Multiscale Modeling of Plant Growth, Pattern Formation and Actuation (22w5179)

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1 Overview of the Field

Plant growth and development involve the flux of molecules from one cell to another, the mechanical deformation of structures, and the exchange of signals between cells and tissues. Mathematical modeling of these complex biological processes has allowed life scientists to better understand the regulatory principles that govern plant functioning and development. However, translating 'biology' into mathematical algorithms is challenging. The power of a modeling approach is determined by the conceptual understanding of biological processes and their causal relationships, as well as the ability of the researcher to quantify essential input parameters.

The workshop is focused at the intersection of three areas: molecular signaling (hormonal control and exchange of signaling molecules), network modeling (mathematical representation of biological feedback mechanisms), and biomechanical concepts (physical and mechanical analysis of force driven deformation or cells and tissues). The workshop will provide a forum for mathematicians, physicists and engineers to develop, exchange and challenge novel approaches to simulate these complex biological processes in integrated manner. The long term goal is to improve our understanding of plant growth, pattern formation and motion.

2 Workshop Structure and Format

13 participants were in-person (as per limitation of max 15 in-person participants specified by BIRS), 36 participants were online.

Three types of activities were conducted:

- Regular talks with question periods (20 min timeslots)
- Working sessions consisting of presentations and discussions (60 min)
- Breakout work (follow-up of working sessions; variable length)

All sessions were hybrid except for a couple of afternoon Breakout work session that were incompatible with the time zones in which most online participants were located (Europe).

3 Working sessions on open problems and tools

Enrico Coen - Principles of Plant Morphogenesis

The growth and shape of plants depend on the mechanical properties of the plant's mesh of interconnected cell walls. Because adhering cell walls prevent cell migrations, morphogenesis is simpler to study in plants than in animals. Spatiotemporal variations in the rates and orientations at which cell walls yield to mechanical stresses—ultimately powered by cell turgor pressure—underlie the development and diversity of plant forms. In my session we reviewed and discussued new insights and points of current contention in our understanding of plant morphogenesis, starting fromwall components and building up to cells and tissues.

Daniel Cosgrove - Mechanobiology: connecting molecular structure to mechanics of primary cell walls

What are the tensile load-bearing polymers in the growing cell wall? How is force transmitted between cellulose? These questions arose from our studies of how expansins loosen cell walls and is relevant to understanding cell wall mechanical properties, including wall elasticity, plasticity, and yield threshold, as well as mechanisms of wall loosening & cell growth.

The primary cell wall contains three major polysaccharides: cellulose comes in the form of stiff microfibrils, hemicelluloses such as xyloglucan are much more flexible and binding tightly to cellulose, while pectins form hydrophilic gels that bind extensively but weakly to cellulose. In the past 70 years, numerous molecular concepts of cell wall organization have been proposed, largely based on information from microscopy (e.g. electron and atomic force microscopy) and wall biochemistry (polymer structure and extractability). The concepts are often presented as schematic depictions of the spatial arrangement, noncovalent bonding, and covalent crosslinks between the cell wall components. Imagination, focus and artistic talents greatly influence the appearance of these "models", which may be grouped into three distinctive concepts of the wall as: (A) a pectic hydrogel reinforced with cellulose microfibrils; (B) a covalently-linked network of matrix polymers bonded noncovalently to cellulose microfibrils; or (C) polylamellate arrays of cellulose microfibrils tethered by xyloglucan and embedded in a pectic gel.

From these depictions one may make inferences about cell wall mechanics and potential mechanisms of cell wall enlargement, but these models are not quantitative and thus are difficult to validate by mechanical testing. Our experimental tests of these ideas, based upon mechanics and enzyme digestions, have been qualitative, but the results appear to contradict the models.

One feature common to these models, perhaps originating in a pioneering electron microscopy study by Frey-Wyssling (1), is that cellulose microfibrils are shown as well separated from each other, not making direct contact. With this arrangement, matrix polysaccharides would have to transmit tensile forces between cellulose microfibrils.

