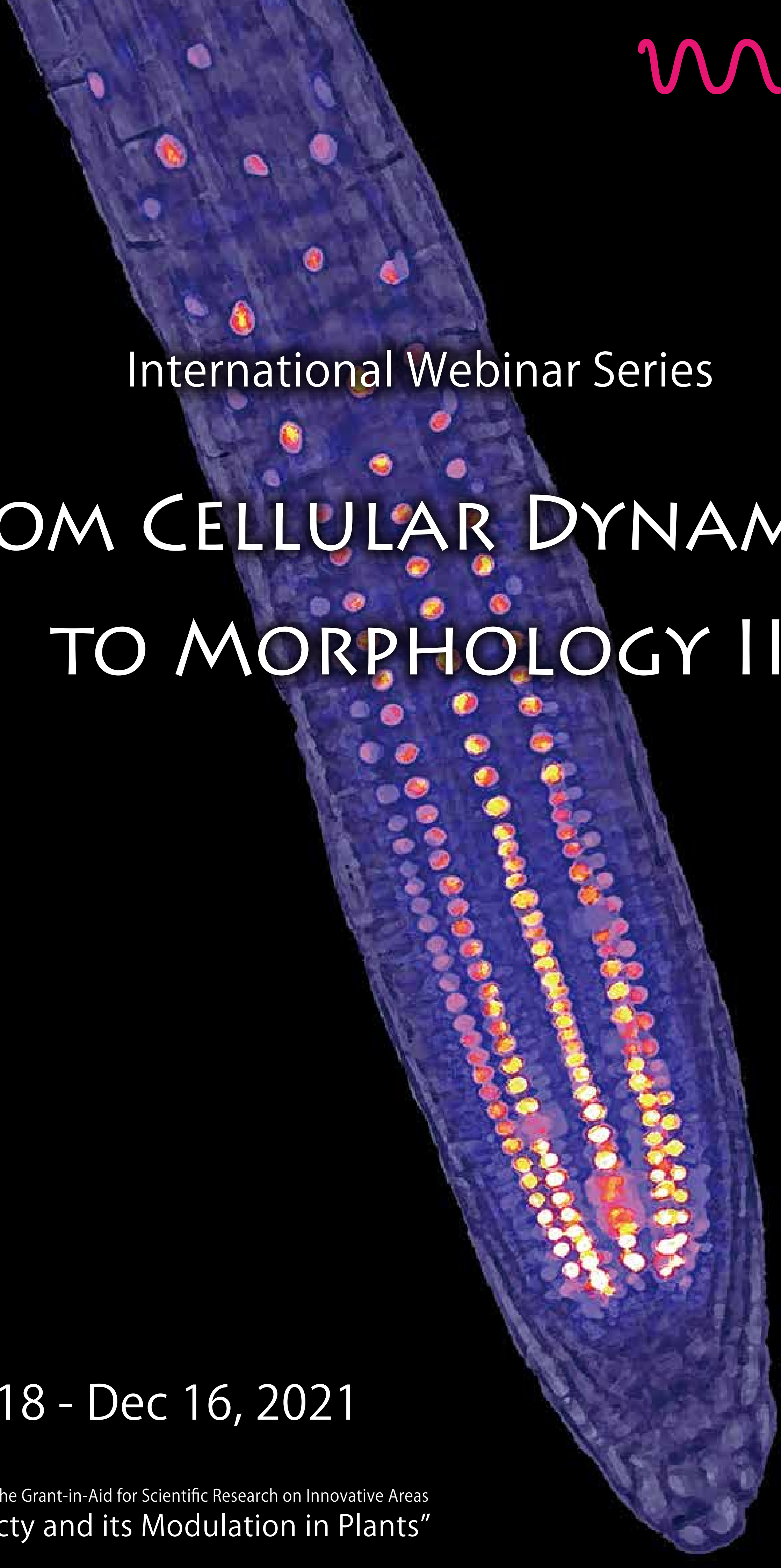
Periodicity and
its Modulation in Plants
植物の周期と変調



International Webinar Series

FROM CELLULAR DYNAMICS TO MORPHOLOGY II

Nov 18 - Dec 16, 2021

Sponsered by the Grant-in-Aid for Scientific Research on Innovative Areas
“Periodicty and its Modulation in Plants”

