VII. European Workshop on Plant Peptides & Receptors

September 11-13, 2019
Freudenstadt, Germany

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Location
The FRITZ LAUTERBAD (formerly WALDHOTEL ZOLLERNBLICK) is located in
Am Zollernblick 1
72250 Freudenstadt-Lauterbad
+49 7441 95099-0

Directions
*By train:*
There are two train stations in Freudenstadt, Hauptbahnhof (main station) and
Stadtbahnhof. From both stations you could take a walk to the FRITZ Lauterbad (see
map) or take a taxi (~10 €; Taxi-Rumpf: 07441-2484; Taxi-Schumacher: 07441-88066).

Alternatively,
- from main station you can use our shuttle (please wait for further
  information by email) or
- from Stadtbahnhof take a bus in direction of “Lauterbad / Zollernblick /
  Freudenstadt” (more info at www.bahn.de). The bus stop
  is located about 200 meters downhill to the hotel.
By foot:
The hotel can be reached by a 30 minutes stroll from the main station of Freudenstadt.

By car from Basel and Strasbourg:
Highway A5 direction Frankfurt, exit Appenweier, B28 towards Freudenstadt. In Freudenstadt at first traffic light turn right towards Lauterbad (Lauterbad Straße). Drive about 2 km away from town, the hotel banner WALDHOTEL ZOLLERNBLICK will be on the right side.

..from Karlsruhe / Frankfurt:
Highway A5 direction Basel, exit Rastatt, then B462 towards Freudenstadt. After Huzenbach turn left towards Freudenstadt / Freiburg (B 294). At the 3rd exit (L460) in Freudenstadt you head right towards Lauterbad. The WALDHOTEL ZOLLERNBLICK will be on your left.

..from Stuttgart and Singen (lake of constance):
Highway A81, exit Horb, take B28, B14 and L370 towards Freudenstadt. In Schopfloch turn left, direction Glatten, from there you’ll pass through Dietersweiler and reach the WALDHOTEL ZOLLERNBLICK before entering the city of Lauterbad.

Information
Free wireless LAN called “fritzlovesyou” is provided by the hotel.
Sponsors

We thank the following companies for their support:

Building blocks for the peptide synthesis (a large variety of protected amino acids), cofactors of plant peptides (e.g. FAD as found in flavoproteins) as well as chromophores of photoreceptor proteins (e.g. bilirubin) and a wide range of products for protein analysis are available at Carl ROTH for your research projects!
Wednesday, 11.9.2019

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<td><strong>June Nasrallah</strong></td>
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<td>14:00</td>
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<td>The receptor-ligand determinants of mating system in the Brassicaceae: functional and evolutionary studies</td>
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<td>Thomas Dresselhaus</td>
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<td>A battlefield: signaling along the pollen tube journey in maize</td>
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<td>AtLURE1/PRK6-mediated signaling controls conspecific pollen precedence in <em>Arabidopsis thaliana</em></td>
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<td>Investigation of the signaling between two different species at the site of pollen tube reception</td>
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<td>Stefanie Sprunck</td>
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<td>Sperm adhesion and fusion is mediated by egg cell-secreted EC1 peptides</td>
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<td><strong>pecha kucha / flash talk (3 x 2 min)</strong></td>
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<td>Yan Ma</td>
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<td>Mind the gaps in the SCHENGEN pathway</td>
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<td>MAKR3 is a novel regulator of shoot gravitropic response</td>
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<td>Nils Stührwohldt</td>
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<td>Hydroxyproline-dependent processing of CLE40 from Arabidopsis</td>
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<td>Alexandra Furch</td>
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<td>FLS2 sensors located in epidermal and subepidermal cells trigger occlusion of flg22-insensitive sieve tubes in <em>Arabidopsis thaliana</em> and <em>Vicia faba</em></td>
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<td>Volker Hegenauer</td>
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<td>Tomato’s immune system recognizes Cuscuta infection by sensing a cell wall associated protein</td>
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<td>Julia Pastor Fernandez</td>
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<td>Tomato systemin is perceived by <em>Arabidopsis thaliana</em> and triggers metabolic rearrangements promoting defense against fungal pathogens</td>
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<td>Shinichiro Sawa</td>
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<td>Parasitic nematode hijacks plant systemic CLE-CLV1 mechanisms for successful infection</td>
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<td>Anja Fuglsang</td>
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<td>RALF and RALFLike peptides both trigger alkalinization but are perceived differently by FERONIA</td>
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<td>Alicia Abarca</td>
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<td>Regulation of RALF peptide processing by the subtilase S1P during immunity</td>
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Thursday, 12.9.2019

07:30 - 08:30  Breakfast

08:30 - 10:30  Session III  DEVELOPMENT  
   Chair: Yvon Jaillais

08:30  Christian Hardtke  Keynote lecture
   A phloem-centric perspective of CLE peptide signaling in root development

09:10 Yaping Zhou  
   Regulation of cluster roots of white lupin by small peptides

09:30 Ana Fernandez  
   GOLVEN/RGB/CLEL peptide signaling through RGF1 Insensitive (RGI) receptors and MAPK6 restricts asymmetric cell division during lateral root initiation

09:50 Zengxiang Ge  
   The roles of RALF/CrRLK1L-mediated signaling in plant reproduction

10:10 Barbara Berckmans  
   Identification of the role and mode of action of plant defensins during plant defense responses and in root development

10:30 - 11:00  Coffee Break

11:00 - 13:00  Session IV  PEPTIDES AND IMMUNITY  
   Chair: Thomas Boller

11:00 Ralph Hückelhoven  
   Arabidopsis thaliana cell surface receptor signalling for recognition of peptide elicitors of Fusarium spp.

11:20 Lisha Zhang  
   A conserved peptide pattern from fungal endopolygalacturonase triggers plant immunity in Arabidopsis

11:40 Martin Stegmann  
   Identification of novel phytocytokines regulating plant immunity

12:00 Kyle Bender  
   EFR protein kinase activity is dispensable for elf18-induced PTI signaling

12:20 Frank Menke  
   Targeting post translational modifications to open the black box pattern recognition receptor signaling

12:40 Birgit Kemmerling  
   A TIR-NBS-LRR protein is necessary for BAK1 autoimmune phenotypes and links BAK1-mediated cell death to effector triggered immunity

13:00  Lunch

14:00 - 18:00  Social Activities  
   Guided tour at the Brewery Alpirsbacher Klosterbräu

18:20 - 19:40  Session V  ROOT DEVELOPMENT  
   Chair: Judith Fliegmann

18:20 Florian Frugier  Keynote Lecture
   Signaling peptides acting in the systemic regulation of root system architecture in legumes

19:00 Yvon Jaillais  
   Control of root gravitropism dynamics by reversible inhibition of TMK1 plasma membrane signaling

19:20 Reidunn Aalen  
   The involvement of the IDL1-HSL2 peptide-receptor signaling pair in root cap development and sloughing

19:40  Poster Awards

20:00  Dinner: Berghütte Lauterbach
07:30 - 08:30  **Breakfast**

09:00 - 10:40  **Session VI**  **SIGNALING AT THE CELL WALL**
Chair: Birgit Kemmerling

09:00  Steven Moussu  Structural basis for recognition of RALF peptides by LRX proteins during pollen tube growth

09:20  Kay Schneitz  The receptor kinase STRUBBELIG regulates the cell wall stress response in Arabidopsis

09:40  Chao Li  GPI-anchor proteins act as chaperones and coreceptors in CrRLK1L Receptor Like kinases-mediated signaling in Arabidopsis

10:00  Nicolas Doll  Subtilase mediated activation of a novel GSO1/GSO2 ligand provides spatial information during embryonic cuticle integrity monitoring

10:20  Hugo Mélida  Plant immunity regulated by cell wall integrity: unveiling novel carbohydrate-based molecular patterns

10:40 - 11:10  **Coffee Break**

11:10 - 12:50  **Session VII**  **NEW METHODS, NEW PATTERNS**
Chair: Melinka Butenko

11:30  Elwira Smakowska-Luzan  Reactive oxygen species as a signaling nexus in receptor kinase interaction networks

11:50  Anna Philippova  *Physcomitrella patens* moss’s intracellular and extracellular peptidomes and their role in plant immune responses

12:10  Grégoire Denay  Over the rainbow: a practical guide for fluorophore selection in plant FRET experiments

12:30  Stefanie Ranf  Sensing of 3-hydroxy fatty acid metabolites by the LORE receptor complex

12:50  **Concluding remarks**

13:15  **Lunch**

Departure
Keynote lectures
The Receptor-Ligand Determinants of Mating System in the Brassicaceae: Functional and Evolutionary Studies

JUNE B. NASRALLAH
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Section of Plant Biology, School of Integrative Plant Science, Cornell University, Ithaca, NY 14853, US

The S-locus Receptor Kinase (SRK), a member of the S-Domain (SD) receptor kinase family, and its ligand, the S-locus Cysteine-Rich (SCR) peptide, are highly-polymorphic and co-evolving proteins that are encoded by haplotypes of the S locus, which determines specificity in the self-incompatibility response of the Brassicaceae. The signaling cascade that culminates in the inhibition of self pollen is triggered by allele-specific interaction between the ectodomain of an SRK variant with the SCR encoded in the same S-locus haplotype. Analysis of the recognition and response phases of self-incompatibility have been facilitated by two developments: (1) the establishment of an efficient transgenic self-incompatible Arabidopsis thaliana model, and (2) the solution of the crystal structure of the SRK ectodomain in complex with its cognate SCR. Ongoing studies that make use of these developments for functional studies as well as evolutionary studies aimed at understanding the diversification of receptor-ligand gene pairs and their possible relationship to other members of the SD receptor kinase family will be presented.
A phloem-centric perspective of CLE peptide signaling in root development

CHRISTIAN HARDTKE
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Department of Plant Molecular Biology, University of Lausanne, Biophore Building, CH-1015 Lausanne, Switzerland

Angiosperms, the extant plants that dominate terrestrial ecosystems, are characterized by extensive vascular xylem and phloem networks, which permit nutrient distribution as well as systemic coordination of physiology and development. Molecular mechanisms of vascular differentiation and their relation to plant hormone pathways are the major research focus of my lab. In this context, the development of phloem sieve elements is particularly interesting, because during their differentiation, sieve elements reduce some organelles and lose others (notably the nucleus) as they interconnect via sieve plates to form continuous sieve tubes. Thus, sieve elements represent a unique cell type that retains complex functionality in the absence of a nucleus. A major question in our research is how the onset of the peculiar sieve element differentiation process is controlled at the molecular level? The Arabidopsis root is particularly well-suited to investigate this process, because vascular tissues are continuously formed from stem cells at its tip and phloem formation can be followed along the spatio-temporal gradient of single cell files. Over the last years we have built up an extensive molecular genetic network that governs the differentiation of sieve element precursors. This network comprises angiosperm-specific positive regulators, which drive sieve element differentiation through tipping a delicate quantitative balance, opposing negative regulators of the process. Both auxin transport regulation and brassinosteroid signaling are key aspects of the positive regulatory output, whereas CLE peptide signaling is central to the negative regulatory output. I will present data that illustrate how these pathways intersect to guide sieve element differentiation.
Signaling peptides acting in the systemic regulation of root system architecture in legumes