A conceptually different model has emerged from our coarse-grained model of the primary cell wall (2). Simple noncovalent binding interactions in the model generate bundled cellulose networks resembling that of primary cell walls and possessing stress-dependent elasticity, stiffening, and plasticity beyond a yield threshold. Plasticity originates from fibril-fibril sliding in aligned cellulose networks. This physical model provides quantitative insight into fundamental questions of plant mechanobiology and reveals design principles of biomaterials that combine stiffness with yielding and extensibility.

1. Frey-Wyssling, A. (1954). The fine structure of cellulose microfibrils. Science 119, 80-82.

2. Zhang, Y. et al. (2021). Molecular insights into the complex mechanics of plant epidermal cell walls. Science *372*, 706-711. 10.1126/science.abf2824.

Christophe Eloy - The shape of the longest branch
This (interactive) working session was aimed at demonstrating a possible modeling approach on a concrete example. Drawing inspiration from the classical paper of J.B. Keller entitled "The tallest column" (1966), we looked for a model that could predict the shape of the branch with the largest horizontal extension. This problem is somewhat related to the S-shape sometimes observed in large horizontal tree branches. However, it would be pointless to try to model the full complexity of a real branch, which includes not only self-weight bending, but also primary and secondary growth as a response to stimuli such as light, gravity, and proprioception. For the sake of clarity, and as a first modeling step, we simplified the problem drastically. Inspired by Keller's approach, we considered the problem of finding the shape of a beam of a given volume such that its horizontal extent is maximum when submitted to its own weight.

Christophe Godin - Fractals from genes: a cauliflower recipe
Fractals forms are ubiquitous in nature, clouds, lightenings, coastlines, snowflakes in the inorganic world, but also trees,ferns, lungs, and corals in the living world. One of the most iconic example of a biological fractal is certainly the cauliflower, whose fractal appearance culminates in the Romanesco variety. A bit more than 10 years ago, I met François Parcy, a specialist of the genetic regulation of the passage from inflorescences to flowers during plant growth. We both were very intrigued by this ability of plants to make so remarkable fractals. François knew already that the cauliflower was the result of the failure of a plant to make flowers, due to a couple of mutations. However, why and how the change in the gene activity would produce a fractal-like shape remained a mystery. In this presentation, I explained what we understood, i.e. basically that such fractal forms are produced because, despite their failure to make flowers, the growing tissues keep memory of of their transient passage in a floral state. Additional mutations affecting growth can induce the production of conical structures reminiscent of the conspicuous fractal Romanesco shape. Interestingly, the way plants produce fractals has commonalities with the way mathematical fractals are constructed, but they are not exactly similar. This study reveals how fractal-like forms may emerge from the combination of specific perturbations of floral developmental programs and growth dynamics. This presentation introduced a number of questions related to both biological and modeling aspects (see lelow) followed by a debate between the participants:

1. Biological aspects: what new genetic insights do we need to continue such an investigation of flower development
- How can we determine the genes that control the memory of transitory LFY expression?
- How general can we construct a generic inflorescence regulation network
• to generalize to other cabbages shapes (kale, brussels sprout, cabbage, white cabbage)
• to generalize to other inflorescence architectures
- How to find genes causal to domesticated cauliflower
• to determine the multiple mutations responsible for the domesticated plants
• to explain different genomes (brocoli, …), understand where are their genomic variations, if they are associated with particular morphotypes?

2. Modeling aspects: the need to define new formalisms to model mesoscopic systems
The presentation illustrated the need to develop new computational models for mesoscopic structure, able to account for gene interaction, competition of territories and gene patterning, signaling regulation and growth. These model must be able to address multicellular and branching

structures, often both continuous and discrete and showing at the same time lineic, surfacic and volumetric properties and shapes. We discussed the following questions:

- How to measure mesoscopic structures (confocal microscope are often limited in depth of acquisition, microCT, other ?)
- How to model mesoscopic structures (need new mathematical/computational concepts)
- How to handle the massive amount of computation required by these systems?