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New fluorescent probes for the analysis of plant cell behavior
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Lateral root priming emerges from synergy between root tip growth and auxin reflux dynamics
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Polymorphism in the symmetries of gastric pouch arrangements in the sea anemone *D. lineata*
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Chair: Keiji Nakajima (NAIST), Hidehiro Fukaki (Kobe University)

The phloem nexus of root meristem organization
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Robust control of the cambium maintenance during vascular development
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Root nodule formation controlled by host molecular networks in response to nitrogen-fixing bacteria in Lotus japonicus
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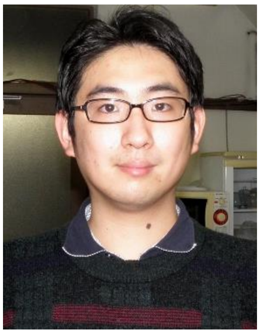
[Session I] Thu 18. Nov. 17:00-19:30 JST; 19:00-21:30 AEDT

Periodic plant organogenesis and its modulation at the shoot apex

Marcus Heisler
University of Sydney, Australia

Over the last decade or so important progress has been made in identifying and understanding a core set of patterning mechanisms that help shape plant aerial architecture. These include a feedback loop between mechanical stress and interphase microtubules, the role of auxin and mechanical stress in regulating cell polarity and the role of adaxial and abaxial cell type boundaries in modulating auxin response. What is perhaps most intriguing is how these mechanisms integrate in a combinatorial manner to provide a means to generate a large variety of commonly seen plant morphologies. Here I will discuss our current work on understanding these mechanisms and the links between them.

[Session I] Thu 18. Nov. 17:00-19:30 JST; 19:00-21:30 AEDT



Mathematical model analysis on the generation of a steep spiral of spiromonostichy

Takaaki Yonekura
The University of Tokyo, Japan

Most plants are known to exhibit a regular and periodic pattern of leaf arrangement, and this pattern is called phyllotaxis. In particular, spiral phyllotaxis, in which leaves are arranged at a constant angle to each other, have interested mathematicians and physicists because their divergence angle is related to the Fibonacci sequence, and the requirements for their generation have been theoretically elucidated. As a result, it has come to be considered that the molecular entity of the process is that the position of a new primordium is determined in such a way as to avoid the effects of inhibition emitted by existing leaf primordia. Recent progress in molecular biology has also revealed that the essence of the inhibitory effect is the "up-the-gradient dynamics" of auxin transport toward higher auxin concentrations.

Despite the progress of research, the requirements for the generation of minor phyllotactic patterns remain largely unknown. Using morphological analysis and mathematical modeling, we are trying to elucidate the requirements for the generation of these unaddressed patterns. Recently, we have focused on the requirements for the generation of spiromonostichy in *Costaceae*. Spiromonostichy is a kind of spiral phyllotaxis with extremely small divergence angle. It has been called a "genuine puzzle" because it seems to disagree with the inhibitory effect-based mechanism. We focused on the extremely large plastochron ratio of the *Costaceae* and found that the inductive effect from existing leaf primordia is necessary to explain this generation. Based on this hypothesis, we developed a new mathematical model and found that this model can explain the generation of spiromonostichy. Based on the result, I would like to give an overview of the extent to which the previously reported phyllotactic patterns can be explained.

[Session I] Thu 18. Nov. 17:00-19:30 JST; 19:00-21:30 AEDT

Dimorphic leaf development in the aquatic plant *Callitriche palustris*

Hiroyuki Koga
The University of Tokyo, Japan

Aquatic plants, the plants that grow on wetlands or in water, often show significant phenotypic plasticity in the leaf form. When the shoots of such plants are submerged in water, they sometimes form specific leaves that are drastically different from the leaves formed in the air. This ability is called heterophylly. It is of interest in both developmental and evolutionary biology because it provides an opportunity to elucidate the different modes of leaf development in the same individual. We are addressing the molecular developmental basis of the heterophylly and the evolutionary mechanism for acquiring such drastic phenotypic plasticity, using *Callitriche* plants (water-starworts: Plantaginaceae, Lamiales) as a model. We established laboratory culture lines of a heterophyllous species *C. palustris* and its closely related species and explored the genetic factors involved in the differential leaf formation by comparing gene expression patterns during the leaf development. In this talk, I will discuss how *C. palustris* controls dimorphic leaf development depending on the surrounding environment, and the differences and similarities in the mechanism of heterophylly to the other aquatic plants that acquired heterophylly independently.

