IN PARTNERSHIP WITH:
CIRAD

INRA

Activity Report 2016

Project-Team VIRTUAL PLANTS

Modeling plant morphogenesis at different scales, from genes to phenotype

IN COLLABORATION WITH: Amélioration génétique et adaptation des plantes (AGAP)

RESEARCH CENTER
Sophia Antipolis - Méditerranée

THEME
Computational Biology

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Creation of the Project-Team: 2007 July 01

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1. Members

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2. Overall Objectives

2.1. Overall Objectives

The Virtual Plants team is a joint team between Inria, CIRAD and INRA located in Montpellier. The long-term focus of the project is to study plant development, its modulation by the environment and its control by genetic processes.

Plants are branching living organisms that develop throughout their lifetimes. Organs are created by small embryogenetic regions at the tip of each axis, called *apical meristems*. In the project Virtual Plants, we are interested in studying plant apical meristem functioning and development. We develop a detailed analysis of apical meristem processes, based on advanced mathematical and computational methods and tools, to get a deeper and better understanding of plant development.

This study is performed from two complementary perspectives.

- First, at a macroscopic level, we develop an extensive methodology to analyze *the structures produced by meristems*. This can be seen as a methodology that aims to solve an inverse problem in which one tries to infer meristem functioning from the complex structures they produce. This analysis is carried out at different spatial and temporal scales.
- Second, at a more microscopic level, we intend to exploit the recent spectacular scientific and technological progresses in developmental biology in order to understand how physiological and genetic processes control meristem growth at cell scale.

To develop these two scientific axes, we carry out research in three main categories of models and methods:

- multiscale models for the spatial (topological and geometrical) representation of structured biological objects (which range from meristem tissues to branching structures),
- methods and models for deciphering the organization of these complex biological objects,
- and models for morphogenesis.

In order to make our methods and models available to our partners, all our tools are integrated in a common software platform: *V-Plants*. Based on this platform, we coordinate the development of an open software platform, *OpenAlea*, for plant modeling at a national and international level.

3. Research Program

3.1. Analysis of structures resulting from meristem activity

To analyze plant growth and structure, we focus mainly on methods for analyzing sequences and tree-structured data. Theses methods range from algorithms for computing distance between sequences or tree-structured data to statistical models.

- *Combinatorial approaches*: plant structures exhibit complex branching organizations of their organs like internodes, leaves, shoots, axes, branches, etc. These structures can be analyzed with combinatorial methods in order to compare them or to reveal particular types of organization. We investigate a family of techniques to quantify distances between branching systems based on non-linear structural alignment (similar to edit-operation methods used for sequence comparison). Based on these techniques, we study the notion of (topology-based) self-similarity of branching structures in order to define a notion of degree of redundancy for any tree structure and to quantify in this way botanical notions, such as the physiological states of a meristem, fundamental to the description of plant morphogenesis.
- *Statistical modeling*: We investigate different categories of statistical models corresponding to different types of structures.

  - Longitudinal data corresponding to plant growth follow up: the statistical models of interest are equilibrium renewal processes and generalized linear mixed models for longitudinal count data.
  - Repeated patterns within sequences or trees: the statistical models of interest are mainly (hidden) variable-order Markov chains. Hidden variable-order Markov chains were in particular applied to characterize permutation patterns in phyllotaxis and the alternation between flowering and vegetative growth units along sympodial tree axes.
  - Homogeneous zones (or change points) within sequences or trees: most of the statistical models of interest are hidden Markovian models (hidden semi-Markov chains, semi-Markov switching linear mixed models and semi-Markov switching generalized linear models for sequences and different families of hidden Markov tree models). A complementary approach consists in applying multiple change-point models. The branching structure of a parent shoot is often organized as a succession of branching zones while the succession of shoot at the more macroscopic scale exhibit roughly stationary phases separated by marked change points.

  We investigate both estimation methods and diagnostic tools for these different categories of models. In particular we focus on diagnostic tools for latent structure models (e.g. hidden Markovian models or multiple change-point models) that consist in exploring the latent structure space.