Richard S. Smith - Modeling plant growth with MorphoDynamX

Computational Morphodynamics is an emerging field that aims to understand morphogenesis and development through an interdisciplinary approach. Experimental data from live imaging of growing biological tissue is analysed in order to understand how gene expression controls cell and organ shape change. Hypotheses are formulated and then tested in simulation models, which then create predictions which can then be tested experimentally, forming a cycle of experiments, image analysis and modelling. Our image analysis software MorphoGraphX (www.MorphoGraphX.org) is specialized for the quantification of cell shape change and gene expression on surface layers of cells. It uses a triangular mesh to represent the surface shape of a sample, projecting signal from 3D images onto the vertices that represent the pixels of the image, something we call "2.5D". These curved surface images are able to capture the organ curvature and cell outlines for segmentation on samples where full 3D time-lapse is not possible. This abstraction was inspired by simulation modelling approaches, as it much simpler to simulate growth and cell division on a curved surface than in full 3D. In practice, we have found that many of the tools and methods we use for image processing on meshes are also useful for modelling and vice versa. In some cases, such as the visualization and quantification of stresses, simulations are required for the quantifications. To this end we are developing a software called MorphoDynamX (ww.MorphoDynamX.org) that extends MorphoGraphX to include modelling. Borrowing paradigms from image processing workflows, models are constructed from pipelines of reusable processes, that implement specific features of the model such as growth, cell division, genetic networks and cell-cell communication. This allows models to be directly compared with imaging data, often using the same tools, and cells extracted from biological samples can be used as geometric templates for simulations. MorphoDynamX provides a significant step towards an integrated framework for computational morphodynamics.

4 Presentation Highlights (Regular Presentations)

Atef Asnacios - Root hair growth : mechanics and mechanotransduction from the cell wall to the nucleus

Root hair (RH) cells are important for plant growth and survival, mainly by favoring nutrients and water uptake. To invade the soil, RH cells have to penetrate dense and mechanically resistant media. Thus, the soil’s physical properties impact the growth and survival of plants. Here we presented the effect of the mechanical resistance of the culture medium on RH length, time, and speed of growth. We also show the impact of the environment on the positioning, and movement of the nucleus inside the growing RH cells. Arabidopsis thaliana seedlings were cultured in a custom-made microfluidic-like system, in solid media with agar concentrations ranging from 0.5% to 1.25%. We found that the time of growth of RH cells is independent of the mechanical resistance of the surrounding environment, while the RH speed decreases when the mechanical resistance increases. As a consequence, the RH cells are shorter in stiffer environments. Moreover, we show that the speed of the nucleus adapts to the mechanical resistance of the environment and follows the same trend as the average speed of the RH tip. Eventually, during RH growth, the nucleus-to-tip distance was found to decrease when the stiffness of the environment was increased, indicating mechanotransduction from the cell surface to the nucleus.

Amir J. Bidhendi - Microscale geometrical features in the plant leaf epidermis confer enhanced resistance to crack propagation

We aimed to understand the significance of the jigsaw puzzle-like pattern of cells in the epidermal tissues of leaves and petals in many plant species. We propose a novel hypothesis that links this pattern to the role of the epidermal tissue as a skin that protects the plant interface with the environment. To test this hypothesis, we combined computational and physical modeling of crack propagation and fracture tests on real plant leaves. The results showed that the wavy cell geometry toughens the plants' protective skin by promoting crack deflection and forcing growing fissures to meander, thus enhancing the tissue's resistance against microcrack propagation. These findings provide insights into the design principles of plant tissues, plant evolution, could inform selective plant breeding and inspire the design of human-made materials.

