

Keynote Lecture - ISPS2019-101

Balancing variability and stability in leaf patterning by multiple auxin response regulators

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Auxin signal transduction is mediated by the antagonistic activity of transcriptional activators and inhibitors. Both activators and inhibitors belong to gene families with partially redundant activities, but the biological importance of this complexity is not clear. We addressed this question using tomato leaf development as a model, by generating mutants in multiple auxin-response components. In developing compound tomato leaves, auxin promotes leaflet formation and blade growth, and in the intercalary regions between leaflets, auxin response is inhibited by the Aux/IAA protein ENTIRE (E). *e* mutants form simple leaves due to ectopic blade growth in the intercalary domain. Using this unique loss-of-function phenotype, we identified the contribution of specific ARFs to the *e* phenotype. Mutations in *SIMP*, *SIARF19A* and *SIARF19B*, but not the closely related *SIARF7*, reduced leaf blade and suppressed the *e* phenotype in a dosage-dependent manner that correlated with their relative expression, leading to a continuum of shapes. While single *e* and *slmp* mutants affected blade growth in an opposite manner, leaves of *e slmp* double mutants were similar to the wild type. However, leaf shape of *e slmp* was less stable than the wild type, and showed increased sensitivity to changes in auxin level. Therefore, the existence of multiple auxin-response inhibitors and activators stabilizes the developmental output of auxin, and tuning their activity enables shape variability. The increased complexity of auxin response therefore balances stability and flexibility in leaf patterning.

ISPS2019-102

Solving the riddle of the evolution of Shine-Dalgarno based translation in chloroplasts

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The chloroplast, a photosynthetic organelle found in all plant and algae species, originates from an ancient event in which a cyanobacterium was engulfed by a larger eukaryote. Thus, modern chloroplasts still harbor a bacterial-like genome and carry out all stages of gene expression, including mRNA translation by a 70S ribosome. However, the Shine-Dalgarno model, which predominantly regulates translation initiation by base-pairing between the ribosomal RNA and the mRNA in model bacteria genera, was reported to have ambiguous effects on chloroplast gene expression. Here we show that while the Shine-Dalgarno motif is clearly conserved in proteobacterial mRNAs, its general absence from chloroplast mRNAs is common to cyanobacteria as well, promoting the idea that the evolutionary process of reducing the centrality of the Shine-Dalgarno mechanism began well before chloroplast endosymbiosis. A main difficulty in understanding this decline in Shine-Dalgarno generality is the strict conservation of the ribosomal RNA anti-Shine-Dalgarno element. By computational simulation we show that upstream point mutations render the ribosomal RNA local folding in chloroplasts, creating significantly tighter complexes around the anti-Shine-Dalgarno nucleotides, which in turn reduce the probability of ribosome binding via the Shine-Dalgarno mechanism. To validate our model, we expressed a mCherry gene harboring a Shine-Dalgarno motif in the *Chlamydomonas reinhardtii* chloroplast. We show that co-expressing it with a 16S ribosomal RNA, modified according to our model, significantly enhances its expression compared to co-expression with an endogenous 16S gene.

ISPS2019-103

The proof is in the bulb: glycerol influences key stages of lily development

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A geophyte's bulb comprises both food reserves and important developmental history, which may affect its whole growth. In Easter lily (*Lilium longiflorum*), bulb size is associated with the plant's flowering pathway- vernalization or photoperiod- and also affects sprouting, flower quality and abortion rate. The aim of this study was to investigate the reasons for the major physiological differences between large and small bulbs. Lily bulbs start their development from secondary meristems along the stem, with large bulbs being heavier and bearing more scales than small ones. Peeling the outer scales of a large bulb converts its physiological responses into those of a small bulb, implying that the physiological discrepancies in plants developing from large or small bulbs are mediated by factors inherent to the bulb. We therefore performed broad analyses of the metabolite composition in the scales of bulbs subjected to temperature regimes affecting further plant development. We found a striking association between the level of glycerol, a primary metabolite mostly synthesized in the outer scales, and a delay in sprouting and flowering time, and reduction in abortion rate. Exogenous glycerol application to the bulbs before planting corroborated these results. Moreover, transcriptome analyses showed that flowering-promoting gene expression was down-regulated in the bulb after glycerol treatment, while potential flowering inhibitor as well as a dormancy-related gene expressions were up-regulated. Based on these studies we postulate that glycerol is a major factor influencing both vegetative and reproductive development in lily.