FLORIAN FRUGIER¹, Pierre Gautrat¹, Carole Laffont¹, Emeline Huault¹, Ariel Ivanovic², Mathias Brault¹, Michael Djordjevic²
(florian.frugier@cnrs.fr)

¹ Institute of Plant Sciences Paris-Saclay (IPS2), CNRS, INRA, Univ Paris Sud, Univ Evry, Univ Paris-Diderot, Université Paris-Saclay, Rue de Noetzlin, 91190 Gif-sur-Yvette, France
² Division of Plant Sciences, Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia

Plant growth is limited by soil nutrient availability and symbiotic nitrogen-fixing nodulation allows legume plants to use the atmospheric nitrogen source as an alternative. Legumes tightly regulate nodule number to balance the cost of supporting symbiotic rhizobial nitrogen-fixing bacteria growth with nitrogen fixation’s benefits. Two antagonistic pathways involving signalling peptides regulate nodule numbers systemically from shoots: under low nitrogen conditions, CEPs (C-terminally Encoded Peptides) are produced in roots and promote rhizobial infection and nodule formation through the CRA2 (Compact Root Architecture 2) Leucine-Rich Repeats Receptor-Like Kinase (LRR-RLK) acting in shoots; and after symbiotic rhizobia have initiated nodulation, CLE (CLAVATA3-like) peptides are produced to limit the energetically costly nodulation in relation to the plant’s needs, through the SUNN (Super Numeric Nodules) LRR-RLK receptor acting in shoots. Molecular mechanisms explaining how these two signalling peptide hormonal pathways are coordinated to fine-tune nodule number remains however poorly understood. Progress will be reported on different aspects of these peptide systemic signalling pathways, notably in relation with their interaction with other types of hormonal regulations and with the characterization of potential common downstream shoot-to-root signals.
Oral presentations
A Battlefield: Signaling Along the Pollen Tube Journey in Maize

Liangzi Zhou, Lele Wang, THOMAS DRESSELHAUS  
(thomas.dresselhaus@ur.de)

Cell Biology and Plant Biochemistry, Regensburg Center for Biochemistry, University of Regensburg, 93053 Regensburg, Germany

In the majority of plants including Arabidopsis and all grasses, pollen tubes carry two sperm cells as a passive cargo for fertilization. During their journey, pollen tubes have to overcome a number of prezygotic hybridization/speciation barriers including penetration of papilla hair cells/stigmata, growth towards and inside the transmitting tract, guidance inside the egg apparatus ultimately leading to pollen tube burst, gamete activation and double fertilization. Intensive cellular communication takes place along the pollen tube pathway to distinguish self from alien pollen tubes and to promote own and reject foreign tubes. Outcrossing with individuals of the same species shall be promoted to avoid fertilization failures and inbreeding leading to sterility. The underlying molecular mechanisms appear to be partly adapted from defense signaling including the involvement of ROS production and Ca\(^{2+}\) spiking. However, polymorphic cysteine-rich peptides (CRPs) of the defensin-like DEFL, RALF and LTP subgroups generated by specific reproductive cells appear to specific signaling processes during pollen tube invasion and growth after binding to more broadly expressed receptors. With a focus on maize, we will report on various peptide-receptor interactions and highlight differences between the grasses and Arabidopsis.
AtLURE1/PRK6-mediated signaling controls conspecific pollen precedence in Arabidopsis thaliana

SHENG ZHONG¹§, Meiling Liu¹§, Zhijuan Wang¹§, PeiLiu², Ya-Long Guo³, Juan Dong⁴, Thomas Dresselhaus⁵, Hongya Gu¹, LI-JIA QU¹
(qulj@pku.edu.cn)

¹State Key Laboratory for Protein and Plant Gene Research, Peking University, China; ²China Agricultural University, China; ³Institute of Botany, CAS, China; ⁴Rutgers the State University of New Jersey, USA; ⁵University of Regensburg, Germany
§Equal contribution

Reproductive isolation prevents members of different species from producing offspring and is a prerequisite for speciation. Failure of communication between female tissues of the pistil and paternal pollen tubes represent major hybridization barriers in flowering plants. Polymorphic maternal LURE peptides and one identified male receptor PRK6 were involved in pollen tube attraction. Here we report that knock out of the whole Arabidopsis thaliana LURE1 gene family did not affect fertility, indicating that AtLURE1/PRK6-mediated signaling is dispensable for successful fertilization within one Arabidopsis species. Instead, we report a novel role of AtLURE1s as conspecific pollen tube emergence accelerators that favor conspecific pollen over pollen from other species and thus promote reproductive isolation. We further identified maternal XIUQIU1-4 peptides that attract pollen tubes in a non-species-specific manner. Cooperation between at least two types of attractants promotes fertilization success and the recently-evolved peptides AtLURE1s represent a key mechanism for reproductive isolation.
Investigation of the signaling between two different species at the site of pollen tube reception

BENCIVENGA S¹, Muller L², Pires N, Gagliardini V¹, Grossniklaus U¹
(stefano.bencivenga@botinst.uzh.ch)

¹University of Zurich, Switzerland
²Cornell University, Itaca, USA

Pollen tube (PT) reception is a cell-cell communication process allowing the recognition of the male gametophyte (the PT) by the female gametophyte necessary for fertilization. One important step is the distinction at the level of the female gametophyte of a same-species pollen from a different species pollen. We are investigating how this process happens. As tool we use two closely related species, *Arabidopsis thaliana* and *Arabidopsis lyrata*. Depending on the *A. thaliana* accession, *A. lyrata* pollen is recognized with a variable degree of success. If recognition does not occur, the PT is not properly received, keeps growing inside the ovule, and fertilization fails. This recognition step takes place in the cells at the contact point between the embryo sac and PT, the synergids, through a highly regulated signaling manner. Preliminary results identified a gene coding for a LysM-domain containing glycan-binding peptide as a key player for species-specific PT recognition, pointing at glycosylation patterns for the distinction of intra- and interspecific PTs, a mechanism already known to be important in symbiosis and immunity. We found that differences in the regulation in distinct species is responsible for recognition, as the amino acid sequence does not differ among *A. thaliana* accessions.

We propose to attest and manipulate the expression profile of the gene in analysis in different accessions to correlate its regulation with its function and to analyse its molecular mechanism.
Sperm adhesion and fusion is mediated by egg cell-secreted EC1 peptides

SPRUNCK S, Cyprys P, Malka R, Flores-Tornero M, Lindemeier M (stefanie.sprunck@ur.de)
Cell Biology and Plant Biochemistry, University of Regensburg, Germany

Unlike all other species, flowering plants have evolved the unique mechanism of double fertilization in which two female reproductive cells (egg cell and central cell) are fertilized by two male gametes (sperm cells). During double fertilization one pollen tube enters the ovule and bursts, ejecting a pair of sperm cells close to the fertilization site between the egg cell and central cell. In Arabidopsis thaliana, only a few minutes later two gamete fusion events take place. Previously, we and others have shown that successful double fertilization requires sperm repositioning and adhesion, mutual gamete activation and the physical separation of the sperm pair. Nevertheless, the molecular mechanism permitting sperm-egg fusion whereas the second sperm almost simultaneously fuses with the central cell remains to be understood. We identified a small family of small cysteine-rich EGG CELL 1 (EC1) proteins, which are only secreted from the egg cell when the two sperm cells are delivered to the fusion site. We will present our most recent results showing that the function of EC1 peptides is evolutionary conserved among flowering plants and that they mediate both sperm adhesion and activation.
FLS2 sensors located in epidermal and subepidermal cells trigger occlusion of flg22-insensitive sieve tubes in *Arabidopsis thaliana* and *Vicia faba*

FURCH ACU¹, Buxa SV², van Bel AJE², Noll GA³, Wrobel L³, Hafke JB⁴, Ehlers K⁵, Zimmermann MR¹, Mrozinska A¹, Scholz S¹, Koch AM², Maaß J-P⁶, Peiter E⁶, Oelmüller R¹, Kogel K-H²

(Alexandra.Furch@uni-jena.de)

¹Department of Plant Physiology, Matthias-Schleiden-Institute for Genetics, Bioinformatics and Molecular Botany, Faculty of Biological Science, Friedrich-Schiller-University, Jena, Germany
²Institute of Phytopathology, Centre for BioSystems, Land Use and Nutrition, Justus Liebig University, Giessen, Germany
³Institute of Biology and Biotechnology of Plants, Plant Biotechnology, Westfälische-Wilhelms-University, Münster, Germany
⁴Institute of Plant Physiology, Justus Liebig University, Giessen, Germany
⁵Institute of Botany, Justus Liebig University, Giessen, Germany
⁶Plant Nutrition Laboratory, Institute of Agricultural and Nutritional Sciences, Faculty of Natural Sciences III, Martin Luther University of Halle-Wittenberg, Halle (Saale), Germany

In *Arabidopsis thaliana*, the flagellin epitope flg22 induced inhibition of mass flow by sieve-element occlusion (SEO), which was absent in *fis2* mutants of the pattern recognition receptor FLAGELLIN SENSING2 (FLS2). Despite the flg22-induced SEO, the number of FLS2 receptors was almost none in sieve elements (SEs) in contrast to their abundance in epidermal cells. The apparent signal transfer from flg22-sensing epidermal and subepidermal cells to SEs was further investigated in *Vicia faba* because of a better accessibility, larger cell sizes, and the presence of innate Ca²⁺ level indicators, the forisomes. Therefore we identified and characterized a yet unknown FLS2 homolog from *Vicia faba* with 53% amino acid sequence identity to FLS2 from Arabidopsis. Thereby, we could localize the protein to the plasma membrane. Consistent with the observations in *Arabidopsis*, application of flg22 induced forisome dispersion and stop of mass flow in intact plants. However, flg22 did not provoke forisome dispersion in *V. faba* SE protoplasts. Electrophysiology indicated that flg22-induced depolarizations in subepidermal cells propagate to SEs as electropotential waves, triggering an elevated Ca²⁺ level in SEs and associated forisome dispersion. Aequorin-based Ca²⁺ measurements showed two successive Ca²⁺ waves in SEs: the first wave occurred one min after flg22 application followed by a second one, three min later, the latter of which may be responsible for SEO. In conclusion, flg22-triggered SEO initiated by surface cells may restrict pathogen spread and potentiate systemic alarm signals.
Tomato`s immune system recognizes *Cuscuta* infection by sensing a cell wall associated protein

HEGENAUER¹ V., Körner¹ M., Slaby¹ P., Hollmann² J., Burggraf¹ R., Kaiser¹ B., Löffelhardt¹ B., Droste-Borel⁴ I., Sklenar³ J., Menke³ F., Maček⁴ B., Ranjan⁵,⁶ A., Sinha⁵ N., Felix¹ G., Krause² K., Stahl¹ M. and Albert¹ M. (volker.hegenauer@zmbp.uni-tuebingen.de)