Mark Blyth - Variation potential transmission: a new viewpoint on the Ricca factor hypothesis

A variation potential (VP) is an electrical signal that is unique to plants and that occurs in response to flaming or wounding. However, it is known that the particular propagation mechanism is not to be electrical. In this talk we discussed our hypothesis that VP transmission happens through the transport of a chemical agent in the xylem, known traditionally as a Ricca factor. We assume that the electrical signal is generated locally by the activation of an ion channel at the plasma membrane of cells adjacent to the xylem, and do not discuss this further except for working on the assumption that the ion channels are triggered when the chemical concentration goes beyond a critical value. We show through numerical computations the combined effect on on chemical transport in a tube flow of advection and diffusion. The central proposition of the talk is that so-called shear-enhanced dispersion, also known as Taylor dispersion, can works as a candidate mechanism to explain the VP rates that observed in experiments where plant stems are wounded by flaming.

Elena Dimitrova - PlantSimLab - a modeling and simulation web tool for plant biologists

In the talk we introduced PlantSimLab, app.plantsimlab.org, a web-based application developed to allow plant biologists to construct dynamic mathematical models of molecular networks, interrogate them in a manner similar to what is done in the laboratory, and use them as a tool for biological hypothesis generation. It is designed to be used by experimentalists, without direct assistance from mathematical modelers, and includes a natural language parser that allows the user to create text-based models.

Clinton H. Durney - Revisiting the 'mechanical advantage' of grass stomatal subsidiary cells through a computational model

Stomata are tiny adjustable pores on the surface of plants that balance gas exchange for photosynthesis with water loss. The mechanical interactions of a pair of cells, known as guard cells, are responsible for the reversible opening and closing of each pore, reliably regulating this dynamic process. Grasses, which inhabit dry environments, have evolved specialised stomatal complexes. Grass stomata consist of dumbbell shaped guard cells plus a pair of subsidiary cells, and this is thought to enable them to open and close more rapidly. We study the biomechanics of grass stomata through a combination of microscopy and Finite Element Method (FEM) modelling. We investigated the mechanical interactions of the guard cells with the subsidiary cells and take a closer look at the 'mechanical advantage' hypothesis presented by Franks and Farquhar. Our results are contrasted with a FEM model of a two-cell kidney shaped stomata, underscoring the unique properties present in grass stomata that enhance their performance. Overall, this research provides a deeper understanding of the interplay between cellular geometry and material properties for biomechanical mechanisms that enable efficient gas exchange in grasses.

Thomas Fai - Nuclear size control by osmotic forces in S. pombe

The size of the nucleus scales robustly with cell size so that the nuclear-to-cell size ratio is maintained during cell growth in many cell types. To address the fundamental question of how cells maintain the size of their organelles despite the constant turnover of proteins and biomolecules, we consider mathematical models of organelle size control rooted in the physicochemical principles of transport, chemical kinetics, and force balance. In particular, we consider how a model based on osmotic force balance predicts the stable nuclear-to-cell size ratio observed experimentally and test key predictions in the fission yeast Schizosaccharomyces pombe. We further demonstrate that the N/C ratio is maintained by a homeostasis mechanism through the synthesis of macromolecules during growth. These studies demonstrate the functions of colloid osmotic pressure in intracellular organization and size control, and suggest general principles of organelle size control.

Frédérick P. Gosselin - Can a wrinkling instability play a role in the morphogenesis of kelp blades?

Brown macroalgae, also known as kelp, have a holdfast to attach them to the substrate, a stipe to rise from the sea floor to the surface and one or many blades that act as "leaves" for plants. Ruffling instabilities have already been observed on these blades. We can also wonder if wrinkling instabilities play a role in kelp morphogenesis and what would be the mechanical behavior behind their formation. Ruffles can be considered as plate instabilities, created by the difference of speed growth between the edges and the midline of the blade. Wrinkles are surface instabilities caused by the growth differential of the growing outer layers stretching the passive core. As blades can be broken down in three layers (medulla and cortex combined together into a passive core covered on both sides by a growing meristoderm), wrinkling is specifically linked to the still little-known models of tri-layers. Our goal is to simulate wrinkling instabilities with the finite element method, then to study the influence of different mechanical and geometrical parameters (thickness, modulus ratio, boundary conditions…) on blades strain and stress. In order to create a model, a systematic analysis of periodic buckling modes (symmetric and anti-symmetric) is done. This model has many applications. It will improve our understanding of the kelp growth mechanism, and also highlight the combination of biology and physics. The results could also lead us to biomimicry, using the benefits of wrinkles and ruffles in the adaptation of floating solids to a low-speed water flow.