[Session II] Wed 24. Nov. 17:00-19:30 JST; 9:00-11:30 CET

Towards new paradigms of movement for adaptive robots: lessons from plants

Barbara Mazzolai
Istituto Italiano di Tecnologia, Italy

Nature is adaptive, constantly learning and evolving. In the 3.8 billion years, nature has evolved and selected billions of species with characteristics most suited to their environment to be more likely to survive and to sustain life for generations. Perfection is not nature's goal. Nature focuses on evolution. Therefore, nature experiments, re-combines the existing and adapts according to results. Thus, why are roboticists looking at natural organisms for the robot revolution? By looking at natural organisms' life and evolution strategies, nature can provide engineers with the rules to design novel materials, devices able to adapt to unstructured and even dangerous environments, and develop new manufacturing processes.

In this talk, I will present our approach to bioinspiration based on the investigation of plants and soft animals' features, with the double goal to identify and extract the key principles underlying these biological functions and to translate them in a technological solution, and to improve scientific knowledge on the biological system that we take as a model.

[Session II] Wed 24. Nov. 17:00-19:30 JST; 9:00-11:30 CET

Human augmentation x Botany: Seeing touch, experiencing data, and plant inspired physicality

Zendai Kashino
The University of Tokyo, Japan

Human Augmentation is a field that commonly aims to extend human ability using machines. However, the essence of human augmentation is not to extend one's ability through external assistance, but to augmented one's ability while maintaining a sense of physicality. By achieving human augmentation while maintaining physicality, we can allow the augmented to feel a sense of ownership their actions and perceptions. This, in turn, allows the conversion of "information" into "experiences" which can facilitate an intuitive understanding of the natural world.

As humans, botanists are both a subject of research and potential application area in this field. Through human augmentation, it may be possible to allow an understanding of plants which was previously unimaginable, leading to new avenues of botanical research. In this talk, I introduce some of our work which aims to achieve this by imbuing botanical data and its acquisition a sense of physicality and touch on how working with botanists has, in turn, inspired exploration into novel forms of human physicality as well.

[Session II] Wed 24. Nov. 17:00-19:30 JST; 9:00-11:30 CET

P-MIRU (Polarized Multi-spectral Imaging of Reflection compatible with field Use) Polarized light as a quick exploration tool for botanical and biological research

Alfonso Balandra
The University of Tokyo, Japan

Usually, the presence or absence microstructures in the leaves and flowers of plants could be observed using circular polarization imagining, since these structures change the polarization characteristics of the incident light, these could be responsible of hidden interactions with pollinators capable to perceive such changes in light polarization in the surface of plants' flowers and leaves. P-MIRU is an imaging system that visualizes the surface and polar surface structure of an object by irradiating the object with linearly polarized light of monochromatic light and measuring and analyzing the degree of change in the reflected light. The system also enables the quick management and analysis of the captured data using cloud services. The capture and quick analysis system will enable the rapid exploration of a great number of botanical and biological specimens.

In this talk we are going to overview the P-MIRU imagining system. First the project origin and motivations are going to be explained. Then the talk will follow with an introduction of the optical and electronic technologies used to develop the system and a general description of how the complete system works. Also, the current technique used to analyze the degree of change in the reflected light will be introduced (Stokes Parameters). In the talk P-MIRU's last obtained results and the current status of the project will be presented. Finally, future applications of the camera and future features for data management and analysis using free cloud services will be discussed.

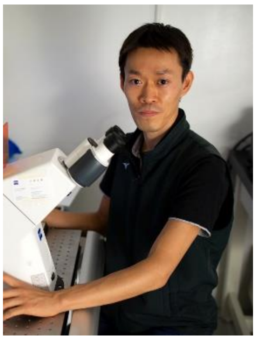
[Session III] Fri 26. Nov. 17:00-19:30 JST; 9:00-11:30 CET

Are microtubules their own mechanosensors?

