New Phytologist

Meetings

Schooling PhD students in plant development

12th International PhD School in Plant Development, Retzbach, Germany, 2–4 October 2019

Plant development is a dynamic field of research that is inherently multi-scale and multi-disciplinary. For these reasons, it has become increasingly important for scientists to communicate and collaborate on research projects across subject and geographical boundaries. The PhD School in Plant Development (www.plant-development.org) has been running successfully for the past 12 years to immerse early career scientists in exciting research at the very forefront of plant developmental biology, and to train them in the skills needed to communicate their science with peers and international leaders in the field. This year's topics ranged from membrane signaling, cell wall dynamics, organ growth and patterning; through to the evolution of plant form and function (Fig. 1). These topics reflect multiple scales of investigation using approaches from multiple disciplines including structural biology, live-cell imaging, genetics, computational modeling and fluid dynamics. Here, we highlight some of the excellent science that inspired the recent cohort of students in plant development.

Patterning

Edwige Moyroud (Sainsbury Laboratory Cambridge University (SLCU), UK) kicked off the meeting with an exciting presentation of boundary formation in petals. Her group uses the nonmodel species *Hibiscus trionum*, which has a striking, iridescent bullseye pattern that is important for insect pollination (Moyroud *et al.*, 2017). This pattern relies on the precise formation of a boundary between two regions of the petal that differ in cell type, including cell shape, color and cell surface structure. The Moyroud group are using forward and reverse genetic approaches to dissect the mechanisms that regulate each of these cellular features and control the positioning of a boundary between different cell types to produce an iridescent bullseye.

Ari Pekka Mähönen (University of Helsinki, Finland) used sophisticated lineage tracking in Arabidopsis roots to identify the origin of vascular cambium stem cells. Mähönen demonstrated that cells with xylem identity act as organizers that direct adjacent cells to divide and function as stem cells (Smetana *et al.*, 2019). He showed that xylem identity is determined by a local maximum of auxin signaling and downstream expression of HD-ZIP III transcription factors. Moreover, inducing high levels of ectopic auxin signaling in activation clones was sufficient to specify a stem-cell organizer – these cells differentiated as xylem vessels and promoted cell division and expression of cambial and phloem markers in neighboring cells.

Staying with Arabidopsis roots, Sabrina Sabatini (Sapienza University, Rome, Italy) moved the focus from stem cells to the dynamics of root growth. Root growth is largely determined by the regulation of meristem size, which is controlled by a precise balance between cell division and differentiation (Dello Ioio *et al.*, 2008). Sabatini demonstrated the importance of hormone gradients and how they interact in genetic networks to regulate meristem size (Di Mambro *et al.*, 2017). She presented work from a collaborative computational modeling approach and highlighted the importance of combining such an approach with molecular genetics to understand dynamic processes.

Membrane signaling

Membrane signaling in plants is very distinct from animals and less well understood. However, recent work from Michael Hothorn (University of Geneva, Switzerland) is shedding new light on plant membrane signaling. He highlighted the importance of membrane receptor-like kinases in plant development and presented the work his group is doing to dissect the molecular mechanisms of these signaling pathways. Hothorn showed that several pathways involving different receptor-like kinases differ in how they bind their hormone peptide ligands, but often share co-receptors, suggesting a conserved mechanism of ligand binding and activation that is relevant for plant development (Hohmann *et al.*, 2018).

A striking example of the importance of receptor-like kinases in plant development was highlighted by work from Niko Geldner (University of Lausanne, Switzerland) on the Casparian strip. His laboratory combines cell biology and genetics to understand the formation of this apoplastic barrier in the Arabidopsis root endodermis. He recently identified a barrier surveillance pathway, involving SCHENGEN (SGN) receptor-like kinases, that ensures that the supracellular Casparian strip network is effectively sealed (Alassimone *et al.*, 2016; Doblas *et al.*, 2017). Geldner showed that this surveillance pathway depends on the precise and distinct distribution of SGN1 and SGN3 in the plasma membrane, such that signaling interactions with the sulfated peptide ligand CASPARIAN STRIP INTEGRITY FACTOR 2 (CIF2) only occur when the Casparian strip is breached. Such a breach triggers a kinase signaling relay that produces reactive oxygen species and lignification with micrometer-scale precision in the cell wall (Fujita *et al.*, 2019). Recently, the Hothorn group identified the molecular mechanism of SGN3-CIF2 binding by producing a crystal structure of SGN3 (Okuda *et al.*, 2020). A surveillance pathway involving SGN3 and another receptor-like kinase, GASSHO2, was also shown to safeguard the integrity of the embryonic cuticle by interacting with the sulfated peptide ligand TWISTED SEED 1