Charlotte Kirchhelle - A concept for edge-based growth control in plants

Polyhedral plant cells control directional growth through modification of cell wall mechanical properties at different cell faces. According to the leading paradigm of plant cell growth, directional growth is principally driven through oriented deposition of cellulose at different cell faces, which is in turn controlled by cortical microtubules. Cell edges (where two faces meet) can act as organisers of microtubule patterning through selectively stabilising and nucleating microtubules. We have recently shown that cell edges can also influence directional growth independently of oriented cellulose deposition. In lateral root cells, an edge-directed transport pathway mediated by a plant-specific small GTPase is required for directional growth at the cell and organ level. Based on our latest genetic and biochemical data, we propose that edge-directed transport is involved in establishing growth-limiting mechanical hotspots at cell edges, which are targets of expansing-mediated growth. We furthermore propose that such spatial patterning of growth-limiting hotspots may facilitate targeting of expansins to hotspots through geometric sorting of soluble proteins within the apoplast.

Alexis Maizel - Morphodynamics of lateral root initiation
Morphogenesis in plants depends on local growth rates and directions. Since plant cells are confined and linked together by rigid extracellular cell walls, spatial differences in growth can generate mechanical stresses within tissues. The resulting mechanical tensions caused by cells pulling or pushing on their neighbors serve as instructive signals during development and an essential element of the feedback mechanism coupling tissue geometry to gene expression. The lattice of cortical microtubules (CMTs) plays an important role in translating mechanical signals during morphogenesis and are essential regulators of anisotropic growth at the crossroads of biochemical and mechanical growth control. The Maizel lab uses the formation of lateral root primordia (LRP) as an example of morphogenesis that entails a difference in growth behavior between tissues. LRPs initiate deep within the primary root, in the xylem pole pericycle (XPP). In response to auxin, lateral root founder cells (LRFCs) swell, their nuclei migrate towards each other, and they divide asymmetrically to form a stage I LRP. The endodermis that overlies the forming LRP accommodates the radially expanding LRFCs through a change in cell shape and volume loss. Interference with this step results in a complete block of LRP formation and the absence of endodermis remodeling. The cellular mechanisms that license and ensure the coordination of these events have yet to be discovered. The lab combines live imaging with confocal and light sheet microscopy with cell and tissue-specific perturbations and modelling to capture and analyze these initial events of lateral root formation. Results related to the role of cell wall mechanical properties in correctly positioning the asymmetric division plane, re-directing auxin flow and canaliszing growth were presented along a overview of the dynamics of cytoskeleton reorganisation necessary for the expansion and emergence of the lateral root promordia.

Olivier Martin - Roots probe their nearby soil environment through ethylene sensing
Plants arrest root growth when confronted with compact soils, associated with morphological changes such as reduced cellular elongation and larger root diameters. This talk reported experiments on rice and Arabidopsis seedlings, showing that (1) exposure to ethylene (in uncompacted soils) phenocopies the root behavior in compact soils, (2) the ethylene signaling pathway is activated when roots are subject to increased soil compaction, (3) mutants of the ethylene signaling pathway are insensitive to soil compaction and thus maintain root growth in spite of compaction. We have also measured and modeled diffusion of gas in soil for increasing compactions. We propose that root growth arrest in compact soils is likely an adaptive response rather than just caused by a physical limitation, and that plants use ethylene diffusion in soil to best allocate resources when exploring their nearby soil environment.

Outcome from discussion period following the talk:
- The mechanism could be responsible for root - root avoidance.
- This last possibility suggests that ethylene signaling likely drives redistribution of auxin.