¹Center for Plant Molecular Biology, Tübingen, Germany
²Department of Arctic and Marine Biology, Norway
³The Sainsbury Laboratory, Norwich Research Park, United Kingdom
⁴Quantitative Proteomics & Proteome Center, Tübingen, Germany
⁵Department of Plant Biology, UC Davis, United States
⁶National Institute of Plant Genome Research, New Delhi, India

Holoparasitic plants of the genus *Cuscuta* are obligate biotrophs and possess neither roots nor expanded leaves and exhaust solutes and carbohydrates from the host plants. During a successful infection, *Cuscuta* spp. penetrate host plants by haustoria that directly connect to the vasculature of the infected host. *Cuscuta reflexa* can successfully infect a broad range of dicotyledonous plants. The cultivated tomato (*Solanum lycopersicum*) represents a notable exception since it is able to block the infection and responds to *C. reflexa* extracts with defence reactions typical for defence against microbial pathogens (induction of ethylene, oxidative burst). By using recombinant inbred lines of *S. lycopersicum* and *S. pennellii* we mapped a region within the tomato genome responsible for the recognition of the *Cuscuta* peptides. We could identify the LRR-RLP CuRe1 (*Cuscuta Receptor 1*) as the receptor for the perception of *C. reflexa*. CuRe1 significantly contributes to resistance when stably expressed in otherwise susceptible hosts. In search for the epitope that triggers CuRe1 we analysed extracts of *C. reflexa*. With HPLC we purified a set of small peptides with masses of ~2-3.5 kDa, that were able to trigger defense responses in CuRe1 expressing plants. We analysed and sequenced the peptides using MS/MS and found that the epitope is a peptide (CrCrip) which is a part of a cell wall associated protein. The identified peptide CrCrip is able to trigger immune responses in a CuRe1 specific manner unlike homologs from other plants.
Tomato Systemin is perceived by *Arabidopsis thaliana* and triggers metabolic rearrangements promoting defense against fungal pathogens


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Metabolic Integration and Cell Signaling Laboratory, Plant Physiology Section, Department of Ciencias Agrarias y del Medio Natural, Universitat Jaume I, Castellón, Spain

Systemin is a tomato peptide that regulates the plant response against herbivores. It is released upon wounding or pathogen attack and induces a cascade of plant defenses producing the accumulation of protease inhibitors in local and systemic tissue. There are also evidences of the involvement of Systemin in tomato defenses against pathogens such as the necrotrophic fungus *Botrytis cinerea*. Although the tomato Systemin receptor and processing has been recently described, very little is known about the perception and function of Systemin in heterologous species.

In the present study, we found that tomato Systemin was perceived by the taxonomically distant species *Arabidopsis thaliana* at very low concentrations. Additionally, Systemin induces resistance against the necrotrophic fungus *Plectosphaerella cucumerina*. Systemin triggers resistance by activating the plant immune system, since in vitro assays revealed that Systemin has not direct antifungal activity.

In order to understand the mechanisms behind Systemin-induced Resistance (Sys-IR) we performed non-targeted metabolomic analysis to study the metabolic fingerprint of Systemin in Arabidopsis before and after a challenge in Arabidopsis plants. Overall the Systemin treatment alone had a major impact in the Arabidopsis metabolome, whereas after infection treated plants showed an overlapping profile with the control plants. Nevertheless, we could also find some groups of compounds that were over or down accumulated in systemin treated plants after infection comparing with control plants.
Parasitic nematode hijacks plant systemic CLE-CLV1 mechanisms for successful infection

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Plants develop plenty number of systemic signals in many aspect of their successful growth events including biotic or abiotic stress responses. Here we show plant parasitic nematodes (PPN), Meloidogyne incognita, induce four CLAVATA3 (CLV3)/EMBRYO SURROUNDING REGION (CLE) genes expression at infection site in Arabidopsis. Plants deficient in this pathway show PPN resistance, whereas CLE overexpression showed hypersusceptibility. Grafting analysis showed clv1 mutation in upperground tissue provide PPN resistance. Together with the result of split root experimente, our results reveal that translocated root derived CLE signal are perceived by CLV1 at upperground tissue as a systemic singal to support successful gall formation and successful PPN reproduction.
RALF and RALFLike peptides both trigger alkalinization but are perceived differently by FERONIA

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Acidification of the apoplastic space followed by cell wall loosening is a key step in cell expansion. PSY1 is a secreted tyrosine-sulfated glycopeptide that activates the plasma membrane H⁺-ATPase, lowers the apoplastic pH and, as a result, triggers cellular expansion. Peptides belonging to the Rapid Alkalinization Factor (RALF) family inhibit the plasma membrane H⁺-ATPase, resulting in reversal of this effect and alkalinization of the apoplastic space. Here we show that PSY1 treatment induced the transcription of genes encoding three RALF peptides, RALF22, RALF33 and RALFL36. The apoplastic alkalinization in roots induced by RALF peptides is preceded by a rapid burst of intracellular Ca²⁺, with isoform-specific signatures. RALF-induced alkalinization was prevented by blocking Ca²⁺ channels, indicating that the Ca²⁺ signal is an obligatory part of the response. Furthermore, fer mutants lacking the FERONIA receptor kinase responded to RALF33, but not RALFL36, indicating a different mechanism for RALFL36 perception.
Regulation of cluster roots of white lupin by small peptides

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White lupin cluster roots are specialized brush-like root structures that are formed in some species under phosphorus (P)-deficient conditions. They intensely secrete protons and organic acid anions for solubilization and acquisition of sparingly soluble phosphates. Phytohormones and sucrose modulate cluster root number, but the molecular mechanisms of cluster root formation have been elusive. Here, we blast a CEP1 homologous gene, LaCEP1, in white lupin transcriptomic dataset. It belongs to the C-TERMINALLY-ENCODED PEPTIDE (CEP) family. Members of that family arrest root growth and modulate branching in model species. The study aimed at characterizing its function in cluster root formation and morphology. LaCEP1 was highly expressed in the pre-emergence zone of clusters. Over-expression of the gene encoding the LaCEP1 propeptide resulted in moderate inhibition of cluster root formation. The primary and lateral root lengths of lupin were little affected by the overexpression, but LaCEP1 reduced cluster rootlet and root hair elongation. Addition of a 15-mer core peptide derived from LaCEP1 similarly altered root morphology and modified cluster activity, suggesting that a core sequence of the propeptide is functionally sufficient. Stable overexpression in Arabidopsis confirmed the LaCEP1 function in root growth inhibition across species.

Peptide and its corresponding receptor kinase regulate root development and nutrients uptake. Sucrose and LaCEP1 core peptide addition resulted in a similar cluster root morphology, indicating a co-receptor may exist and coordinate cluster root development and function. Later study will focus on the CEP1 receptor (CEPR) and sucrose induced cluster root formation. This study will provide a comprehensive understanding of peptide and sugar signaling involved in cluster root formation and function in white lupin.
Lateral roots (LRs) in the model plant Arabidopsis thaliana develop from the pericycle, a stem cell layer surrounding the vascular bundle. Although present as a contiguous tissue layer spanning over the entire length of the main root, only a subset of pericycle cells become specified as lateral root founder cells (LRFC). During LR initiation, LRFCs undergo one or two rounds of asymmetric cell divisions (ACDs) to form a single-layered primordium stage. The initial ACDs generate daughter cells with different size and fate thereby guaranteeing correct subsequent primordium organogenesis. We recently reported that excess of the GOLVEN (GLV) 6/ROOT GROWTH FACTOR (RGF) 8 disrupts these ACDs resulting in more symmetric divisions and failure to achieve LR organogenesis. Here we show that loss-of-function GLV6 and its homologue GLV10 leads to increased ACDs during LR initiation providing evidence for the existence of a restraining mechanism on ACDs plants are making use of. We also identified three members of the RGI1 Insensitive (RGI)/RGF1 receptors (RGFRs) as likely GLV receptors during LR initiation. Furthermore, through a suppressor screen, we found that the MITOGEN-ACTIVATED PROTEIN KINASE6 (MPK6) is a downstream regulator of the GLV pathway. Our data altogether indicate that GLV6 and 10 are inhibitors of ACDs and signal through RGI receptors and MPK6 to restrict the initial ACDs that take place in LRFCs during LRI.
The roles of RALF/CrRLK1L-mediated signaling in plant reproduction

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In angiosperms, the precise delivery of gametes for double fertilization depends on complex cell-to-cell communications between pollen tubes and female tissues/gametophytes. At the male side, these communications including pollen tube reception were primarily controlled by the tube cells, rather than sperm cells. It was established that RAPID ALKALINIZATION FACTORS (RALFs) peptides and their receptors Catharanthus roseus RLK1-like receptors (CrRLK1Ls) are intensively involved in male-female interactions. For instance, synergid cell-expressed FERONIA and HERK1/ANJEA, together with the glycosylphosphatidylinositol-anchored protein (GPI-AP) LRE, are involved in pollen tube reception, since loss of function of these factors resulted in defects in pollen tube reception. We have also identified RALF4/19 peptides serving as the signals for the male-expressed ANXUR1/2 and BUPS1/2 receptors in pollen tube rupture control; knocking out these RALFs or their receptors leads to pollen tube reception defects. We further identified LRE-like GPI-AP 2/3 (LLG2/3) as the co-receptors for ANX/BUPS receptors in pollen tube integrity control, since llg2 llg3 showed precocious tube rupture. Interaction between LLG2/3 and ANX/BUPS receptors was significantly enhanced by the treatment of RALF4/19. We propose a model that multiple CrRLK1L receptors form a heteromeric complex, stabilized by LLG proteins on the membrane, to perceive RALF peptide signals for different signaling pathways.
Identification of the role and mode of action of plant defensins during plant defense responses and root development

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Fungal plant pathogens are a major threat to food production worldwide. For example the necrotrophic fungal pathogen Botrytis cinerea, causing grey mould disease, can infect over 200 plant species leading to annual losses of up to $100 billion. The production of antimicrobial peptides plays an important role in plant immunity. Plant defensins are such small highly stable peptides originally isolated based on their antifungal activity. They are regarded as being an important part in plant innate immunity responses directed against fungal pathogens, which is supported by enhanced disease resistance in diverse plants upon overexpression of specific PDFs. The antifungal mode of action of PDFs is partly regulated through interaction with a fungal membrane target. Recent data indicate that their role is not restricted to the defense response, but also includes important biological functions, such as root development, nodule formation and reproduction. Surprisingly, despite the broad international interest in plant defensins, their mode of action in plant defense responses is still unclear as well as their possible involvement in (other) biological functions. We aim to unravel the biological function (during root development and defense) and mode of action (in planta and against fungi) of the plant defensin AtPDF2.3 and its closest homologue AtPDF2.2.
Arabidopsis thaliana cell surface receptor signalling for recognition of elicitors of Fusarium spp.