- *A new generation of morphogenesis models*: Designing morphogenesis models of the plant development at the macroscopic scales is a challenging problem. As opposed to modeling approaches that attempt to describe plant development on the basis of the integration of purely mechanistic models of various plant functions, we intend to design models that tightly couple mechanistic and empirical sub-models that are elaborated in our plant architecture analysis approach. Empirical models are used as a powerful complementary source of knowledge in places where knowledge about mechanistic processes is lacking or weak. We chose to implement such integrated models in a programming language dedicated to dynamical systems with dynamical structure $(DS)^2$, such as L-systems or MGS. This type of language plays the role of an integration framework for sub-models of heterogeneous nature.

3.2. Meristem functioning and development

In this second scientific axis, we develop models of meristem growth at tissue level in order to integrate various sources of knowledge and to analyze their dynamic and complex spatial interaction. To carry out this integration, we need to develop a complete methodological approach containing:

- algorithms for the automatized segmentation in 3D, and cell lineage tracking throughout time, for images coming from confocal microscopy,
- design of high-level routines and user interfaces to distribute these image analysis tools to the scientific community,
- tools for structural and statistical analysis of 3D meristem structure (spatial statistics, multiscale geometric and topological analysis),
- physical models of cells interactions based on spring-mass systems or on tensorial mechanics at the level of cells,
- models of biochemical networks of hormonal and gene driven regulation, at the cellular and tissue level, using continuous and discrete formalisms,
- and models of cell development taking into account the effects of growth and cell divisions on the two previous classes of models.

4. Highlights of the Year

4.1. Highlights of the Year

- *Stochastic model of Phyllotaxis*: Exploration of developmental mechanisms classically relies on analysis of pattern regularities. Whether disorders induced by biological noise may carry information on building principles of developmental systems is an important debated question. In this work, we addressed theoretically this question using phyllotaxis, the geometric arrangement of plant aerial organs, as a model system. Phyllotaxis arises from reiterative organogenesis driven by lateral inhibitions at the shoot apex. Motivated by recurrent observations of disorders in phyllotaxis patterns, we revisited in depth the classical deterministic view of phyllotaxis. We developed a stochastic model of primordia initiation at the shoot apex, integrating locality and stochasticity in the patterning system. This stochastic model recapitulates phyllotactic patterns, both regular and irregular, and makes quantitative predictions on the nature of disorders arising from noise. Altogether, we show that disorders in phyllotaxis instruct us on the parameters governing phyllotaxis dynamics, and thus that disorders can reveal biological watermarks of developmental systems [27].
- *Statistical methods*: One of our main activities consists of identifying and characterizing developmental patterns in plant phenotyping data. Phenotyping data are very diverse ranging from the tissular to the whole plant scale but are often highly structured in space, time and scale. We intend to analyse such data using state-of-the-art methods at the crossroad between statistical modelling, machine learning and pattern recognition. This generates regularly new methodological results as illustrated this year by [18] and [25].

5. New Software and Platforms

5.1. OpenAleaLab

KEYWORDS: Bioinformatics - Biology - Workflow - Modelling Environment
FUNCTIONAL DESCRIPTION

OpenAleaLab is an integrated modelling environment (IME) designed for scientists based on IPython and on OpenAlea components. This open source environment is extensible via plug-ins and allows user to work with a set of diverse modelling paradigms like imperative languages (Python, R), scientific workflows (visual programming) or rule-based language (L-System). This IME, built using PyQt, provides an IPython shell, a text editor, a project manager, a graphical package installer and a world, containing the objects and state variables shared by the different paradigms. The world can be graphically interpreted in 3D or 2D. Different paradigms and tools for plant modelling are available as plug-ins, such as a visual programming environment, a L-system language, a 3D viewer, and an R editor and interpreter. The plug-in system is based on setuptools entry-points and provide both functional and GUI components. This environment is designed to be easily extensible in order to include new plant modelling paradigms in the future or to be customized for other scientific domains. Several dedicated extensions (TissueLab, PlantLab) have been developed or are in development.

- Participants: Christophe Pradal, Christophe Godin.
- Contact: Christophe Pradal, Christophe Godin
- URL: http://virtualplants.github.io/

5.2. TissueLab

KEYWORDS: Bioinformatics - Biology - Modelling Environment
FUNCTIONAL DESCRIPTION

TissueLab is an OpenAleaLab extension dedicated to study plant morphogenesis at the scale of the tissues. This extension was built on the basis of several key concepts of OpenAleaLab (project, world, interactive panels, etc.) and using its plugin mechanism (dynamically discovered, modular, extensible, etc.). TissueLab provides a framework for the visualization, exploration, interaction, reconstruction, analysis and simulation of tissue development based on image sequences. It contains for instance the PyThor module, dedicated to 3D real-time interaction and modification of segmented images for the creation of ground truth segmentations.