Bruno Moulia - Investigating the control of the shaping of plant axes and crowns through model-assisted (top-down) phenotyping

Shoot morphogenetic plasticity is crucial to the adaptation of plants to their fluctuating environments. Major insights into shoot morphogenesis have been compiled studying the shoot apical meristem (SAM) through a methodological effort in multiscale systems biology and biophysics [1]. However, morphogenesis at the SAM is robust to environmental variability. Plasticity emerges later on during post-SAM development. The purpose of this talk was to show that multiscale systems biology and biophysics is insightful for the shaping of the whole plant as well. More specifically, I reviewed the shaping of axes and crowns through tropisms and elasticity, combining the recent advances in morphogenetic control using physical cues and by genes. I focused on land angiosperms, with growth habits ranging from small herbs to big trees. Generic morphogenetic processes have been identified, revealing feedforward and feedback effects of global shape on the local morphogenetic process, involving proprioception [2]. Major advances have also been made in the analysis of the major genes involved in shaping axes and crowns, revealing conserved genic networks [3,4]. These two approaches are now starting to converge through the definition of a quadruplet of dimensionless morphogenetic numbers (B,M,W,El) that fully defines the control over axis and crown shaping at the scale of the tropic control apparatus (i.e. a segment of stem in the growth zone below the apical meristem). These dimensionless numbers are quantitative macro-characters that can be more readily related to multi-cellular models and to relative expressions of genes and/or to QTLs [5]. Moreover, methods for model-assisted phenotyping are now available [6].

References

1. Vernoux, T., Besnard, F. & Godin, C. What shoots can teach about theories of plant form. Nat. Plants 7, 716–724 (2021). https://doi.org/10.1038/s41477-021-00930-0
2. Moulia B, Douady S, Hamant O. 2021. Fluctuations shape plants through proprioception. Science 372: eabc6868.
3. Hill JL, Hollender CA. 2019. Branching out: new insights into the genetic regulation of shoot architecture in trees. Current Opinion in Plant Biology 47: 73–80.
4. Hollender CA, Hill JL, Waite J, Dardick C. 2020. Opposing influences of TAC1 and LAZY1 on lateral shoot orientation in Arabidopsis. Scientific Reports 10.
5. Moulia, B., Badel, E., Bastien, R., Duchemin, L., & Eloy, C. (2022). The shaping of plant axes and crowns through tropisms and elasticity: an example of morphogenetic plasticity beyond the shoot apical meristem. New Phytologist, 233(6), 2354-2379.
6. Hartmann F; H Chauvet-Thiry , J Franchel , S Ploquin , B Moulia, N Leblanc-Fournier, Decourteix M. 2022 “Methods for a quantitative comparison of gravitropism and posture control over a wide range of herbaceous and woody species” in Elison B. Blancaflor. Plant Gravitropism, 2368, Springer US, pp.117-131, 2021, Methods in Molecular Biology, 978-1-0716-1677-2.

Wojtek Palubicki - Ecoclimates

Over the last years, the role of forests in climate change has received increased attention. This is due to the observation that not only the atmosphere has a principal impact on vegetation growth but also that vegetation is contributing to local variations of weather resulting in diverse microclimates. The interconnection of plant ecosystems and weather is described and studied as ecoclimates. In this work we take steps towards simulating ecoclimates by modeling the feedback loops between vegetation, soil, and atmosphere. In contrast to existing methods that only describe the climate at a global scale, our model aims at simulating local variations of climate. Specifically, we model tree growth interactively in response to gradients of water, temperature and light. As a result, we are able to capture a range of ecoclimate phenomena that have not been modeled before, including geomorphic controls, forest edge effects, the Foehn effect and spatial vegetation patterning. To validate the plausibility of our method we conduct a comparative analysis to studies from ecology and climatology. Consequently, our method advances the state-of-the-art of generating highly realistic outdoor landscapes of vegetation.