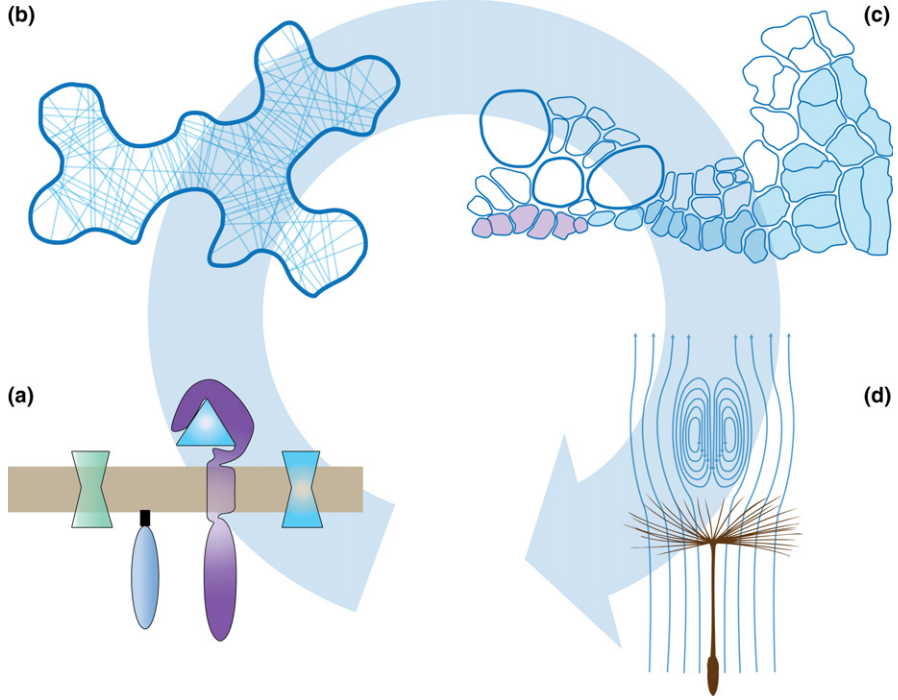

Fig. 1 Multi-scale and multi-disciplinary investigations of plant development. Arrow indicates the increasing length scale of biological processes addressed at the 12th International PhD School in Plant Development. (a) Membrane signaling at the molecular scale, for example, SCHENGEN pathway proteins, including receptor-like kinase and ligand. (b) Cell wall and cytoskeleton dynamics at the cell scale, for example alignment of cortical microtubules in a jigsaw puzzle-shaped cell. (c) Growth and patterning at tissue and organ scales, for example clonal sector (blue) in the root vascular cambium. (d) Evolution of form and function at organ and whole plant scales, for example a dandelion seed and the vortex that it generates during flight.

(Doll *et al.*, 2020). Therefore, the same receptor-like kinase evolved distinct integrity monitoring functions within the plant.

Cell wall dynamics

Marie-Cécile Caillaud (Reproduction and Development of Plants Laboratory Lyon, France) kept the focus on membrane signaling, but moved the context to cell division. Plant cells cannot migrate since they are surrounded and locked in place by cell walls; therefore, cell elongation and cell division are crucial for plant morphogenesis. In this context, positioning of the division plane is of key importance. Caillaud presented the work of her group investigating the interplay between anionic membrane phospholipids and the cytoskeleton in plant cell division (Caillaud, 2019). They use live imaging of phosphoinositide (PIP) biosensors and PIP perturbation tools to investigate the precise role of PIPs in positioning the cell division plane.