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Fusarium is a large genus of fungi causing severe economic damage in many species of cultivated plants exemplified by Fusarium Head Blight of wheat or Panama Disease of banana. Non-self molecular patterns (termed elicitors) can be perceived by plants resulting in disease resistance via the activation of pattern-triggered immunity (PTI). However, knowledge of these elicitors or corresponding plant immunity components is lacking for Fusarium. We describe a new peptide elicitor fraction present in several Fusarium species, which elicits canonical PTI responses in monocots and dicots but depends on a thus far unknown signalling pathways. We hence employed a forward-genetics screen in Arabidopsis aequorin cytosolic calcium reporter plants to isolate mutants strongly impaired in multiple PTI marker responses to an enriched elicitor fraction derived from Fusarium oxysporum. We termed the mutant with a nearly full loss of function fere1 (Fusarium Elicitor Reduced Elicitation1) and mapped the causal mutation to a gene with a hitherto undescribed role in PTI pathways but functions in other cell surface signalling pathways. PTI loss-of-function in fere1 was fully complemented with the full-length recombinant protein. The strength of the phenotype in fere1 mutants supports that it is a new immune receptor or key component in sensing Fusarium. FERE also contributes towards basal resistance to Fusarium wilt. This identified FERE as a novel PTI player relevant for Fusarium resistance in Arabidopsis. Partial genetic interaction of FERE with known PTI signalling components is discussed.
A conserved peptide pattern from fungal endopolygalacturonase triggers plant immunity in Arabidopsis

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Plant plasma membrane pattern recognition receptors are key to microbe sensing and activation of immunity to microbial invasion. The Arabidopsis leucine-rich repeat receptor-like protein (LRR-RP) RLP42 (also known as Responsiveness to Botrytis PolyGalacturonase 1, RBPG1) mediates plant immunity by perceiving fungal endopolygalacturonases (PGs). RLP42 recognizes several PGs from the plant pathogen Botrytis cinerea and from the saprotroph Aspergillus niger. In this study, we showed that RLP42 recognizes a conserved 9-amino-acid peptide from fungal PGs (pg9), but not from plant PGs, thereby triggering plant immune responses, including ROS burst, MAPK activation, ethylene production, and defense-related gene expression. RLP42 forms a ligand-independent complex with LRR receptor kinase (LRR-RK) SOBIR1 (Suppressor of Brassinosteroid insensitive 1 (BRI1)-associated kinase (BAK1)-interacting receptor kinase 1). In addition, we show that RLP42 recruits LRR-RKs SERK proteins into a tripartite complex upon ligand perception. Expression of RLP42 in Arabidopsis Br-0 (an accession that is non-responsive to fungal PGs) confers pg9 pattern recognition and enhances immunity against bacterial pathogen Pseudomonas syringae pv. tomato after pg9-priming.
Identification of novel phytocytokines regulating plant immunity

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Endogenous plant signalling peptides play an important role in regulating diverse physiological responses where they control e.g. root growth, cell expansion, stem cell fate or cell separation events. Furthermore, several classes of these peptides have regulatory functions in the control of plant immune responses. For example, it has been shown that RAPID ALKALINISATION FACTOR (RALF) peptides act as suppressors or activators of PRR-triggered immunity via the FERONIA (FER) receptor kinase. Thus, immune-modulatory peptides can be classified as phytocytokines as they share similar functions with animal cytokines.

To identify novel phytocytokines we mined publically available gene expression data in the model species Arabidopsis thaliana and found several specific members of plant endogenous peptide genes with a differential transcriptional regulation in response to elicitors and/or pathogen infection, suggesting that they play a role during plant-microbe interactions. We focussed on peptide families with described functions regulating growth and development. Here, we show that overexpression of distinct peptide genes alters PRR-triggered immunity and antibacterial resistance. In addition, treatments with synthetic peptides show similar alterations of immunity. We are currently trying to dissect the molecular mechanisms governing the regulation of plant immune responses by these newly identified modulatory phytocytokine peptides.
**EFR protein kinase activity is dispensable for elf18-induced PTI signaling**

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Several leucine rich-repeat receptor kinases (LRR-RKs) function as cell surface immune receptors that activate plant immunity in response to conserved microbial molecules called pathogen-associated molecular patterns (PAMPs). PAMP perception activates a battery of rapid cellular responses, culminating in changes in gene expression, and curtailing pathogen ingress. The LRR-RK ELONGATION FACTOR TU RECEPTOR (EFR) perceives the bacterial PAMP elongation factor thermo unstable (or the minimal epitope, elf18) in coordination with the co-receptor BRASSINOSTEROID INSENSITIVE 1 ASSOCIATED KINASE 1 (BAK1). EFR is phosphorylated following PAMP perception, but the importance of EFR phosphorylation in activating PTI is not known. Transgenic *Arabidopsis* expressing EFR protein kinase mutants (D849N and K851E) activate elf18-induced BAK1 and MAPK phosphorylation, and ROS production, and are indistinguishable from the wild-type in seedling growth inhibition assays. Analysis of phospho-null and phospho-mimic mutants of EFR reveals the site-specific impacts of phosphorylation in elf18-induced PTI responses. Collectively, the data indicate that while EFR phosphorylation regulates receptor function, EFR does not play a direct catalytic role in activating PTI signaling following elf18 perception. Future work aims to understand a potential scaffolding function of the EFR cytoplasmic domain in regulating receptor complex composition during PTI.
Physcomitrella patens moss’s intracellular and extracellular peptidomes and their role in plant immune responses

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Plant bioactive peptides play crucial roles in numerous processes from growth and development to biotic and abiotic stress responses. The vast majority of known bioactive peptides are generated via processing of inactive protein precursors. However, recent studies have shown that bioactive peptides can also be generated from functionally active proteins. It is still unclear whether such peptides are just merely breakdown products or they have a significant role in immune responses. Using the model organism Physcomitrella patens we performed comprehensive analyses of the cell and extracellular endogenous peptide pools. Mass-spectrometry and bioinformatics approaches allowed us to identify thousands of intracellular and extracellular peptides. Treatments with methyl jasmonate (MeJA) and salicylic acid (SA) induced specific proteolysis of new functional proteins and the release of endogenous peptides. We then proposed a list of proteases, which might be responsible for generation of endogenous peptides. Using in silico and in vivo analyses of peptides generated from functionally active proteins upon MeJA-treatment we also detected antimicrobial activity. Our special interested was attracted by one peptide, which in addition to its antimicrobial activity altered the transcription of defense genes involved in immune responses. Thus, degradation of functionally active proteins might play an important role in defense mechanisms by generating a new source of bioactive peptides.
A TIR-NBS-LRR protein is necessary for BAK1 autoimmune phenotypes and links BAK1-mediated cell death to effector triggered immunity

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The co-receptor BRASSINOSTEROID INSENSITIVE1-ASSOCIATED RECEPTOR KINASE1 (BAK1/SERK3), regulates different signaling pathways including growth and development, immune response, and cell death control by directly interacting with and positively regulating multiple ligand binding receptors. The BAK1-interacting RK BIR3 can prevent BAK1-ligand binding receptor interaction by directly interacting with both ligand-binding receptors and BAK1 (and all members of the SERK family). The interaction of BIR3 with SERKs stabilizes BAK1 and its closest homolog BKK1/SERK4. The interactome of BIR3 revealed a BIR3 interacting TIR-NBS-LRR (TNL) protein (BIT1). Double mutants in bit1 bak1 show reduced cell death compared to bak1 single mutants upon inoculation with the necrotrophic fungus Alternaria brassicicola. Double mutants in bir3 bak1 show a severe dwarf phenotype and spontaneous cell death. Our investigations revealed that mutations in bit1 also suppress bir3bak1-mediated cell death. Both bak1 and bak1 bir3-mediated cell death can be partially suppressed by mutations in ENHANCED DISEASE SUSCEPTIBILITY (eds1), a common downstream component of TNLs. Taken together, BIT1 interacts with BAK1 and BIR proteins, is necessary for BAK1-mediated cell death and links BAK1 to TIR-NBS-LRR-mediated cell death usually involved in effector triggered immunity. BIT1 likely guards the integrity of BAK1 and BAK1 BIR complexes and initiates autoimmune cell death when BAK1 complexes are impaired.
Control of root gravitropism dynamics by reversible inhibition of TMK1 plasma membrane signaling

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Plants are able to orient their growth according to gravity, which ultimately controls both shoot and root architecture. Gravitropism is a dynamic process whereby gravistimulation induces the asymmetric distribution of the plant hormone auxin, leading to asymmetric growth, organ bending and subsequent reset of auxin distribution back to the original pre-gravistimulation situation. While differential auxin accumulation during the gravitropic response depends on the activity of polarly localized PIN-FORMED (PIN) auxin-efflux carriers, it is poorly understood how the timing of this dynamic response is regulated. Here, we show that MEMBRANE ASSOCIATED KINASE REGULATOR2 (MAKR2) controls the pace of the root gravitropic response. We found that MAKR2 is required for the PIN2 asymmetry during gravitropism by acting as a negative regulator of the cell surface signaling mediated by the receptor-like kinase TRANSMEMBRANE KINASE1 (TMK1) and the Rho-GTPase of Plants 6 (ROP6). Furthermore, we show that the MAKR2 inhibitory effect on TMK1 signaling is antagonized by auxin itself, which triggers rapid MAKR2 membrane dissociation in a TMK1-dependent manner. Our findings suggest that the timing of the root gravitropic response is orchestrated by the reversible inhibition of the TMK1/ROP6 signaling pathway at the cell surface.
The involvemnet of the IDL1-HSL2 peptide-receptor signaling pair in root cap development and sloughing

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The root cap protects the stem cell niche of Angiosperm roots from damage. In Arabidopsis lateral root cap (LRC) cells covering the meristematic zone are regularly lost through programmed cell death, while the outermost layer of the root cap covering the tip is repeatedly sloughed. Efficient coordination with stem cells producing new layers is needed to maintain a constant size of the cap. We have identified a signalling pair, the peptide IDA-LIKE1 (IDL1) and its receptor HAESA-LIKE2 (HSL2), mediating such communication (Shi et al. Nature Plants, 2018). Live imaging over several days characterized this process from initial fractures in LRC cell files to full separation of a layer. Enhanced expression of IDL1 in the separating root cap layers resulted in increased frequency of sloughing balanced with generation of new layers in a HSL2-dependent manner. The NAC transcription factors FEZ, SOMBRERO, BEARSKIN1 and BEARSKIN 2 are involved in maturation, cell separation and cell division in the root tip. Transcription data link HSL2 to these transcription factors. Programmed cell death seems to be involved in the initiation of sloughing of the distal cap, in an HSL2-dependent manner. In light of these findings, a detailed presentation will be given of root tip development from germination to the mature stage.
Structural basis for recognition of RALF peptides by LRX proteins during pollen tube growth