Adam Roddy - Localized growth drives spongy mesophyll morphogenesis
The spongy mesophyll is a complex, porous tissue found in plant leaves that enables carbon capture and provides mechanical stability. Unlike many other biological tissues, which remain confluent throughout development, the spongy mesophyll must develop from an initially confluent tissue into a tortuous network of cells with a large proportion of intercellular airspace. How the airspace in the spongy mesophyll develops while the tissue remains mechanically stable is unknown. Here, we use computer simulations of deformable polygons to develop a purely mechanical model for the development of the spongy mesophyll tissue. By stipulating that cell wall growth and remodelling occurs only near void space, our computational model is able to recapitulate spongy mesophyll development observed in Arabidopsis thaliana leaves. We find that robust generation of pore space in the spongy mesophyll requires a balance of cell growth, adhesion, stiffness and tissue pressure to ensure cell networks become porous yet maintain mechanical stability. The success of this mechanical model of morphogenesis suggests that simple physical principles can coordinate and drive the development of complex plant tissues like the spongy mesophyll.

Anne-Lise Routier-Kierzkowska - How to model apical hook growth?
I presented the challenges associated with modeling the process of apical hook formation and maintenance, which is an ongoing project in my lab. I also proposed some solutions, inspired by mathematical models of gravitropic responses. Since this type of modeling is new to my group, I was particularly keen on getting feedback from the workshop participants.

Jingyi Yu - Nonlinear mechanics of epidermal cell walls
The discussion about the interpretation of cell wall stress and how it might differ in different lamella of cell walls were particularly insightful. How cell wall structure changes during wall growth and expansin mediated wall loosening is also of great interests. These discussions provide insight into my work on studying the relationship between wall growth and wall mechanics.

5 Insights gained in the words of the participants

- Based on L Mahadevan’s talk, I thought more about the potential biological/mechanical feedback mechanisms to maintain leaf flatness. This led to a nascent collaboration with a colleague to analyze leaf flatness in the context of cell wall modification.
- Based on Tatiana Gorshkova’s talk, I thought more about how pectin degradation-mediate cell separation might facilitate cavity formation in the stems of flax and other plants.

- Christophe Godin's talk inspired me to consider more deeply how the gene regulatory networks that control flower development might engage in feedback loops with cell wall modification; recent RNAseq data we have collected implies that this is indeed the case.
- Clinton Durney's talk presenting a computational model of the "see-saw" hypothesis for how subsidiary cells in grass stomatal complexes interact with guard cells to allow for rapid stomatal opening and closure, expanding my own work on the biomechanics of guard cells and neighboring pavement cells in Arabidopsis.
- I came home from the BIRS workshop with a headful of ideas. Ideas to port biological growth phenomena into the mechanical engineering modelling realm. How could be model the deposition of micro-tubules/micro-fibers in response to stress/strain distribution in growing cell walls? How to explain interdigitating pavement cells? How to create fast actuation from slow growing media? How can slipping fiber networks explain the viscoelastic behaviour of plant wall material? I am still digesting these ideas. As an outsider to the world of plant biology, I am a mechanical engineer, this conference reenergized my conviction to study plant biomechanics problems!
- The participants, some of whom are experts in modeling gravitropic responses, gave very precise and helpful feedback, for example concerning the type of referential that would be most optimal for solving our specific problem. This workshop presented a unique opportunity to get this kind of insight on ongoing projects.
- Multi-scale modelling appears as a general need.
- There was a lot of editorial processing of the information by the speakers. This made it much more accessible and highlighted the limitations and important stuff.
- The general conversations about micro-scale cell wall growth dynamics were very useful. The elaboration for the need for mesoscopic models and the pavement cell discussion was extremely fun and interesting.
- There is a need for an article to clarify wall mechanical properties and their relations to growth; insights into the aspects of wall plasticity
- Very valuable novel insights into biomechanics in plant biology from talks covering a wide range of topics. The focus on modeling mechanical properties of cell walls and role of microtubules was most helpful to me. Also, emphasis on using specific experimental data for model calibration was important to me as well. Lastly, talk on modeling formation of fractal structure of cauliflower baes on genetic data was very interesting and helpful to my group.
- There are various modeling tools being developed to simulate plant cell growth patterns. They could factor in gene regulation patterns, cell geometry and cell wall anisotropy.
- Relationships between plastic deformation, creep and wall growth are not well understood.
- Multiscale modeling is a popular idea among the groups but there hasn't been a systematic/coordinative way to do it?
- State of mind of physicists and modellers.
- Many talks covered topics (open questions) not covered usually by papers
- Several talks, especially the very pedagogical one by Coen, clarified for me the nature of the cell wall and the fact that the field still has basic controversies.
- These presentations allowed me either to discover
    - new researches on subjects a little distant from plant-microbe interactions,
    - to have a more direct presentation of papers which seem to me to have consequences for plant-microbe interactions,