- Participants: Sophie Ribes, Guillaume Baty, Guillaume Cerutti, Alizon Konig, Grégoire Malandain, Christophe Pradal, Christophe Godin.
- Contact: Christophe Godin
- URL: https://github.com/virtualplants/tissuelab

5.3. Draco-Stem

KEYWORDS: 3D Reconstruction - Triangular Mesh - Biomechanical Simulations
FUNCTIONAL DESCRIPTION

A computational tool called DRACO-STEM (Dual Reconstruction by Adjacency Complex Optimization - SAM Tissue Enhanced Mesh) has been made available, with the aim of bridging the gap between experimental data and tissue biomechanics models. It provides the necessary tools to generate a FEM-ready, topologically accurate, complete 3D triangular mesh of meristematic tissue, based on a segmented image obtained from a confocal microscopy acquisition. The produced meshes proved to be useable as an input for computational simulations of biomechanical and physiological cellular processes.

- Participants: Guillaume Cerutti, Christophe Godin, Olivier Ali
- Contact: Guillaume Cerutti
- URL: https://github.com/VirtualPlants/draco_stem/

5.4. ASTEC

KEYWORDS: Segmentation - Tracking - High resolution
FUNCTIONAL DESCRIPTION

A new algorithmic pipeline, ASTEC (Adaptative Segmentation and Tracking of Embryonic Cells), has been developed to segment and track cell shapes in 3D from movies with high spatio-temporal resolution of embryos where the membranes have been labeled (using dye or genetic markers for example). To segment the 3D embryo image at a given time-point, ASTEC takes advantage of the high spatial resolution of the movie in order to propagate the segmentation of the previous time points. This, coupled to biological knwoledge on the studied system, allows to constrain the segmentation and to track cells throughout time simulataneously. Moreover, the propagation allows to bound the potential mistakes of segmentation (e.g. a cells cannot disappear) which enables powerful post-correction based on the study of the resulting tracking.

- Participants: Léo Guignard, Emmanuel Faure, Grégoire Malandain, Patrick Lemaire, Christophe Godin
- Contact: Christophe Godin
- URL: https://gforge.inria.fr/projects/marsalt/

5.5. AutoWIG

KEYWORDS: Syntaxic Analysis
FUNCTIONAL DESCRIPTION

High-level programming languages, such as Python and R, are popular among scientists. They are concise, readable, lead to rapid development cycles, but suffer from performance drawback compared to compiled languages. However, these languages allow to interface C, C++ and Fortran code. In this way, most of the scientific packages incorporate compiled scientific libraries to both speed up the code and reuse legacy libraries. While several semi-automatic solutions and tools exist to wrap these compiled libraries, the process of wrapping a large library is cumbersome and time consuming. We developped AutoWIG [40], [47], a Python library that wraps automatically compiled libraries into high-level languages. Our approach consists in parsing C++ code using the LLVM/Clang technologies and generating the wrappers using the Mako templating engine. Our approach is automatic, extensible, and applies to very complex C++ libraries, composed of thousands of classes or incorporating modern meta-programming constructs. The usage and extension of AutoWIG have been illustrated on a set of statistical libraries (StructureAnalysis).

- Participants: Pierre Fernique, Christophe Pradal
- Contact: Pierre Fernique
- URL: https://github.com/VirtualPlants/AutoWIG

5.6. Phenomenal

KEYWORDS: Image Analysis, Phenotyping
FUNCTIONAL DESCRIPTION

Phenomenal [65] is a Python library dedicated to the analysis of high throughput phenotyping data and models. It has been developed in the frame of the Phenome high throughput phenotyping infrastructure. It is based on the OpenAlea platform [76], [77] that provides methods and softwares for the modelling of plants, together with a user-friendly interface for the design and execution of scientific workflows. OpenAlea is also part of the InfraPhenoGrid infrastructure that allows high throughput computation and recording of provenance during the execution [26].

