors in the establishment of PTI.

Nietzschmann, L.; Smolka, U.; Perino, E. H. B.; Gorzolka, K.; Stamm, G.; Marillonnet, S.; Bürstenbinder, K.; Rosahl, S.; The secreted PAMP-induced peptide StPIP1_1 activates immune responses in potato *Sci. Rep.* **13**, 20534, (2023) DOI: 10.1038/s41598-023-47648-x

Abstract
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Treatment of potato plants with the pathogen-associated molecular pattern Pep-13 leads to the activation of more than 1200 genes. One of these, StPIP1_1, encodes a protein of 76 amino acids with sequence homology to PAMP-induced secreted peptides (PIPs) from Arabidopsis thaliana. Expression of StPIP1_1 is also induced in response to infection with Phytophthora infestans, the causal agent of late blight disease. Apoplastic localization of StPIP1_1-mCherry fusion proteins is dependent on the presence of the predicted

signal peptide. A synthetic peptide corresponding to the last 13 amino acids of StPIP1_1 elicits the expression of the StPIP1_1 gene itself, as well as that of pathogenesis related genes. The oxidative burst induced by exogenously applied StPIP1_1 peptide in potato leaf disks is dependent on functional StSERK3A/B, suggesting that StPIP1_1 perception occurs via a receptor complex involving the co-receptor StSERK3A/B. Moreover, StPIP1_1 induces expression of FRK1 in Arabidopsis in an RLK7-dependent manner. Expression of an RLK from potato with high sequence homology to AtRLK7 is induced by StPIP1_1, by Pep-13 and in response to infection with P. infestans. These observations are consistent with the hypothesis that, upon secretion, StPIP1_1 acts as an endogenous peptide required for amplification of the defense response.

Heuermann, D.; Döll, S.; Schweneker, D.; Feuerstein, U.; Gentsch, N.; von Wirén, N.; Distinct metabolite classes in root exudates are indicative for field- or hydroponically-grown cover crops *Front. Plant Sci.* **14**, 1122285, (2023) DOI: 10.3389/fpls.2023.1122285

Abstract
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Introduction: Plants release a large variety of metabolites via their roots to shape physico-chemical soil properties and biological processes in the rhizosphere. While hydroponic growth conditions facilitate accessibility of the root system and recovery of root exudates, the natural soil environment can alter root metabolism and exudate secretion, raising the question to what extent the quantity and composition of root exudates released in hydroponic growth systems reflect those recovered from soil-grown roots. Methods: Using a root washing method, we sampled root exudates from four field-grown cover crop species with wide taxonomic distance, namely white mustard, lacy phacelia, bristle oat, and Egyptian clover. A set of primary metabolites and secondary metabolites were analysed in a targeted and untargeted LC-MS-based approach, respectively, for comparison with exudates obtained from hydroponically cultured plants. Results and discussion: We found that hydroponically cultivated plants released a larger amount of total carbon, but that the recovery of total carbon was not indicative for the diversity of metabolites in root exudates. In the field, root exudates from phacelia and clover contained 2.4 to 3.8 times more secondary metabolites, whereas carbon exudation in hydroponics was 5- to 4-fold higher. The composition of the set of metabolites identified using the untargeted approach was much more distinct among all species and growth conditions than that of quantified primary metabolites. Among secondary metabolite classes, the presence of lipids and lipid-like molecules was highly indicative for field samples, while the release of a large amount of phenylpropanoids, organoheterocyclic compounds or benzenoids was characteristic for clover, mustard or oat, respectively, irrespective of the cultivation condition. However, at the compound level the bulk of released metabolites was specific for cultivation conditions in every species, which implies that hydroponically sampled root exudates poorly reflect the metabolic complexity of root exudates recovered from field-grown plants.

Zönnchen, J.; Gantner, J.; Lapin, D.; Barthel, K.; Eschen-Lippold, L.; Erickson, J. L.; Landeo Villanueva, S.; Zantop, S.; Kretschmer, C.; Joosten, M. H. A. J.; Parker, J. E.; Guerois, R.; Stuttmann, J.; EDS1 complexes are not required for PRR responses and execute TNL-ETI from the nucleus in Nicotiana benthamiana *New Phytol.* **236**, 2249-2264, (2022) DOI:

10.1111/nph.18511

Abstract
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Heterodimeric complexes incorporating the lipase-li ke proteins EDS1 wi th PAD4 or SAG101 are central hubs in plant innate immunity. EDS1 functions encompass signal relay from TIR domain-containing intracellular NLR-type immune receptors (TNLs) towards RPW8-type helper NLRs (RNLs) and, in A. thaliana, bolstering of signaling and resistance mediated by cell-s u r face pattern recognition receptors (PRRs). Increasing evidence points to the activation of EDS1 complexes by small molecule binding. •We used CRISPR/Cas-generated mutant lines and agroinfiltration-based complementation assays to interrogate functions of EDS1 complexes in N. benthamiana. •We do not detect impaired PRR signaling in N. benthamiana lines deficient in EDS1 complexes or RNLs. Intriguingly, in assays monitoring functions of SlEDS1-NbEDS1 complexes in N. benthamiana, mutations within the SlEDS1 catalytic triad can abolish or enhance TNL immunity. Furthermore, nuclear EDS1 accumulation is sufficient for N. benthamianaTNL (Roq1) immunity.•Reinforcing PRR signaling in Arabidopsis might be a derived function of the TNL/EDS1 immune sector. Although Solanaceae EDS1 functionally depends on catalytic triad residues in some contexts, our data do not support binding of a TNL-derived small molecule in the triad environment. Whether and how nuclear EDS1 activity connects to membrane pore-f orming RNLs remains unknown.

Vogt, S.; Feijs, K.; Hosch, S.; De Masi, R.; Lintermann, R.; Loll, B.; Wirthmueller, L.; The superior salinity tolerance of bread wheat cultivar Shanrong No. 3 is unlikely to be caused by elevated Ta-sro1 poly-(ADP-ribose) polymerase activity *Plant Cell* **34**, 4130–4137, (2022) DOI: 10.1093/plcell/koac261

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