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Plant reproduction relies on the highly regulated growth of the pollen tube for proper sperm delivery. This process is controlled by secreted RALF signaling peptides, which have been previously shown to be perceived by CrRLK1Ls membrane receptor-kinases and leucine-rich (LRR) extensin proteins (LRXs). Here we demonstrate that RALF peptides are active as folded, disulfide bond-stabilized proteins, which can bind to the LRR domain of LRX proteins with nanomolar affinity. Crystal structures of the LRX-RALF signaling complexes reveal LRX proteins as constitutive dimers. The N-terminal LRR domain containing the RALF binding site is tightly linked to the extensin domain via a cysteine-rich tail. Our biochemical and structural work reveals a complex signaling network by which RALF ligands may instruct different signaling proteins – here CrRLK1Ls and LRXs – through structurally different binding modes to orchestrate cell wall remodeling in rapidly growing pollen tubes.
The receptor kinase STRUBBELIG regulates cell wall stress response in Arabidopsis

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Cell wall remodeling is essential for the control of growth and development as well as the regulation of stress responses. However, the underlying cell wall monitoring mechanisms remain poorly understood. The Arabidopsis atypical receptor kinase STRUBBELIG (SUB) mediates tissue morphogenesis. Present evidence indicates that this process involves a complex between SUB and the C2 domain protein QUIRKY (QKY) at plasmodesmata. Here, we show that SUB also regulates the cellular response to reduced levels of cellulose, a central component of the cell wall. SUB signaling affects several cell wall damage responses induced by the cellulose biosynthesis inhibitor isoxaben, including the increase in intracellular reactive oxygen species, stress gene induction, ectopic lignin and callose accumulation as well as the maintenance of cell shape and root growth recovery. SUB is also required for root growth arrest in mutants with defective cellulose biosynthesis. Genetic data further indicate that SUB controls the isoxaben-induced cell wall stress response independently from other known receptor kinase genes mediating this response, such as THESEUS1 or MIK2, but also in part independently of QKY. Thus, we propose SUB to function in at least two distinct biological processes: the control of tissue morphogenesis and the response to cell wall damage. Our results reveal a novel signal transduction pathway that contributes to the molecular framework underlying cell wall integrity signaling.
Glycosylphosphatidylinositol-anchor proteins act as chaperones and coreceptors in CrRLK1L Receptor Like kinases-mediated signalings in Arabidopsis

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The Catharanthus roseus Receptor-Like Kinase1-like (CrRLK1L) family genes have been widely studied in a variety of biological processes. We previously found that the female gametophyte-expressed glycosylphosphatidylinositol-anchored protein (GPI-AP) LORELEI and the seedling-expressed LORELEI-like GPI-AP1 (LLG1) acting as chaperones and co-receptors for an extensively investigated CrRLK1L member, FERONIA. Homologs of FERONIA expressed in the pollen tubes, ANXUR (ANX)/BUPS receptor kinase complex was revealed controlling pollen tube growth in response to RAPID ALKALINIZATION FACTOR4/19 signaling. We found that pollen-specific LORELEI-LIKE GPI-ANCHORED PROTEINS 2 and 3 (LLG2/3) promoted pollen tube growth in vitro and in vivo. LLG2/3 interacted with extracellular J domain of ANX/BUPS, and knockdown of LLG2/3 function induced cytoplasmic retention of ANX1/2, suggesting that LLG2/3 assist the secretion of ANX1/2 to the apical plasma membrane. We further demonstrated that LLG2/3 were components of the ANX/BUPS-ROP signaling complex which control the pollen tube growth through the production of reactive oxygen species. Together our studies support LORELEI GPI-APs acting as chaperones and coreceptors for CrRLK1L family proteins and elucidate a mechanism by which GPI-APs enable the signaling capacity of cell surface receptors.
Plants in the terrestrial environment crucially depend on their ability to effectively limit water loss. In aerial tissues this is achieved by the production of a hydrophobic cuticle. In many angiosperms, such as the model plant Arabidopsis thaliana, the first organs to emerge upon germination, the cotyledons, are already covered by a functional cuticle, which is produced by the embryo within the protected environment of the seed. Embryonic cuticle establishment is controlled by multiple proteins including a subtilisin protease and the receptor-like kinases, GASSHO1/SCHENGEN3 (GSO1/SGN3) and GASSHO2 (GSO2). Recent studies have shown that GSO1/SGN3 is involved in the formation of another diffusion barrier, the Casparian strip, where it acts by binding sulphated peptides (CIFs) that come into contact with GSO1/SGN3 when barrier closure is incomplete or defective. Here we demonstrate that the currently known GSO1/SGN3 ligands show no embryo cuticle defects. Nonetheless, the unique tyrosine sulfatase in plants, TPST does display defect in embryonic cuticle formation, pointing to the role of as yet unknown sulphated peptides in this process. We find that a sulphated peptide, CHICKPEA (CHP), is necessary for embryonic cuticle formation. The active CHP peptide can recapitulate CIF-activity in roots in a GSO1/SGN3 dependent manner, and, physically binds the extra-cellular domains of GSO1/SGN3 and GSO2. However, the spatial organisation of the CHP signalling pathway in seeds is dramatically different to that of the CIF pathway in roots. Notably the pathway is dependent upon a spatially regulated peptide processing event. Together, our data elucidate a complex molecular dialog between the embryo and the endosperm, required for the formation of a continuous cuticle in advance of its deployment upon germination.
Plant immunity regulated by cell wall integrity: unveiling novel carbohydrate-based molecular patterns

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Plant innate immune system can be activated by microbe-associated molecular patterns (MAMPs), but also by damage-associated molecular patterns (DAMPs) that trigger immune responses upon recognition by plant Pattern Recognition Receptors (PRRs). DAMPs are signalling molecules released from host cellular structures (i.e. plant cell walls) upon pathogen infection or wounding. Despite the hypothesized important role of DAMPs in plant-pathogen interactions, a very limited number of DAMPs are well characterized. Typical examples of carbohydrate-based DAMP/MAMPs are oligogalacturonides, β-glucans and chitin.

Carbohydrate-enriched extracts from cell wall mutants showing altered susceptibility/resistance to several pathosystems were chemically and chromatographically fractionated. Those fractions were tested for their capacity to activate the plant innate immune system and those showing the highest triggering capacities were characterized. These analyses pointed to a role of pentose oligosaccharides triggering plant immune responses. Further research revealed that β-1,4-xylooligosaccharides of specific degrees of polymerization carrying arabinose decorations are sensed as DAMPs by plants. The molecular mechanisms of these and other potential novel DAMPs in the regulation of plant immunity are being characterized and will be presented.
Reactive Oxygen Species as a Signaling Nexus in Receptor Kinases Interactions Networks

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In plants communication between cells and the extracellular environment is largely controlled by Receptor Kinases (RKs), where the Leucine-Rich Repeat Receptor Kinases (LRR-RKs) and the Cysteine-Rich Receptor-Like Kinases (CRKs) represent more than two-thirds of all RKs in Arabidopsis. Moreover, the Reactive Oxygen Species (ROS) also play a critical role in the communication between the environment and the interior of the cell and its generation is one of the most common responses to different environmental challenges. A long-standing question is what are the ROS extracellular sensors that integrate seemingly independent RKs signalling to produce optimal growth and immune responses. CRKs have frequently been associated with ROS signalling and processes involving ROS accumulation. One potential mechanism of ROS-sensing by CRKs involves redox-mediated modifications in the extracellular domain (ECD) that modulate interactions with other RKs and downstream signalling. Alternately, CRKs may also bind a ligand that is oxidatively modified resulting in RKs interactions. Either mechanism would suggest that the presence of ROS modulates the physical interactions between CRKs and LRR-RKs upstream of signalling. Here, we will present how using systems biology, multi-omics approaches, quantitative biochemistry, and cell biology, we are planning to explore how signalling networks of RKs influence and are influenced by ROS signalling.
Targeting Post Translational Modifications to open the black box
Pattern Recognition Receptor Signaling

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Pattern recognition receptors (PRRs) play a key role in the first line of defense in plant innate immunity. PRR binding of their cognate ligand, so called pathogen-associated molecular patterns (PAMP), triggers a signaling network that ultimately results in an immune response. Despite recent advances, it has still remained largely an open question how activated PRR are connected to downstream defense activation. However, it is evident that changes in phosphorylation play a major role and changes in ubiquitination play an emergent role. We have used quantitative phosphoproteomics approaches to identify a large array of verified and potential components involved in PRR signaling. Some of the earliest changes in phosphorylation, immediately downstream of activated PRRs, were identified on receptor like cytosolic kinase, mitogen activated protein kinase kinase kinases and calcium dependent protein kinases. Our initial analysis using a ubiquitin-remnant enrichment approach suggests that PRRs as well as immediate downstream components of PRR signalling also become rapidly ubiquitinated. To unravel the interplay between this two post translational modifications in PRR signalling we are using targeted proteomics. By measuring PAMP-triggered temporal changes in both phosphorylation and ubiquitination on components of the PRR signaling network we hope to sign a light on the black box in PRR signaling.
Over the rainbow: a practical guide for fluorophore selection in plant FRET experiments

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Receptor-like kinases and receptor-like proteins often interact in combinatorial manner, depending on the tissue identity, membrane domain, or endo- and exo- genous cues. Same RLKs or RLPs can produce different signalling outputs depending on the composition of the receptor complexes they are involved in. Investigation of their interaction partners in a spatial and dynamic way is therefore of prime interest to understand their functions. This is however limited by the technical complexity of assessing it in endogenous conditions. A solution to close this gap is to assess protein interaction directly in the relevant tissues at endogenous expression levels using Förster resonance energy transfer (FRET). The ideal fluorophore pair for FRET must however fulfil specific requirements: consequent overlap of the emission and excitation spectra of the donor and acceptor respectively; allow proper folding, activity, and localisation of the fusion proteins; be photostable in plant cells. Additionally, to apply FRET in plant tissues, the donor must yield sufficient photon count at near-endogenous protein levels. Although many fluorescent proteins were reported to be suitable for FRET experiments, only a handful were actually described in plants and comparative data are scarce. We have therefore undertaken a comparison of several popular fluorescent tags and assessed their usability to study RLK interaction by lifetime fluorescence imaging (FLIM) FRET in *N. benthamiana* as a prerequisite for the setup of FRET measurements in Arabidopsis.
Sensing of 3-hydroxy fatty acid metabolites by the LORE receptor complex

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Sensing of microbe-associated molecular patterns (MAMPs) by cell-surface immune receptors activates pattern-triggered immunity. Previously, we identified the S-domain receptor-like kinase LORE (LipoOligosaccharide-specific Reduced Elicitation) as a key component required for immune sensing of bacterial lipopolysaccharide (LPS) preparations. Recently, we demonstrated that LORE does not sense LPS but synthetic and bacterial medium chain 3-hydroxy fatty acid (mc-3-OH-FA) metabolites that co-purify with LPS (1). mc-3-OH-FAs are sensed in a chain length-specific manner with free (R)-3-hydroxydecanoic acid representing the strongest elicitor. Apparently, LORE binds mc-3-OH-FAs directly. Candidate binding sites are currently evaluated through biochemical and genetic studies. To mechanistically resolve how the LORE receptor complex and downstream signalling is activated upon mc-3-OH-FA elicitation we identify LORE interactors and assess their role in LPS immune sensing. We show that LORE does not require any of the well-known co-receptors but forms homodimers independent of elicitation. LORE signalling attenuation is mediated through a Plant U-Box-dependent feed-back module. Downstream of LORE, mc-3-OH-FA-induced signal transduction converges on common signalling hubs to activate typical immune responses. LORE loss- and gain-of-function approaches reveal a role for LORE in pre-invasion immunity against Pseudomonas syringae infection.