- Participants: Simon Artzet, Jérôme Chopard, Tsu-Wei Chen, Nicolas Brichet, Christian Fournier, Christophe Pradal
- Contact: Christian Fournier, Christophe Pradal
- URL: https://gitlab.inria.fr./phenome/phenomenal

5.7. Platforms

5.7.1. Platform OpenAlea

OpenAlea is an open-software platform for interdisciplinary research in plant modeling and simulation. This scientific workflow platform is used for the integration and comparison of different models and tools provided by the research community. It is based on the Python (http://www.python.org) language that aims at being both a *glue* language for the different modules and an efficient modeling language for developing new models and tools. *OpenAlea* currently includes modules for plant simulation, analysis and modeling at different scales (*V-Plants* modules), for modeling ecophysiological processes (*Alinea* modules) such as radiative transfer, transpiration and photosynthesis (*RATP*, *Caribu*, *Adel*, *TopVine*, *Ecomeristem*) and for 3D visualization of plant architecture at different scales (*PlantGL*).

OpenAlea is the result of a collaborative effort associating 20 french research teams in plant modeling from Inria, CIRAD, INRA and ENS Lyon. The Virtual Plants team coordinates both development and modeling consortia, and is more particularly in charge of the development of the kernel and of some of the main data structures such as multi-scale tree graphs and statistical sequences.

OpenAlea is a fundamental tool to share models and methods in interdisciplinary research (comprising botany, ecophysiology, forestry, agronomy, applied mathematics and computer science approaches). Embedded in Python and its scientific libraries, the platform may be used as a flexible and useful toolbox by biologists and modelers for various purposes (research, teaching, rapid model prototyping, communication, etc.).

New methodological developments around scientific workflows in *OpenAlea* have been done recently.

5.7.2. Platform Sofa

Our team is increasingly using the platform SOFA developed at Inria by other teams, in conjunction with OpenAlea, to model biomechanics of plant tissues. SOFA (https://www.sofa-framework.org) is an Open Source framework primarily targeted at real-time simulation, with an emphasis on biological simulation. It is mostly intended for the research community to help develop new algorithms, but can also be used as an efficient prototyping tool. Based on an advanced software architecture, it allows the creation of complex and evolving simulations by combining new algorithms with algorithms already included in SOFA, the modification of most parameters of the simulation (deformable behavior, surface representation, solver, constraints, collision algorithm, etc.) by simply editing an XML file, the building of complex models from simpler ones using a scene-graph description, the efficient simulation of the dynamics of interacting objects using abstract equation solvers, the reuse and easy comparison of a variety of available methods. It has been extensively used by our team in the recent years to conduct virtual mechanical experiments on plant tissues (see section 6.2.3).

6. New Results

6.1. Analysis of structures resulting from meristem activity

6.1.1. Acquisition and design of plant geometry

Participants: Frédéric Boudon, Christophe Pradal, Christophe Godin, Christian Fournier, Ibrahim Chedaddi, Mathilde Balduzzi, Julien Diener.

Virtual 3D model of plants are required in many areas of plant modeling. They can be used for instance to simulate physical interaction of real plant structures with their environment (light, rain, wind, pests, ...), to set up initial conditions of growth models or to assess their output against real data. In the past decade, methods have been developed to digitize plant architectures in 3D [81], [68]. These methods are based on direct measurements of position and shape of every plant organ in space. Although they provide accurate results, they are particularly time consuming. More rapid and automated methods are now required in order to collect plant architecture data of various types and sizes in a systematic way. In this aim, we explore the use of laser scanner and pictures.

- *Reconstruction of tree structures from 3D laser scanner data.* (Olivier Simler [AFEF, AGAP], Chakkrit Preuksakarn, Frédéric Boudon, Christophe Godin, Benoit Pallas [AFEF, AGAP], Evelyne Coste [AFEF, AGAP])

  We investigate the possibility to use 3D laser scanners to automate plant digitizing. We are developing algorithms to reconstruct branching systems without leaves or foliage from scanner data or from scan simulated on plant mock-up obtained using different digitizing method.

  For the branching systems, we previously proposed a reconstruction method to reconstruct plausible branching structures from laser scanner data based on the concept of space colonization [78]. Additionally, a number of automatic methods were proposed in the literature. A graphical editor has been developed and makes it possible to test these different methods and correct manually the reconstruction on laser scans. An additional validation pipeline makes it possible to compares automatic reconstruction with ground truth data using two indices of geometrical and structural similarities [59].