ISPS2019-104

Meristems development at the single cell level

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Plants are able to dramatically alter their body plan and regenerate from severe damage by de novo formation of meristems – organized regions of patterning and organ formation containing the plant's stem cells. Recent work has shown that meristems originate at a cooperative process from a group of 15-40 cells. The composition of these cells, and the mechanisms coordinating early steps in meristem formation remain mostly unknown. To address this question, we have established a novel model system, the tomato stem-borne root initiation. Unlike other systems, tomato generates meristems de novo from highly accessible tissue without the need for injury or hormonal perturbations, ensuring a natural development context. We isolated meristem primordia at ~40 cell stage from tomato stems, and using an optimized cell separation protocol, dissociated them to individual cells. Single-cell RNA sequencing of several hundred cells was used to profile the entire primordium at single cell resolution. Surprisingly, as early as the 40 cells, we could already identify a complex structure in the meristem primordium, with several distinct cell types and strict separation between hormone production and response. Analysis of the dynamics of multiple patterning genes uncovered unexpected parallels to shoot meristems, suggesting a possible convergence of root and shoot meristems at early initiation stages. Overall, here, we provide the first comprehensive single-cell level profiling of a forming root meristem in a natural context. We are currently extending this profile to later stages in meristem formation in order to construct a spatiotemporal trajectory of all cells in the forming meristem and enhance our understanding of de novo meristem formation and plant developmental plasticity.

Keynote Lecture - ISPS2019-105

Aphid resistance in perennial soybeans: Two genomes are better than one

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Enhanced resistance to pests and pathogens, resulting from the additive effects of two sets of defensive genes, may provide a selection for polyploidy, which has arisen frequently in the course of plant evolution. The allotetraploid perennial soybean *Glycine dolichocarpa* has resistance to both *Aphis glycines* (soybean aphid) and *Acyrtosiphon pisum* (pea aphid), whereas its diploid progenitors, *Glycine tomentella* D3 and *Glycine syndetika*, show resistance to only *A. glycines* or *A. pisum*, respectively. Transcriptomic and metabolomic assays demonstrated species-specific variation in the responses of perennial soybeans to *A. glycines* and *A. pisum* infestation. Resistance to *A. pisum* feeding was associated with isoflavone accumulation, whereas resistance to *A. glycines* increased with flavone content. This observation was recapitulated in artificial diet assays, where isoflavones had a greater negative effect on *A. pisum* and flavones had a greater negative effect on *A. glycines*. Correlative analysis of gene expression and aphid resistance in the three perennial soybean species identified likely resistance (*R*) genes. The functions of two cysteine-rich receptor-like protein kinases were confirmed through overexpression and expression silencing. Together, the observed additive effects of flavonoids and *R* genes in aphid resistance support the hypothesis that allotetraploidy in perennial soybeans provides an evolutionary advantage through the combination of two plant defense systems.

ISPS2019-106

An alternative pathway for apocarotenoid production highlights the utility of the new tomato pan-genome

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The experience of flavor results from a combination of taste, texture and aroma, with the significance of the latter often underestimated. We used RNA-sequencing data of a recombinant inbred line (RIL) population, derived from a cross between *Solanum lycopersicum* cv. NC EBR-1 and *Solanum pimpinellifolium* LA2093, to map quantitative trait loci (QTL) for fruit aroma volatiles. QTLs for nine apocarotenoids, important volatiles arising from catabolism of various carotenoid pigments, were mapped to a 16-gene interval on chromosome 1. Among these genes include a fatty-acid catabolic enzyme, 13-lipoxygenase (*TomLoxC*), whose expression is tightly correlated with apocarotenoid levels. Transgenic repression of this gene in tomato and of its homologous gene in Arabidopsis, resulted in reduced apocarotenoid levels in the fruits and leaves, respectively. These results indicate a new role for this enzyme in an alternative *in vivo* pathway to apocarotenoid volatiles in addition to the well-characterized carotenoid cleavage dioxygenase (CCD) pathway. Since no differences in the *TomLoxC* promoter were seen in previous sequencing studies of LA2093, we used our novel tomato pan-genome to search for a structural variation that might explain its reduced expression. The tomato pan-genome is based on *de-novo* assembly of the tomato genome combining 725 tomato accessions, and holds additional 351 Mb of non-reference sequences. We found a rare allele of *TomLoxC* promoter that accounts for the reduced apocarotenoid phenotype. These findings expand our understanding of carotenoid catabolism in general and of volatiles production in particular, and highlight the usefulness of the tomato pan-genome for capturing alleles with important roles to breeders and researchers that have been discarded in traditional mapping-to-reference pipelines.