Olivier Hamant
INRAE, CNRS, UCBL, ENS de Lyon, France

In plant cells, cortical microtubules (CMTs) generally control morphogenesis by guiding the synthesis of stiff cellulose microfibrils in the wall. CMT orientation has been proposed to depend on geometrical cues, with microtubules aligning with the cell long axis in silico and in vitro. Yet, CMTs are usually transverse in vivo, i.e., along predicted maximal cortical tension, which is transverse for cylindrical pressurized vessels. Here, we confined protoplasts laterally to impose a curvature ratio and modulated pressurization through osmotic changes. We find that CMTs can be longitudinal or transverse in wall-less protoplasts and that the switch in CMT orientation depends on pressurization. In particular, longitudinal CMTs become transverse when cortical tension increases, consistent with observations in planta. To search for upstream regulators, we investigated the contribution of Receptor-Like Kinase (RLK) to the CMT response to tensile stress. We found that both CMT and RLK pathways independently control the mechanical integrity of the cell. Conversely, when both RLK signaling and CMTs are impaired, plant cells behave like passive material. Altogether, these results reveal the key role of microtubule response to cortical tension in plant cell morphogenesis, and further support the idea of an autonomous microtubule mechanosensing pathway.

[Session III] Fri 26. Nov. 17:00-19:30 JST; 9:00-11:30 CET



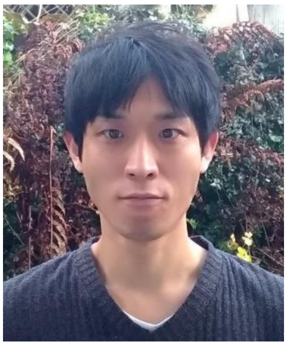
Secretory activity is required for normal morphogenesis of the oil body in Marchantia polymorpha

Takehiko Kanazawa
National Institute for Basic Biology, Japan

Eukaryotic cells possess a variety of endomembrane organelles with specific sets of proteins, lipids, and polysaccharides to fulfill functions specific to each organelle. Delivery and localization of the various substances are accomplished by membrane traffic. In addition to endomembrane organelles conserved among eukaryotes, eukaryotic cells have acquired unique organelles in a lineage-specific manner. The emergence of a novel endomembrane organelle is thought to be accompanied by the development of novel membrane trafficking pathways to and from the organelle, whose mechanism, however, still remains elusive. We are interested in the oil body, which was uniquely acquired by liverworts in bryophytes, as a model of lineage-specific organelles. Recently, we discovered that secretory cargos are targeted to the oil body in oil body cells in the liverwort, Marchantia polymorpha, which indicated that the oil body is formed by the redirection of the secretory pathway followed by fusion of secretory vesicles inside the cell (Kanazawa et al., 2020). We also isolated mutants with aberrant morphology of the oil body, one of which was caused by a mutation in a key machinery component of secretory trafficking. This finding suggests that unknown factors required for normal oil body morphogenesis are transported to the oil body via the redirected secretory pathway.

Kanazawa et al., (2020) The liverwort oil body is formed by redirection of the secretory pathway. Nat Commun, 11: 6152

[Session III] Fri 26. Nov. 17:00-19:30 JST; 9:00-11:30 CET



Dynamics of microtubule structure during cell division in land plants

Takema Sasaki
National Institute of Genetics, Japan

Eucaryotes have evolved diverse mechanisms for cell division. Land plants undergo cell division by forming cell plates, which eventually partition their cytoplasm. Proper positioning and construction of the cell plate require plant-unique microtubule structures, preprophase band (PPB) and phragmoplast. We have identified a novel microtubule-associated protein family, CORD (Sasaki et al. 2017 Plant Cell). CORD is conserved exclusively among land plants, implying that CORD is involved in the evolution of microtubule structures in land plants. In Arabidopsis, CORD genes were expressed in various tissues including xylem vessels and mitotic meristem. We revealed that Arabidopsis CORD localizes to mitotic microtubules and regulate the dynamics of microtubules in phragmoplast (Sasaki et al. 2019 Curr Biol). We recently found that, in liverwort, CORD plays distinct roles in mitotic microtubules. Here, I will present how CORD is involved in mitotic microtubules in land plants and will discuss possible roles of CORD in the evolution of plant cell division.