Poster presentations
Regulation of RALF peptide processing by the subtilase S1P during immunity

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Plants have evolved a vast repertoire of cell-surface receptor kinases (RKs) which allow them to cope with an ever-changing environment. A number of plant pattern recognition receptors (PRRs) are RKs that recognize pathogen-associated molecular patterns (PAMPs) to trigger pattern-triggered immunity (PTI). PRRs form dynamic complexes with other RKs at the plasma membrane to activate immune responses. For instance, FLAGELLIN-SENSING 2 (FLS2) perceives bacterial flagellin and associate with the co-receptor BRASSINOSTEROID-INSENSITIVE 1-ASSOCIATED RECEPTOR KINASE 1 (BAK1). Recently, our laboratory identified that the malectin-like RK FERONIA (FER) associates with FLS2 and BAK1 to regulate positively their complex formation and thus immunity (Stegmann et al., 2017). Interestingly, this function of FER is hindered upon perception of its ligand RAPID ALKALINIZATION FACTOR 23 (RALF23), an endogenous peptide produced upon proteolytic cleavage by the subtilase SITE-1-PROTEASE (S1P) (Stegmann et al., 2017). Notably, S1P-mediated RALF23 cleavage is increased upon PAMP perception (Stegmann et al., 2017), as part of a proposed negative feedback regulation. We will present recent results trying to shed light on the molecular mechanisms underlying the increased S1P-dependent RALF23 cleavage during PTI.
MAKR3 is a novel regulator of shoot gravitropic response

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Membrane-localized Receptor-Like Kinases (RLKs) are key determinants of plant architecture and need to be tightly regulated during development and adaptation to changing environmental conditions. Negative regulation of RLKs by inhibitory intracellular proteins is a process widely studied in animals but still an emerging field in plants. BKI1 (BRI1 kinase inhibitor 1), a negative regulator of the brassinosteroid receptor, is one of the best described RLK inhibitor in plants and is the founding member of the Membrane Associated Kinase Regulators (MAKR) family. Because MAKR proteins are putative RLK inhibitors, we used MAKR overexpression (OxMAKR) in order to reveal phenotypes mimicking those of the loss-of-function of their targeted RLKs. In particular, OxMAKR3 is involved in the shoot gravitropic response and, its lateral inflorescences grow downward instead of upward, suggesting a role of MAKR3 in the modulation of lateral inflorescences gravitropic set-point angle. These results suggest that MAKR3 may target a yet unknown RLK involved in shoot gravitropism. Next, we conducted a structure-localization-function approach to determine how MAKR3 functions at the molecular/cellular levels. We showed that MAKR3 localizes to the plasma membrane (PM) by electrostatic interactions through a polycationic region present at the MAKR3 N-terminus part of the protein. In addition, we showed that PM localization as well as the C-terminal kinase-interacting peptide are required for MAKR3 function.
A phosphoproteomics approach to unravel the IDA signalling pathway

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The signalling system comprising the related receptor-like kinases HAESA (HAE) and HAESA-LIKE2 (HSL2), SERK co-receptors, and their proline-rich peptide ligand INFLORESCENCE DEFICIENT IN ABSCISSION (IDA) induces cell separation during floral organ abscission and lateral root emergence¹,²,³. Activation of the receptors leads to phosphorylation of a MAP kinase cascade including MKK4 and 5 and MAPK3 and 6⁴. Additional signalling components include KNOX homeodomain transcription factors thought to regulate the expression of genes encoding cell wall remodelling enzymes responsible for the cell separation event⁵. The IDA signalling pathway is also activated by biotic and abiotic stresses and we have shown that the IDA peptide induces a receptor-dependent production of extracellular reactive oxygen species (ROS)⁶. Here we show that IDA also induces an increase in cytosolic Ca²⁺ concentration. With the aim of identifying proteins downstream of IDA perception by HAE and HSL2 that can modulate stress responses as well as cell wall modifications, we have performed a phosphoproteomics experiment. Floral abscission zone tissue from the ida mutant, IDA over-expression lines, the hae hsl2 double mutant and wild type at different developmental stages was collected and subjected to a phosphoproteomics workflow, leading to the identification of differentially phosphorylated proteins between the different genotypes. Results from these experiments will be presented.

Computational modeling identifies PRRs ectodomains recognizing glycan-based DAMPs/MAMPs activating Arabidopsis immune responses

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Fungal and plant cell walls have been selected by the plant immune system as a source of Microbe-Associated Molecular Patterns (MAMPs) and Damage-Associated Molecular Patterns (DAMPs) that are perceived by host Pattern Recognition Receptors (PRRs) triggering immune responses. Arabidopsis has more than 700 PRR coding genes, but only a reduced number of them have their ligands characterized. Moreover, from the vast number of ligands that PRRs can bind, those containing carbohydrate moieties are poorly studied, and only a handful of PRR/glycans pairs have been determined\textsuperscript{1,2}. In order to identify additional PRR/glycan complexes, we have developed a computational protocol based primarily on Molecular Dynamics. This method predicted some PRRs/glycans pairs that were tested by determining the \textit{in vivo} immune response in \textit{prr} mutants upon treatment with the corresponding glycan pair. These analyses demonstrated that there was a correlation between the theoretical modeling data and the \textit{in vivo} immune responses activated by some predicted PRR/glycan pairs. To further validate these interactions as well as to refine the computational protocol’s parameters, protein purifications followed by ITC experiments were performed. These analyses confirmed some interactions as well as contradicted others, allowing the refinement of the computational protocol and producing new clues in the grounds of protein-glycan binding prediction which should contribute to accelerate the discovery of novel ligands of glycan nature and the characterization of plant immune responses activated by these novel DAMPs/MAMPs.

The root morphological change of white lupin under a series of CLE supply

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The legume white lupin (*Lupinus albus*) is a model crop which forms cluster root (CR), releases carboxylates, and then mobilizes and acquires sparingly soluble soil orthophosphate (Pi) under phosphate-deficient conditions. However, the signaling involved in the formation of CR is not clear yet. The initiation of CR is very similar with that of lateral roots, and some peptide signalings were reported to be involved with the formation of lateral roots. In addition, CEP was reported to inhibit the growth of CR under low phosphorus (P). Therefore, we hypothesize that CLE was also involved in the formation of CR. To test the effect of CLE peptides on the CR formation of white lupin, a series of CLE peptides that were found in the RNAseq database of white lupin were chosen and added to the hydroponic pot with (25 µM) and without P supply (0 µM). Root morphological characteristics and shoot P concentrations of white lupins were measured. Interestingly, we found out that when no P added, CLE25 significantly decreased the number of CR, and CLE27 changed the shape of CR. These results confirmed our hypothesis, however, overexpressed and deletion of CLE 25 and 27 are needed to confirm and detail these results.
What determines the composition of receptor complexes in nanodomains of the plasma membrane?

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The small leucine-rich repeat receptor kinase (LRR-RK) BRASSINOSTEROID INSENSITIVE 1 (BRI1)-ASSOCIATED KINASE (BAK1) is known as a general regulator of many other LRR-RKs by acting as a co-receptor and positive regulator of different ligand-binding receptors. The best-studied BAK1 interaction partners are FLAGELLIN SENSING 2 (FLS2), which senses bacterial flagellin, and BRI1, the major Arabidopsis brassinosteroid receptor. FLS2 and BRI1 reside in different nanodomains of the plasma membrane, indicating that receptor-specific nanoclusters are formed with BAK1. In our lab, two novel LRR-RKs have been identified that interact with BAK1 – BAK1 INTERACTING RECEPTOR-LIKE KINASE 2 (BIR2) and BIR3. In mass spectrometry interactome screens with BIR2 and BIR3 a SMALL MEMBRANE ASSOCIATED PROTEIN (SMAP), a common membrane localized interactor, was identified. SMAP interacts with diverse immune receptor classes, affects immune receptor signaling and might function as the determinant of immune receptor nanocluster composition. To investigate the involvement of SMAP in nanocluster formation of BAK1, BIR2, BIR3 and ligand binding receptors such as FLS2 or BRI1, we analyze the mobility, the specific localization and the interaction of the individual receptor kinases in smap mutant background compared to wild type by single particle tracking photoactivated localization microscopy (sptPALM) and single molecule Förster resonance energy transfer (smFRET).
A cell wall-anchored complex nucleates plasma membrane receptor kinase nanoscale dynamics

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Cell surface receptors survey and relay information to ensure the development and survival of multicellular organisms. In the model plant Arabidopsis thaliana, the malectin-like receptor kinase FERONIA (FER) regulates myriad of biological processes to coordinate development, reproduction and immunity. We recently showed that FER positively regulates immune signaling by controlling the ligand-induced complex formation between FLAGELLIN-SENSING 2 (FLS2) and its co-receptor BRASSINOSTEROID INSENSITIVE 1-ASSOCIATED KINASE 1/SOMATIC EMBRYOGENESIS RECEPTOR KINASE 3 (BAK1/SERK3). This function of FER is inhibited upon binding to the peptide RAPID ALKALINIZATION FACTOR 23 (RALF23) (Stegmann et al., 2017). Here, we demonstrate that the function of the FER-RALF23 regulatory module is conserved across several SERK-dependent LEUCINE RICH REPEAT – RECEPTOR KINASE (LRR-RK) - based signaling pathways involved in growth and development. Additionally, we show that cell wall-associated LRR EXTENSIN 3/4/5 proteins are required for FER-dependent regulation of LRR-RK signaling. Using super-resolution microscopy and single-particle tracking, we visualize that FER regulates LRR-receptor kinase plasma membrane nanoscale dynamics. We therefore propose that FER connects the cell wall and the plasma membrane to act as an anchor enabling the nanoscale nucleation of LRR-RK complexes during plant signaling.
CrRLK1L receptor-like kinases HERK1 and ANJ are female determinants of pollen tube reception