ISPS2019-107

MorphDB: Prioritizing Genes for Specialized Metabolism Pathways and Gene Ontology Categories in Plants

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Recent times have seen an enormous growth of "omics" data, of which high-throughput gene expression data are arguably the most important from a functional perspective. Despite huge improvements in computational techniques for the functional classification of gene sequences, common similarity-based methods often fall short of providing full and reliable functional information. Recently, the combination of comparative genomics with approaches in functional genomics has received considerable interest for gene function analysis, leveraging both gene expression based guilt-by-association methods and annotation efforts in closely related model organisms. Besides the identification of missing genes in pathways, these methods also typically enable the discovery of biological regulators (i.e., transcription factors or signaling genes). A previously built guilt-by-association method is MORPH, which was proven to be an efficient algorithm that performs particularly well in identifying and prioritizing missing genes in plant metabolic pathways. Here, we present MorphDB, a resource where MORPH-based candidate genes for large-scale functional annotations (Gene Ontology, MapMan bins) are integrated across multiple plant species. Besides a gene centric query utility, we present a comparative network approach that enables researchers to efficiently browse MORPH predictions across functional gene sets and species, facilitating efficient gene discovery and candidate gene prioritization. MorphDB is available at <http://bioinformatics.psb.ugent.be/webtools/morphdb/morphDB/index/>. We also provide a toolkit, named "MORPH bulk" (<https://github.com/arzwa/morph-bulk>), for running MORPH in bulk mode on novel data sets, enabling researchers to apply MORPH to their own species of interest.

ISPS2019-108

The discovery of a new protein family designated as ‘tandem kinase-pseudokinases (TKPs)’ and its association with plant immune responses

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Yellow rust, caused by *Puccinia striiformis* f. sp. *tritici* (Pst), is a devastating fungal disease threatening much of global wheat production. Race-specific resistance (R)-genes are used to control rust diseases, but the rapid emergence of virulent Pst races has prompted the search for a more durable resistance. Here, we report the cloning of Yr15, a broad-spectrum R-gene derived from wild emmer wheat, which encodes a putative kinase-pseudokinase protein, designated as wheat tandem kinase 1, comprising a unique R-gene structure in wheat. The existence of a similar gene architecture in 92 putative proteins across the plant kingdom, including the barley RPG1 and a candidate for Un8, suggests that they are members of a distinct family of plant proteins, termed here tandem kinase-pseudokinases (TKPs). We found that 175 out of 184 kinase/pseudokinase domains of these TKPs were associated with receptor-like kinases (RLKs), suggesting that TKPs are involved in plant defense mechanisms. A further phylogenetic analysis indicated that TKP family members originated from either gene duplication or gene fusion events, suggesting a polyphyletic origin of the TKPs. The presence of kinase-pseudokinase structure in both plant TKPs and the animal Janus kinases sheds light on the molecular evolution of immune responses across these two kingdoms.

ISPS2019-109

Aphid Induced Terpene Metabolism in *Pistacia palaestina* galls

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The aphid *Baizongia pistaciae* L. induces the formation and inhabits large, banana-like galls on terminal buds of *Pistacia palaestina* Boiss. trees (Anacardiaceae). Gall tissues accumulate high levels of terpenes, probably as part of a chemical defense form of an extended phenotype of the aphids. The terpene composition of galls is different to that present in non-colonized leaves. Galls also possess enhanced monoterpene biosynthesis capacities as compared to leaves. In this study we demonstrate that aphid colonization induce genes encoding for terpene synthases, key genes in the production of mono- and sesquiterpenes. The levels of expression of six novel Tps gene family members were up to 100 fold enhanced in galls as compared to leaves. We identified three monoterpene synthases (PpTPS210, PpTPS281 and PpTPS809) and two sesquiterpene synthases (PpTPS232 and PpTPS5060) by their functional expression in *E. coli*. PpTPS210 produced mainly alpha-pinene and lower levels of beta-pinene from geranyl diphosphate. PpTPS281 produced ()-limonene from geranyl diphosphate, while PpTPS809 produced monoterpenes such as alpha-thujene, sabinene and gamma-terpinene. PpTPS232 catalyzed the formation of sesquiterpenes such as beta-elemene, alpha- and beta-selinene from farnesyl diphosphate and PpTPS5060 catalyzed the formation of germacrene B from farnesyl diphosphate. Most of the compounds produced in vitro are present in gall tissues at higher levels than in intact leaves and were also detected at enhanced levels in enzymatic cell-free extracts derived from the respective tissues. We therefore conclude that aphids manipulate plant terpene metabolism at the transcriptional level in the induced galls.