[Session IV] Tue 7. Dec. 9:00-11:30 JST; Mon 6. Dec. 18:00-20:30 CST

Flattening the curve: Mechanosensitive ion channels in plant cell and developmental biology

Elizabeth Haswell
Washington University in St. Louis, USA

Mechanoperception, the fundamental process by which a physical stimulus is transduced into a biochemical response, is ancient, universal, and critical for cellular function of organisms across the evolutionary tree. Plants must sense gravity, water availability, pathogens, wind, and soil–all while regulating the internal forces that govern cell shape and tissue morphogenesis. We view the membrane as an efficient platform for the perception of internal and external mechanical stimuli and are especially interested in the mechanosensory role of a class of intrinsic membrane proteins called mechanosensitive (MS) ion channels. MS channels are protein pores in the membrane that open in response to lateral tension, translating physical force into a biochemical signal. An open MS ion channel can serve as an osmotic release valve, releasing hydrostatic pressure by allowing ions to exit and/or as a receptor by allowing calcium to enter. Over the past 15 years, we and others have discovered that plant MS ion channels from multiple families transport distinct ions with a range of efficiencies and tension sensitivities, localize to different cellular membranes and perform many different physiological and developmental roles. In my talk, I will discuss our recent published and unpublished investigations into the role of MS ion channels found in the vacuole and the plasma membrane of pollen grains, pollen tubes, and other tip-growing cells.

[Session IV] Tue 7. Dec. 9:00-11:30 JST; Mon 6. Dec. 18:00-20:30 CST

How plants recover from injury and reconstruct their bodies

Momoko Ikeuchi
Niigata University

Life is full of damaging stresses. Plants generate callus upon injury to heal wound sites, yet regulatory mechanisms of tissue repair remain elusive. We recently identified WUSCHEL RELATED HOMEOBOX 13 (WOX13) as a key regulator of callus formation and organ adhesion in *Arabidopsis thaliana* (Ikeuchi et al., 2021). Strikingly, *wox13* mutant is totally deficient in organ reconnection in petiole grafting system, suggesting that WOX13 is pivotal for the establishment of organ reconnection. We uncovered that WOX13 directly regulates various cell wall-modifying enzyme genes. Furthermore, the chemical composition of cell wall monosaccharides was markedly different in the *wox13* mutant. These data together suggest that WOX13 modifies cell wall properties, which may facilitate efficient callus formation and organ reconnection. Noteworthy, WOX13 belongs to the ancient subclade of WOX family, whose sequence is widely conserved across land plants. Our data suggest that molecular function of WOX13 is partially conserved between the moss *Physcomitrium patens* and Arabidopsis. I will discuss an evolutionary perspective on regulatory mechanisms of cellular reprogramming upon injury.

[Session IV] Tue 7. Dec. 9:00-11:30 JST; Mon 6. Dec. 18:00-20:30 CST

New fluorescent probes for the analysis of plant cell behavior

Yoshikatsu Sato
Nagoya University, Japan

Plants have a sessile lifestyle so that must withstand any stress where they germinated, even if they are placed in an unfavorable condition. In order to adapt to fluctuating environmental conditions, plants have evolved their own developmental processes and physiological responses during the course of evolution. The control of turgor pressure is one of the notable examples, which is the intracellular force that pushes the cell membrane against the cell wall. Remarkably, the force is comparable to that of a car tire and plants use the force for their growth as well as their posture regulation. It remained unknown how plant cells would behave when they encountered physical disturbance that were not easily altered by turgor pressure. We used microfluidic devices to analyze the ability of plant cells to penetrate narrow gaps in tip-growing cells, such as pollen tubes and root hairs in angiosperms, and the moss protonemata and showed that all tip-growing cells we tested have a capacity to deform their shape and penetrated the 1 μm gap (Yanagisawa et al. 2017 Sci Rep 7 1403). These abilities are thought to be useful in growing narrow spaces of female tissue for pollen tubes, and in elongating the narrow spaces of soil particles for root hairs. We realized that new tools are needed to further understand the mechanical properties in cell wall and the dynamics of cell nuclei that maintain a certain distance from the elongation end. In this talk, I will present the latest status of our imaging analysis platform aimed at understanding the mechanical optimization of tip-growing cells with flexible mechanical properties.

[Session V] Fri 10. Dec. 17:00-19:30 JST; 9:00-11:30 CET

Lateral root priming emerges from synergy between root tip growth and auxin reflux dynamics

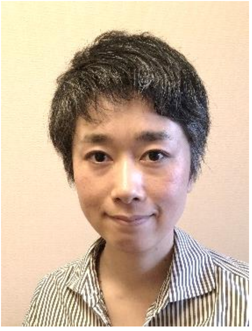
Kirsten ten Tusscher
Utrecht University, The Netherlands

Root system architecture critically determines a plants access to water and nutrients. As a consequence, root architecture has evolved to be a highly plastic property, with the number, length and orientation of root system branches adapting to water and nutrient levels as well as their spatial distribution. Still, the earliest stage of lateral root formation, called priming, in which groups of cells gain the competence for future lateral root development, appears to be highly regular in nature.