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Communication between the gametophytes is vital for angiosperm fertilisation. Multiple CrRLK1L-type receptor kinases prevent premature pollen tube burst, while another CrRLK1L protein, FERONIA (FER), is required for pollen tube burst in the female gametophyte. We report here the identification of two additional CrRLK1L homologues, HERCULES RECEPTOR KINASE 1 (HERK1) and ANJEA (ANJ), which act redundantly to promote pollen tube burst at the synergid cells. HERK1 and ANJ localise to the filiform apparatus of the synergid cells in unfertilised ovules, and in herk\textsuperscript{1} anj mutants a majority of ovules remain unfertilised due to pollen tube overgrowth, together indicating that HERK1 and ANJ act as female determinants for fertilisation. As in fer mutants, the synergid cell-specific, endomembrane protein NORTIA (NTA) is not relocalised after pollen tube reception; however, unlike fer mutants, reactive oxygen species levels are unaffected in herk\textsuperscript{1} anj double mutants. Both ANJ and HERK1 associate with FER and its proposed co-receptor LORELEI (LRE) \textit{in planta}. Together, our data indicate that HERK1 and ANJ act with FER to mediate female-male gametophyte interactions during plant fertilisation.
Three-fluorophore FRET-FLIM enables the study of trimeric protein interactions and complex formation at nanoscale resolution in living plant cells

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Concise integration of differentiation and growth processes is essential for plant life. We recently demonstrated that RECEPTOR LIKE PROTEIN 44 (RLP44) interacts with the brassinosteroid receptor BRI1, the phytosulfokine receptor PSKR1 as well as their coreceptor BAK1 in the plasma membrane (PM) of plant cells and orchestrates vascular cell fate in the Arabidopsis root [Holzwarth et al. PNAS 115, 11838 (2018) and bioRxiv 605923 (2019)]. Here we provide evidence by quantitative in vivo intensity/spectrum- and FLIM-based FRET approaches, that RLP44, BRI1 and BAK1 form a trimeric complex in the PM of N. benthamiana epidermal leaf cells, with respective distances to each other below 20 nm. Remarkably, even though BRI1 and PSKR1 do not interact directly, in the presence of RLP44 they get in close proximity (below 20 nm distance). However, the formation of such a complex is not possible with FLS2 instead of PSKR1 as third component in addition to RLP44 and BRI1.

With our three-fluorophore FRET technique, especially with FRET-FLIM, we now can study complex interactions in the PM with high spatio-temporal resolution. Furthermore, as the fluorescence lifetime of the donor is monitored in FRET-FLIM, our method circumvents the extensive calculations necessary when employing intensity/spectrum-based FRET. In future, our method will provide valuable insights in the dynamics of protein complex composition and subcompartmentalization in the PM of living plant cells.
Small signaling peptides trigger adaptation to abiotic stresses

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Plants possess fascinating abilities to monitor the environment and to adapt their physiological parameters to ensure the optimal growth. Water availability, temperature, nutrients distribution in the soil are among other environmental conditions that shape the plant growth and have to be efficiently communicated within the plant. It has been shown, that small signaling peptides play a key role in drought stress as well as in nitrogen and phosphate availability signaling. My group is interested to identify new peptide-receptor dependent pathways that mediate the stress adaptations. We create a collection of peptide’s promoter-reporter lines that will be screened for different stresses as well as we use the publically available transcriptomic data and we establish a proteomics-based approach. We isolate the peptide candidates and we functionally characterize them. I will present our strategy and preliminary data from our experiments.
YDA MAP3K is a positive regulator of tomato immune responses

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Mitogen-activated protein kinases (MAPK) cascades are conserved signalling modules that play a pivotal role transducing developmental cues and environmental signals into cellular responses. Expression of a constitutively active MAP3K called YDA (CA-YDA plants) confers broad-spectrum disease resistance in Arabidopsis. Despite canonical immune pathways are not altered in CA-YDA plants, many defense-related genes are upregulated suggesting that YDA modulates a novel immune pathway. To evaluate the biotechnological applications of YDA in crop disease resistance, AtCA-YDA was overexpressed into Solanum lycopersicum. The tomato transgenic plants exhibited up to 25-fold AtCA-YDA expression without a negative impact on their fitness and fruit production. Tomato plants overexpressing AtCA-YDA showed a reduction in stomata index as it has been described in Arabidopsis AtCA-YDA plants. Notably, AtCA-YDA expression on tomato conferred enhanced resistance to the bacterium Pseudomonas syringae pv. tomato DC3000 (Pto). Comparative RNAseq analysis of wild type and AtCA-YDA tomato plants identify a subset of defense-associated genes that are up-regulated in AtCA-YDA lines. Moreover, impairing tomato YDA orthologs, SlYDA1 and SlYDA2, by CRISPR/Cas9 leaded to increased susceptibility to Pto. These results indicate that the defence signaling pathways regulated by YDA are functional in tomato, and that the fine tuning of YDA activity might be used as a biotechnological tool to enhance crops disease resistance.
Identification of new *Cuscuta* factors

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Parasitic plants are a constraint on agriculture worldwide. Plants of the genus *Cuscuta* spp. are obligate holoparasites with a broad host spectrum for nearly all dicotyledonous plants. As leaf- and rootless plants, *Cuscuta* spp. wind around stems of host plants and penetrate host tissue with haustoria. They directly connect to the vasculature and withdraw water, nutrients and carbohydrates. Thus, the haustorium development and the establishment of a connection to the host represent essential steps in the parasite’s life cycle.

Little is known concerning the development of such host-parasite connections on molecular level. In this project we want to gain knowledge about specific molecular signals of *Cuscuta* spp. that get sensed by host plants and manipulate them towards susceptibility or resistance, respectively. On the host plant side, we are interested in identifying receptors that recognize parasitic molecules and further induce cellular signaling programs related to susceptibility or development. To identify novel *Cuscuta* factors that reprogram the host cellular signaling, we cloned the promoters of host genes that are upregulated at *Cuscuta* infection sites and fused them to the luciferase reporter gene. In a promotor::luciferase based bio-assay, we now screen different haustorial *Cuscuta*-extract preparations for bioactive Cuscuta factors.
Reconstructing the flagellin response in an early land plant

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Evolutionary molecular plant-microbe interactions (EvoMPMI) is an arising field which closes the gap between molecular phytopathology and evolutionary studies. Little is known about how the first land plants coped with competition and potentially aggressive contemporaries. The starting condition of the ongoing host-pathogen race is thus unknown.

We want to use a model organism for basal land plants, Marchantia polymorpha, to reconstruct the perception of a common Microbe Associated Molecular Pattern (MAMP): flagellin. The most prominent immunogenic epitope of flagellin, flg22, is perceived by the leucine-rich repeat receptor kinase (LRR-RLK) FLS2 in many higher plants. M. polymorpha encodes a number of LRR-RLKs (~90) but no homolog of FLS2. However, there is one homolog for the co-receptor, BAK1 (SERK3), which is however more closely related to SERK1/2. Using stable transformed M. polymorpha lines we want to reconstruct the perception of flagellin by step-wise complementation with genes from higher plants. We also want to investigate the function of SERK in M. polymorpha by generating mutants using the CRISPR/Cas9 approach. These results will contribute to a better understanding of the origins of the highly diversified and specialized pathogen perception capacities in higher plants.
Mind the gaps in the SCHENGEN pathway

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Plants have developed sophisticated barriers in various tissues and organs to safeguard integrity. To monitor barrier integrity, plants appear to have evolved similar systems that share signalling modules. The receptor/ligand signalling pathway initiated by SGN3/CIFs establishes the integrity of the Casparian strip (CS), a root diffusion barrier that is essential for controlling nutrient and water homeostasis. The CS starts off as aligned microdomains that eventually fuse to forge a continuous barrier. The SGN pathway is crucial to “find and seal gaps” between the microdomains. However, the mechanism that ensures perfect domain fusion is not well understood. My research aims to characterise central unknown elements in a proposed, branched SGN pathway. I intend to identify potential SGN3 co-receptors, and also to investigate the elusive role of MAPKs during CS formation. The findings will be crucial to resolve pathway features that the current linear model cannot explain. Identification of the co-receptors is necessary for the understanding of how SGN3 is activated. SGN3 also appears to be involved in embryonic cuticle and pollen coat formation. Therefore, co-receptor identification would clarify whether SGN3 perceives the same or different ligand to govern distinct barrier formation processes. MAPK cascades are activated downstream of many receptor/ligands, and could be important nodes in parallel pathways. Elucidating their function in the SGN pathway will give insights into diverse biological processes.
Functions of systemin and related peptides

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Systemin, a small peptide of 18 amino acids was the first peptide in plants found to have signaling activity. It was originally purified for its capability to induce the expression of proteinase inhibitors, which accumulate in tomato leaves after wounding or insect feeding (Pearce et al., 1991, Science; McGurl et al., 1992, Science). The discovery of the genuine systemin receptor SYR1 (Wang et al., 2018, Nature Plants) proved the importance of systemin perception in the defense of tomato plants against herbivores.

The alkalinization of Lycopersicum peruvianum cell-suspension culture (Felix et al., 1995, The Plant Journal) provides a convenient, sensitive and quantitative bioassay, which we employed to check for the presence of systemin-related species in tomato tissue. Surprisingly, no systemin-type of activity was observed in crude extract of tomato leaves. Furthermore, subsequent treatment with the synthetic peptides, systemin or flg22, demonstrated that the crude extract contained factors which specifically inhibited the activity of systemin. Purification and characterization revealed a peptide with structural and chemical similarity to systemin that competes with systemin for binding to the systemin receptor SYR1.

The aim of my project is to determine the physiological function of the agonistic and antagonistic systemin peptides, whether these peptides and their interaction play a role in the defense mechanism of the plant, or are involved in a different, e.g. developmental, pathway.
Differential involvement of receptor like cytoplasmic kinases in leucine rich repeat receptor kinase and leucine rich repeat receptor like protein signaling

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Leucine rich repeat receptor kinases (LRR-RK) make up a large family of receptors which play diverse roles in defense and development in plants. LRR receptor like proteins (LRR-RPs) are are highly similar to LRR-RKs, but lack an integral kinase domain. Instead, RLPs dimerize with the LRR-RK SOBIR1 to form "bimolecular RLKs." The pattern recognition receptors FLS2 and RLP23 represent prototypical members of the LRR-RK and LRR-RP families, respectively. Comparative analysis of signaling mediated by FLS2 and RLP23 revealed overlapping, but distinct immune outputs triggered by the two pathways. Early responses such as reactive oxygen species production and MAP kinase activation were generally more rapid and stronger upon FLS2 activation than upon RLP23 activation. In contrast, RLP23 signaling resulted in higher production of ethylene, camalexin, and salicylic acid. Screening of selected candidates involved in plant immunity revealed at least three receptor like cytoplasmic kinases (RLCK) subfamily VII proteins as well as potential downstream regulators which play divergent roles in LRR-RLP and LRR-RK signaling. Our studies suggest that LRR-RPs and LRR-RKs involved in plant immunity employ distinct but overlapping signaling pathways and that RLCKs play a key role in determining specific immune outputs.
A peptide pair coordinates regular ovule initiation patterns with seed number and fruit size