ISPS2019-110

Breaking and Entering: Molecular Insights into Fertilization and Viral Infection of Gametophytes and Seeds

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Fertilization is an essential process for the propagation of many flowering plants. Pollen tube growth, guidance and reception involve several cell–cell interactions between the pollen tube and a number of female sporophytic and gametophytic cell types. Despite the numerous signaling events within and between female and male gametophytes, very few of the molecular mechanisms responsible for reproduction have been identified. Classical genetic analysis has likely been hindered by functional redundancy within gene families comprising ca. 65% of the Arabidopsis genome. We established an activation tagging approach that specifically targets the male and female gametophytes and takes advantage of the modular GAL4-VP16-UAS transactivation system. During the screening, we collected a comprehensive set of mutants with potentially disrupted stages in the pollen tube–pistil interactions required for successful fertilization. The highly efficient machinery of pollination and fertilization is used by some plant viruses, such Pelargonium zonate spot virus (PZSV), for propagation and infection. PZSV "hijacks" pollen tubes to infect inner seed tissues, thereby ensuring successful vertical transmission. Our goal is to understand the mechanism(s) by which PZSV infects and interacts with male and female gametophytes, as well as seed parts.

ISPS2019-111

Reshaping wheat root/shoot architecture for changing climate

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Drought is the major environmental factor limiting wheat production and sustainability worldwide. The wild emmer wheat (*T. turgidum* ssp. *dicoccoides*) gene pool harbors a rich allelic diversity for numerous important traits, including drought tolerance. The overall goal of this research is to identify wild alleles for improving root architecture and enhance drought tolerance. A set of Adapted Near Isogenic Lines (NIL) was developed by introgression of wild emmer accession Zavitan into elite durum wheat (*T. turgidum* ssp. *durum*, cv. Svevo). The BC₃F₄ NILs were genotyped using the 90k Illumina array and linked to the wild emmer genome, and phenotyped using high-throughput image-based phenomics approach. A wide range of drought adaptation strategies were found among the NILs. Cluster analysis of morpho-physiological traits revealed five clusters of drought responses. Three drought-tolerant NILs representing different adaptations were selected for detailed characterization. Phenomics experiment including root architecture phenotyping support the drought response strategies. Further, Root phenotyping showed a higher root biomass for all chosen NILs compare to Svevo and high interaction with water availability in one NIL. This NIL showed the highest WUE under water-limited treatment and early vigor in both treatments. Currently we apply RNA-seq to identified candidate genes and reveal their underline mechanisms. While conventional breeding to improve drought tolerance focused on upper ground phenotypes and was limited by narrow allelic variation, the combination of specific wild alleles for vital drought tolerance traits as root architecture can be used for new breeding strategies, oriented drought adaptations for plant productivity.

ISPS2019-112

Reversible Leaf Xylem Collapse: Preventing cavitation under fast transpiration dynamics

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The stomata protect the plants from critical xylem tension that might lead to xylem cavitation and permanent loss of hydraulic conductivity. When VPD increases, the stomatal opening is decreased to regulate a transpiration flux that will maintain the xylem tension above the critical cavitation threshold. However, under some scenarios (e.g. transition from shade to light), VPD increase could be substantially faster (1-2 minutes) than stomatal closure (10-20 minutes). This suggests that a much faster regulation is needed to allow high transpiration rates while coping with sudden changes in VPD.

In this study we compared the onset of collapse in minor veins under tension using cryoSEM while simultaneously monitoring xylem cavitation in an adjacent leaf using the optical vulnerability technique. Our findings show that xylem collapse occurs earlier than xylem cavitation. Models of transpiration transients showed that minor vein collapse and mesophyll capacitance could effectively buffer major veins from cavitation over relevant time scales. The results suggest that vein collapse makes an important contribution to plants' ability to transpire near the brink of cavitation-inducing water potentials.