In Arabidopsis, priming has been characterized to involve regular temporal oscillations in auxin level and/or signaling in the root tip, accompanied by fluctuations in a large number of genes. Through growth, these temporal oscillations subsequently become translated into spatially periodic patches of primed cells along the primary root axis. Previous studies demonstrated that auxin production, transport and sensing are all critical for priming, while also a major correlation with root growth was observed. This led us to speculate that priming may arise from an interplay between root tip auxin and growth dynamics. Given the emergent nature of such a hypothesized mechanism, we used a computational modeling-driven approach for our investigations.

From our modeling approach we deciphered that the so-called reflux loop dictating root tip auxin transport dynamics results in a zone of auxin loading at the boundary of the meristem and elongation zone. Additionally, stem cell driven growth dynamics result in periodic variations in the size at which cells arrive at this, driving oscillatory fluctuations in their passive auxin uptake capacity. Combined this explains the experimentally observed auxin oscillations. We experimentally validated the predictions resulting from our uncovered priming mechanism and contrasted these with predictions emanating from alternative, previously suggested mechanisms. Importantly, our priming mechanisms at least partly explains adaptation of main and lateral root properties to environmental factors such as nutrient levels as two sides of the same coin, rather than needing to invoke two differential adaptation mechanisms.

[Session V] Fri 10. Dec. 17:00-19:30 JST; 9:00-11:30 CET



A theoretical model for leaf shapes with or without branches

Akiko Nakamasu
Kumamoto University, Japan

Diversity in leaf shapes can be observed among plant species or even in a single plant. We are using a simple model for the understanding of how leaf shapes are generated autonomously. In this model, we just treat deformations of a leaf boundary. This assumption may extremely simple, though, it can show characteristics observed in leaf shapes.

For example, growths coupled with a periodicity on the boundary give a steady sequence of a development of branch pattern. It can explain asymmetries and developmental changes in leaf divarications. Then, other leaves than branches can also be obtained by modulations of the periodical growth.

[Session V] Fri 10. Dec. 17:00-19:30 JST; 9:00-11:30 CET

Polymorphism in the symmetries of gastric pouch arrangements in the sea anemone *D. lineata*

Safiye E. Sarper
Osaka University, Japan

Symmetry in the arrangement of organs and body parts is the distinctive morphological feature of plants and animals. Compared to the recurrent evolution of plant symmetry (especially between bilateral and radial symmetries of flowers in many angiosperm orders), such symmetry evolution limitedly appeared in animals where most animal phylum always demonstrate bilateral symmetry. In animals, cnidaria (jellyfish, coral, sea anemone) is a rare phylum including both bilateral and radial symmetrical species. In cnidarians, symmetries appear in their internal organs, such as gastric pouches and muscles. However, how different symmetries appear during the developmental process remains unknown. In this talk, we'll report intraspecific variations in the symmetric arrangement of gastric pouches, muscles, and siphonoglyphs, the Anthozoan-specific organ that drives water into the organism, in *D. lineata* (*Diadumenidae*, Actiniaria-sea anemone). We found that the positional arrangement of the internal organs was constrained to either biradial or bilateral symmetries depending on the number of siphonoglyph organs. Based on the morphological observations, a mathematical model of internal organ positioning was employed to predict the developmental backgrounds responsible for the biradial and bilateral symmetries. In the model, we assumed that the specification of gastric pouches is orchestrated by lateral inhibition and activation, which results in different symmetries depending on the number of siphonoglyph organs. Thus, we propose that a common developmental program can generate either bilateral or biradial symmetries depending on the number of siphonoglyph organs formed in the early developmental stages.