    - to realize that the proximity of the topics plant-microbe interactions and growth and morphogenesis share more common points than I had imagined / hope (e.g. proprioception degradation, the fast release of tension mentionned by Yoël in the closure of Venus flytrap ... among others). "
- In many cases I would have not read the work if I did not attend the workshop and their presentations!
- There was a lot of unpublished material and most importantly, synthesis of the struggles and perspectives that can be shared in a format that is never shared in written form.
- Many insights gained. Many pages of handwritten notes. Current papers gleaned and passed on to my students.
- Yes, a lot of insight gained! Charlotte presented unpublished data and synthesised it with work that I wasn't aware of. This was really helpful for thinking about our (tangental) problems.
- It was really interesting to see the 'questions for the future' slides. It gave a sense that we were all tackling similar questions about different modelling strategies. It's helped me think a bit more broadly about not just trying to answer a biological question, but about the importance of developing modelling strategies and frameworks.
- Discussing face to face in front of a board has been essential.
- I gained a lot of knowledge and discovered new topics by listening to the presentations, participating in the afternoon discussion session, and through in-person and slack discussions. The feedback from experts in plant growth and cell wall mechanics has also been extremely beneficial for my own research. This is invaluable compared to just reading the papers.
- I gained a new appreciation for the mathematical basis of some of the models used to analyze plant biomechanics, and of the utility of different forms of modeling (PlantSimLab, Morphodynamx)
- I got to know a lot regarding the basics of the area of plant biomechanics (which for someone who is very new to this field, is very useful), that are sometimes skipped over in papers. The visual representation in slides and the explanations regarding how some ideas came into existence were very helpful. Also, the discussions after the talks were particularly very useful, in order to also re-evaluate/ gain deeper insights into the area of my own research.
- I gained a better understanding of the mesoscale models and how to interpret the continuum models in light of these.
- I think Eric Mjolsness presentation helped me to better understand the significance of Dynamic Graph Grammars and their usefulness in modelling microtubule dynamics of the cytoskeleton in plant cells.
- There were several presentations which I found very interesting. Perhaps I could get similar insights by reading the papers (if the results were already published), but seeing short presentations of the essence of the work which I might never run into by accident was very useful.
- Was able to get clarity about their work through their presentations and questions asked.
- Nice summaries of currently discussed biological hypotheses, easy to understand review of past modeling efforts at cellular scale. Especially, useful for a person working mostly at other modeling scales of abstraction.

- Talks are better at learning the things that don't make it into papers, so in that regard it's useful seeing talks and hearing other people's questions about talks–that is a good way to learn. Meetings are also good ways of getting up to speed on a field and different methods. So I learned about some methods that are relevant to my own work and have a better understanding of what are the questions in the field.
- What is the frontier of the computational biomechanics in plant cells and tissues.
- I gained a better overview on the theoretical/quantitative/computational biology aspects of plant biology that I would not have gained in the same time by reading papers.
- I think I am understanding Cosgrove work a bit deeper now.
- Some major insights came from the talks from people that I knew really little about their work. Sometimes this provides new ideas!
- It was good to see what people are doing, and for me especially how the modeling compares to what we are doing.
- I particularly enjoyed Daniel Cosgrove's presentation, which made me appreciate sind aspects of the model I did not fully consider from the literature.