ISPS2019-113

Singlet oxygen mediated stress responses are governed by RNA oxidation and attenuation of cellular translation

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Singlet oxygen is a type of reactive oxygen species (ROS) that is highly reactive with a variety of biomolecules including nucleic acids. It is produced in the plant photodynamically in high light stress but can also be produced in the dark in non-chlorophyllous tissue e.g. roots. It has a short half-life and thus is not expected to traverse sufficiently long distances to be a signalling molecule; yet it has been observed to correlate closely with programmed cell death. Interestingly, a variety of abiotic and biotic stresses display a singlet oxygen-like transcriptome. In order to understand this commonality, we examined the mechanism of gene induction by singlet oxygen produced photodynamically via the photosensitizer Rose Bengal. Singlet oxygen was shown to induce the oxidation of RNA as measured by the accumulation of oxidized guanosine residues. This was found to attenuate the rate of ribosomal translation. We hypothesized, that due to such RNA oxidation, the level of short-lived repressor proteins in the cell is lowered, resulting in the release of stress signalling genes from repressor control. We show that this mechanism can bypass a hormonal signalling pathway controlled by repressors such as exemplified by jasmonic acid. The mechanism by which singlet oxygen controls gene expression provides a unifying explanation of how stresses can mediate similar gene induction by any mechanism that leads to the attenuation of cellular translation.

ISPS2019-114

Increasing meiotic crossing over in wheat by virus-induced gene silencing

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Wheat is the most widely grown crop in the world and a major source for human nutrition, therefore a lot of effort is put in developing new varieties. Meiotic recombination is the main engine of genetic diversity in sexually reproducing plants. The rate and location of Crossover (CO) events are regulated by specific genes as well as by genomic and epigenetic marks. In wheat, most COs occur in subtelomeric regions while it is rare in centromeric and pericentric regions. Nevertheless, about 30% of the genes are dispersed along this repressed area. Thus, breaking the linkage between these genes or introducing new allelic variation to these regions is very difficult. The aims of this work were to increase COs in both “hot”, i.e. subtelomeric regions and “cold” (pericentric) chromosomal locations. We used Virus-Induced gene Silencing (VIGS) to downregulate the recombination suppressing genes *XRCC2*, *FANCM* and *RecQ4* as well as the epigenetic maintenance genes *MET1* and *DDM1* during meiosis. The main results are: 1) We found an increase of 76% and 94% in recombination events in *MET1*-VIGS and *DDM1*-VIGS respectively at the sub-telomeric regions. 2) In the *XRCC2*-VIGS treatment, we found an 82% increase of COs at the subtelomeric region, and surprisingly, 57% increase in the pericentromeric region. 3) There was no difference in the total number of the CO events between any of the VIGS treatments and the controls meaning COs distribution was affected rather than total number. We conclude that the rate of CO events can be increased in suppressed as well as nonsuppressed regions by silencing of different genes during meiosis. Thus, the strategy presented here can be used as a simple, fast and non-transgenic way to improve breeding abilities.

Keynote Lecture - ISPS2019-115

Harvesting the desert

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Desert biological soil crusts (BSCs) are among the harshest environments on Earth. They are formed by the adhesion of soil particles to polysaccharides excreted by filamentous cyanobacteria, the pioneers and main primary producers in this habitat. The cyanobacterium *Leptolyngbya ohadii* and the green alga *Chlorella ohadii* were isolated from a BSC near the Egyptian-Israeli border. We are mostly interested in what distinguish organisms able to flourish in the BSC conditions from those that can't. Through comparative physiological, genetic analyses and transcriptome profiling, we uncovered the signals (dawn illumination and the rising temperature) that prepare the cyanobacteria towards the forthcoming dehydration (after early morning dew) and its impact on the network of genes involved. The analysis identified a set of genes present in desiccation-tolerant but not in fresh water model cyanobacteria and a novel means by which the cells protect their proteins during desiccation.

Despite its ability to withstand stress conditions, *C. ohadii* is the fastest growing photosynthetic eukaryote and unlike other plants and algae does not suffer from photodamage. Based on the results obtained using several omics we shed light on the mechanisms involved in its unparalleled performance and on the ability to harvest the right genes to improve plant productivity.