Alexis Maizel (University of Heidelberg, Germany) focused on a specific cell division – the asymmetric division of founder cells that initiate a lateral root. Asymmetric radial expansion and nuclear migration precede the asymmetric division of founder cells. Using mutants as well as pharmacological and tissue-specific genetic perturbations, Maizel showed that reorganization of cortical microtubules differentially constrains founder cell expansion, and polar migration of the nuclei requires the F-actin network (Vilches Barro *et al.*, 2019). Auxin signaling is required to trigger not only these cytoskeletal rearrangements, but also the expression of *EXPANSIN A1*, which encodes a cell wall modifying enzyme that is necessary for asymmetric swelling and division of lateral root founder cells (Ramakrishna *et al.*, 2019).

The use of advanced imaging, such as light sheet microscopy (presented by Maizel), and quantitative, three-dimensional image analysis, was evident in a number of student presentations, including the winner of 'best poster' from Athul Vijayan (Schneitz Laboratory, Technical University of Munich, Germany). Vijayan presented a three-dimensional 'digital ovule' at cellular resolution, reconstructed from 150 ovules covering all stages of ovule development (Tofanelli *et al.*, 2019).

Arun Sampathkumar (Max Planck Institute for Molecular Plant Physiology (MPIMP), Golm, Germany) also followed a quantitative morphodynamics approach, and reminded the audience that plants cope with mechanical forces, which are relevant for directional growth. Mechanical reinforcement occurs via modifications of the cell wall. He showed that cortical microtubules, that guide the direction of cellulose microfibril synthesis in the cell wall, reorganize to cope with stress at the tissue level, for instance in response to cell ablation (Eng & Sampathkumar, 2018). He also showed that cortical microtubules organize within each cell to cope with intracellular differences in stress. Furthermore, he is exploring the contribution of cytoskeleton components in the perception and response to mechanical cues.

Evo-devo

Naomi Nakayama (Imperial College London, formerly University of Edinburgh) also focused on mechanics, but broadened the scale of investigation to address the biomechanics of dandelion dispersal and its interaction with the environment. Nakayama presented her work on the aerodynamics of dandelion diaspore flight. Using computational fluid dynamics and wind tunnel experiments with dandelion pappi, as well as fabricated replicas, she found that the particular geometry and porosity of the pappus allows the generation of a separated vortex ring that keeps them flying (Cummins *et al.*, 2018). Furthermore, she observed differences in pappus detachment depending on environmental conditions (Seale *et al.*, 2019), and is currently exploring the biological significance of these findings.

An interest in the evolution of plant form and function was apparent not only from Nakayama's work, but also from a number of other keynote speakers and students working on organisms other than Arabidopsis, including winner of 'best talk' from Miguel Pérez-Antón (Hay Laboratory, Max Planck Institute for Plant Breeding Research (MPIPZ), Cologne, Germany) on explosive seed dispersal in *Cardamine hirsuta* (Hofhuis *et al.*, 2016).

Cristina Ferrándiz (University of Valencia, Spain) continued this theme by presenting the latest findings of her group on carpel evolution. The carpel encloses and protects the ovules and was a major evolutionary innovation of flowering plants (Ferrandiz *et al.*, 2010). By using the style and stigma as tissues unique to the carpel, Ferrándiz identified a core set of transcription factors that control carpel identity. She showed how a nonhierarchical regulatory network of protein complexes between transcription factors that belong to several families, could explain the patterning of different carpel tissues. Because some of these transcription factors are unique to flowering plants, it may be a testable hypothesis to link the evolutionary origin of this regulatory network to carpel evolution.

Future perspectives

An outstanding feature of the PhD School in Plant Development was the vibrant atmosphere provided by motivated students and enthusiastic speakers. This atmosphere provided great opportunities for students to present their research and establish scientific networks. Career development was another important focus and Stefan Schwarz (KWS Seed Company, Einbeck, Germany) presented his career path as an example of 'PhD to industry' and what working in a company can offer young scientists. Looking forward to the 13th International PhD School in Plant Development 2020, organized by Arp Schnittger, University of Hamburg, we anticipate more excellent science that will stimulate the next generation of plant developmental biologists.

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