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Ovule development in Arabidopsis thaliana involves a pattern formation process which ensures that ovules are regularly arranged in the pistils to reduce competition for nutrients and space. Mechanisms underlying pattern formation in plants, such as phyllotaxis, flower morphogenesis or lateral root initiation, have been extensively studied, and genes controlling the initiation of ovules have been identified. However, how a regular spacing of ovules is achieved is not known. Using genome-wide association studies combined with quantitative trait locus analysis, we found that the spacing of ovules in the developing fruits is controlled by two secreted peptides, EPFL2 and EPFL9, and their receptors from the ERECTA family that act from the carpel wall and the placental tissue. We found that a signalling pathway controlled by EPFL9 from the carpel wall and acting through the LRR-receptor kinases ER, ERL1 and ERL2 promotes fruit growth. Regular spacing of ovules depends on EPFL2, which is also expressed in the carpel wall, and in the inter-ovule spaces where it acts through ERL1 and ERL2. Loss of EPFL2 signalling results in shorter fruits and irregular spacing of ovules or even ovule twinning. The EPFL2 expression pattern between ovules is negatively feedback regulated by auxin which accumulates in the arising ovule primordia. We propose here that the auxin-EPFL2 signalling module evolved to control the initiation and regular, equidistant spacing of ovule primordia, which serves to minimise competition between developing seeds. Together, EPFL2 and EPFL9 coordinate ovule patterning and thereby seed number with fruit growth through a set of shared receptors.
Molecular cues from *Cuscuta*: their perception and effects on host plants

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Parasitic flowering plants occupy a specialized niche in the plant kingdom. They obtain inorganic and organic nutrients, as well as water, from their hosts. The parasite *Cuscuta reflexa* belongs to the genus *Cuscuta* which comprises about 100-150 species. *C. reflexa* is a holoparasite consisting of thread-like vines which coil around the shoots of potential host plants. Upon infection, the parasite produces specialized haustoria which penetrate the aboveground parts of plants. Therefore the host cell wall needs to be overcome followed by the fusion with the host’s xylem and phloem. Receptors, molecular cues as well as susceptibility-related signaling of this plant-plant dialogue remain elusive.

To get any idea about the susceptibility related signaling mainstream, we investigate the role of phytohormones in hosts during the infection. With the help of the COLORFUL biosensor system, which comprises several fluorescence proteins under the control of phytohormone-sensitive promoters in transgenic *Arabidopsis* lines, we aim to monitor the diverse phytohormone activities while *Cuscuta* haustorium penetration. Additionally, we examine the role of yet unknown parasitic molecular triggers and their perception. For this we compared tomato species exhibiting two entirely different phenotypes. In the resistant species *Solanum lycopersicum* one resistance receptor was already identified which recognizes a parasite-associated molecular pattern and induces defense-related responses. In contrast, *Solanum pennellii* a susceptible tomato species does not display defense responses upon treatments. By comparison of sequenced genome parts in recombinant inbred lines, we mapped a further locus that is important for the tomato resistance against *C. reflexa*, and now try to identify the corresponding resistance genes.
Phosphoproteomics analysis of the systemin signaling pathway

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Systemin is a small peptide with important functions in plant wound response signaling. To elucidate systemin perception and signal transduction mechanisms, phosphoproteomic profiling was performed to reconstruct a systemin-specific kinase/phosphatase signaling network. Time course analyses revealed early systemin-induced events at the plasma membrane, such as dephosphorylation of the H⁺-ATPase, and phosphorylation of NADPH-oxidase and Ca²⁺-ATPase. Later responses included transient phosphorylation of small GTPases and vesicle trafficking proteins, as well as transcription factors. Based on a correlation analysis of systemin-induced phosphorylation profiles, substrate candidates were predicted for systemin-responsive kinases and phosphatases. A regulatory circuit was predicted for the regulation of the plasma membrane H⁺-ATPase. In this regulatory model, H⁺-ATPase LHA1 is rapidly dephosphorylated at its C-terminal regulatory residue by phosphatase PLL5, resulting in extracellular alkalization within two minutes of systemin treatment. LHA1 is re-activated by MAP-Kinase MPK2 later in the systemin response. MPK2 showed increased phosphorylation at its activating TEY-motif at 15 minutes of treatment and the predicted interaction with LHA1 was confirmed by in-vitro kinase assays. Our data set provides a valuable resource of proteomic events involved in the systemin signaling cascade with a focus on the prediction of substrates to systemin-responsive kinases and phosphatases.
Hydroxyproline-dependent processing of CLE40 from Arabidopsis

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Plant peptide hormones are essential for regulation of plant growth and development. Peptide hormones are often synthetized as larger pre-pro-proteins that require proteolytic processing and other post-translational modifications within the secretory pathway. One of these small secreted peptides is CLE40 (CLAVATA3/EMBRYO SURROUNDING-REGION RELATED 40) which is expressed in root cells and involved in stem cell differentiation and proliferation. The mature CLE40 peptide consists of 13 amino acids and has to be released from the C-terminus of the precursor. Further, the peptide carries one hydroxyproline. However, the processing mechanisms and the activating proteases are unknown. Subtilisin-like proteases (subtilases, SBTs) are promising candidates for CLE40 cleavage. Here, we focus on the identification of specific SBTs required for the CLE40 processing in Arabidopsis. We address the subcellular site of processing and will present data indicating compartment-specific activation of CLE40 peptide from its precursor. We show that functional redundant SBTs regulate the activity of the CLE40 peptide. We describe a mechanism of proline-dependent activation and inactivation by SBTs and present data leading to the hypothesis that CLE40 proline hydroxylation is a critical step that regulates peptide processing rather than receptor binding and signaling.
Study the biological function of a group of cysteine-rich peptides

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Successful double fertilization requires a series of intensive communications between male and female gametophytes. After pollen grains land on the stigma, pollen tubes emerge and are precisely navigated to grow toward female gametophyte (embryo sac) after interacting with seven different female tissues or cells. A large number of genes encoding small peptides have been identified to highly expressed in male and female tissues, implying that these small peptides may play important roles in male-female interactions.

According to RNA-seq profiles of both male and female tissues in Arabidopsis, we found a group of genes encoding cysteine-rich peptides, named FLM (Flora’s Mind), that are highly expressed in the semi-in vivo pollen tubes. Expression pattern analysis revealed that transcription of FLM genes was induced 2 hours after pollination (HAP) in in vivo-germinated pollen tubes, but not detectable in the in vitro-germinated pollen tubes, suggesting that FLM possibly function in male-female interaction. Interestingly, phylogenetic analysis showed that FLM genes are divided into two groups, one species-specific and the other one with no species specificity. Currently we are adopting CRISPR/Cas9 technology to knock out each group of the peptide genes to characterize their biological function.
A TIR-NBS-LRR protein is necessary for BAK1 autoimmune phenotypes and links BAK1-mediated cell death to effector triggered immunity

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The co-receptor BRASSINOSTEROID INSENSITIVE1-ASSOCIATED RECEPTOR KINASE1 (BAK1/SERK3), regulates different signaling pathways including growth and development, immune response, and cell death control by directly interacting with and positively regulating multiple ligand binding receptors. The BAK1-interacting RK BIR3 can prevent BAK1-ligand binding receptor interaction by directly interacting with both ligand-binding receptors and BAK1 (and all members of the SERK family). The interaction of BIR3 with SERKs stabilizes BAK1 and its closest homolog BKK1/SERK4. The interactome of BIR3 revealed a BIR3 interacting TIR-NBS-LRR (TNL) protein (BIT1). Double mutants in bit1 bak1 show reduced cell death compared to bak1 single mutants upon inoculation with the necrotrophic fungus Alternaria brassicicola. Double mutants in bir3 bak1 show a severe dwarf phenotype and spontaneous cell death. Our investigations revealed that mutations in bit1 also suppress bir3bak1-mediated cell death. Both bak1 and bak1 bir3-mediated cell death can be partially suppressed by mutations in ENHANCED DISEASE SUSCEPTIBILITY (eds1), a common downstream component of TNLs. Taken together, BIT1 interacts with BAK1 and BIR proteins, is necessary for BAK1-mediated cell death and links BAK1 to TIR-NBS-LRR-mediated cell death usually involved in effector triggered immunity. BIT1 likely guards the integrity of BAK1 and BAK1 BIR complexes and initiates autoimmune cell death when BAK1 complexes are impaired.
A Role for N-linked Protein Glycosylation during Pollen Tube Reception

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The crucial role of receptor-like kinases (RLK) for pollen tube reception was uncovered through the isolation of the feronia (fer) mutant, where pollen tubes fail to rupture and keep growing inside the embryo sac (Huck et al., 2003). Forward genetic screen for fer-like phenotypes led to discovery of two mutants impaired in the early steps of N-glycosylation. TURAN (TUN) encodes a uridine diphosphate (UDP)-glycosyltransferase superfamily protein and EVAN (EVN) a dolichol kinase (Lindner et al., 2015). It was also shown that mutations affecting the oligosaccharyltransferase subunit (OST3/6) complex in the artumes (aru) mutant disrupts exclusively the recognition of interspecific pollen tubes (Müller et al., 2016). We have studied whether other endoplasmic reticulum (ER) or Golgi localized enzymes of the N-glycosylation pathway are important for pollen tube recognition. We have observed that mutations of either early- or late-stage enzymes of the pathway affect interspecific pollen tube reception. It is known that FER has ten predicted N-glycosylation sites (Lindner et al. 2012), therefore we are currently preforming systematic mutagenesis of those sites. We will analyse whether impaired N-glycosylation impacts FER protein stability or if they have a role in proper protein-carbohydrate and carbohydrate-carbohydrate interactions and molecular recognition. Our results show a vital role of proper N-glycosylation during plant sexual reproduction.
Late presentations
MtSSPdb - the Medicago truncatula Small Secreted Peptide Database

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Small Secreted Peptides (SSPs) play many roles in e.g. development, stress adaptation or nutrient acquisition. The model legume Medicago truncatula (Mt) is closely related to important forage/food legumes. Since legumes fix atmospheric N2 in root nodules through symbiosis with rhizobia, they are a linchpin for sustainable agriculture. We developed MtSSPdb (http://mtsspdb.noble.org/), a database that hosts genomics and transcriptomics data, with a focus on SSP genes from Mt. MtSSPdb has three main components: (i) re-annotated gene models and annotations of Mt genes, including 4,439 putative/known SSP genes and related family information, (ii) the SSP Gene Expression Atlas (SSP-GEA), which hosts >440 RNA-seq libraries derived from stress or hormone treatments, nodule development, symbiotic interactions and various plant organs. (iii) tools for analysis of expression profiles, differential and co-expression, GO/KEGG enrichment pathway analyses, a SSP gene prediction tool and BLAST. MtSSPdb also hosts information about a synthetic peptide (syP) library, and the syPs’ effects on 24 root and nodule-traits in Mt, Arabidopsis and switchgrass. MtSSPdb is the first database in plants that integrates comprehensive SSP information, large-scale gene expression data and experimental growth data from syP treatments. The database will be expanded to include SSP genes from Arabidopsis thaliana and Brachypodium distachyon. MtSSPdb has potential to become the go-to database for plant SSPs.
Participants of the
VII. European Workshop on Plant Peptides & Receptors

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