[Session VI] Thu 16. Dec. 17:00-19:30 JST; 9:00-11:30 CET

The phloem nexus of root meristem organization

Christian Hardtke
University of Lausanne, Switzerland

Higher animals and plants are two evolutionary outcomes of complex multicellularity. An important driver of cellular specialization and body plan expansion in both phyla was the evolution of vascular distribution networks. Most prominently, the cardiovascular network of mammals distributes oxygen and nutrients throughout the body, driven by the pumping action of the heart. By comparison, the vascular transport systems of the dominant group of higher plants, the angiosperms, are fundamentally different. For instance, transport of photosynthates in the phloem network is governed by dynamic source-sink relations and driven by a pressure differential that builds up through locally controlled cellular osmolarity. The conducting phloem channels are the so-called sieve tubes, which not only transport nutrients but also developmental signals such as the phytohormone auxin. Sieve tubes are formed from interconnected individual sieve elements that are meticulously aligned in cell files as they develop. Sieve elements represent a cellular between-life-and-death state, because they lack numerous organelles, including the nucleus, and are nurtured by their neighboring, so-called companion cells. The peculiar sieve element differentiation process can be observed in growth apices. For example, in the root meristem of Arabidopsis thaliana seedlings their development from stem cell into mature sieve element is laid out in a spatiotemporal gradient. My lab has characterized a molecular network that guides this differentiation process through the interplay between controlled transcellular auxin transport across developing sieve element cell files and autocrine receptor kinase signaling pathways that respond to small peptide ligands. Key players in this network constitute a molecular rheostat that finetunes transcellular auxin flux and contributes to auxin canalization in developing sieve elements. Such intersection with phytohormone pathways also revealed a key role of developing protophloem in root meristem organization, in a sometimes non-cell-autonomous, compensatory fashion.

[Session VI] Thu 16. Dec. 17:00-19:30 JST; 9:00-11:30 CET

Robust control of the cambium maintenance during vascular development

Tomoyuki Furuya
Kobe University, Japan

Like trees, plants undergo continuous radial growth owing to the activity of vascular stem cells in the cambium. Thus, vascular stem cells should be maintained throughout the radial growth. However, it was not fully understood that the molecular mechanism for balancing between the proliferation and the differentiation in vascular stem cells. Here, to discover novel regulators for vascular stem cells, we newly constructed a gene co-expression network equipped with temporal and cell-type information during vascular development by combining multiple transcriptome datasets of an ectopic vascular cell differentiation system, VISUAL. We extracted a total of 394 cambium-related genes based on a gene co-expression network. Of them, a BES/BZR transcription factor BEH3 was found as a potential stem cell regulator. The *beh3* mutants exhibited a larger variation in vascular size than the WT, suggesting the role of BEH3 as a stabilizer of vascular development. BEH3 had a weaker transcriptional repressor activity than other BES/BZR homologs known as negative regulators of vascular stem cell maintenance and inhibits the activity of these other factors via competition to bind to the same DNA motif. Indeed, mathematical modelling supported that the competitive relationship among BES/BZR members leads to decreasing "phenotypic variation" in vascular size, demonstrating the importance of the opposite-behaving member in the robust regulation of stem cell activity.

[Session VI] Thu 16. Dec. 17:00-19:30 JST; 9:00-11:30 CET

Root nodule formation controlled by host molecular networks in response to nitrogen-fixing bacteria in Lotus japonicus

Takashi Soyano
National Institute for Basic Biology, Japan

Legumes form root nodules to host nitrogen-fixing bacteria, collectively called rhizobia. Invasion and release of rhizobia into host cells are restricted in nodule primordia originating root cortical cells. Root nodules provide endosymbiotic bacteria with an environment suitable for nitrogen fixation while avoiding excessive symbiosis by confining nitrogen-fixing bacteria in the symbiotic organ. Nodule formation is indispensable for establishing root nodule symbiosis. We have shown that nodule primordium development is regulated by a lateral root-related transcription factor, ASL18/LBD16, of which expression is positively regulated by a host nodulation-specific transcription factor evolutionarily derived from a member of NIN-like proteins responsible for nitrate responses. Therefore, nodule symbiosis has evolved through cooption and rearrangement of molecular pathways conserved in most plants. Recently, we found that expression of host symbiotic genes oscillates in the susceptible region near the root tip after inoculation with rhizobia, similar to the root clock in Arabidopsis. Stimuli from rhizobia trigger a series of nodulation processes, but it is likely that the host moderately regulates infection and nodule distribution. The periodicity of host symbiotic gene expression may be concerned with the pattering of nodulation in roots growing linearly.