  This year, the editor has been augmented for better user control over the different step of the reconstruction process. Some first alignment procedures of scans and reconstructions made at different times of the year have been also implemented. An application for the reconstruction of an apple tree core collection has been conducted during the internship of O. Simler in a collaboration with the AFEF Team of UMR AGAP.

- *Characterizing wheat canopy characteristics from LiDAR measurements.* (Shouyang Liu [Emmah,Inra], Fred Baret [Emmah,Inra], Frédéric Boudon, Christian Fournier)

Green area index (GAI) has been difficult to estimate accurately at large scales due to the cost prohibitive nature of classical in-situ methods. We propose to use LiDAR to overcome this problem. Through this work, we proposed a self-learning method to estimate GAI using LiDAR-derived metrics over a wheat field.

Specifically, we developed a LiDAR simulator to carry out scanning on digital 3D objects, mimicking the measuring principle and setups of actual LiDAR sensors. The footprint and the geometrical configuration of the LiDAR are explicitly accounted for. Comparison with measurements of actual LiDAR demonstrates that the simulator generates a 3D point cloud having the same statistical properties as those derived from the actual LiDAR measurements.

We then used a machine learning algorithm to correlate LiDAR-derived metrics and GAI over synthetic datasets. 3D wheat canopy scenes were generated with AdelWheat model for two contrasting development stages across a wide range of combination of the model parameters. The scenes were transformed into 3D point clouds using the LiDAR simulator. Results demonstrate that emerging properties, such as leaf area index (GLAI), could be retrieved with a good accuracy.

- *Reconstruction of annual plants from multi-view images.* (Simon Artzet, Jerome Chopard, Christian Fournier, Christophe Pradal, Christophe Godin, Xavier Sirault [CSIRO-HRPPC, Canberra], Tsu-Wei Chen[Inra, LEPSE])

  Image-based phenotyping platforms in semi-controlled conditions offer large possibilities to perform genetic analyses of plant growth, architecture, light interception, and biomass accumulation over large time series for thousands of plants. However, methods for image analysis currently available are still very crude and need improvement and robustness to process huge amount of data. We are developing a python software framework dedicated to the analysis of high throughput phenotyping data and models named Phenomenal. This software framework currently consists of 2D and 3D image analysis workflow which ranges from 2D organs segmentation, 3D multi-view reconstruction, image-base meshing transformation, 2D/3D morphological thinning/skeletonization, 3D segmentation and tracking of plant organs maize (under development). We have processed images from phenoarch platform of the last four years and have built for each plant (maize, cotton, etc.) a voxel point cloud and image-base meshing representation and also for 725 maize plants a voxel point cloud automatically segmented (currently stem and mature leaf). Each process is run on distant server (private or virtual machines on FranceGrille cloud) and results can be viewed via a jupyter notebook server. Furthermore, 3D FSPM model for maize architectural development (named ADEL), is used to help segmenting plant images and to automate the mapping between segmented 3D objects and plant organs defined in the model. The 3D reconstructed model is combined with meteorological data to feed a light distribution model and estimate light use efficiency. This software framework was presented to “BMVA technical meeting: Plants in Computer Vision”.

- *Reconstruction of virtual fruits from pictures.* (Ibrahim Chedaddi, Mik Cieslak, Nadia Bertin [Inra, Avignon], Frédéric Boudon, Christophe Godin, Michel Genard [Inra, Avignon], Christophe Goz-Bac [Université Montpellier 2])

  This research theme is supported by the Agropolis project MecaFruit3D.

  The aim of this work is to provide methods for generating fruit structure that can be integrated with models of fruit function. To this end, a modeling pipeline has been developed in the OpenAlea platform. It involves two steps: (1) generating a 3D volumetric mesh representation of the entire fruit, and (2) generating a complex vascular network that is embedded within this mesh using the concept of space colonization [80]. Previous studies demonstrated the possibility to create species-specific models of fruit structure with relatively low effort [63]. We focus now on validating the vascular networks by comparing them to experimental data from the literature. This work has been presented at the ISHS symposium in Montpellier [60] and resulted in a publication [17].

  Using these fruit virtual structures, a mechanical model of fruit growth is also developed (see section 6.3.2) taking into account the distribution of water fluxes in the fruit.

- *Review on morphological plant modelling.* (Christophe Pradal, Mathilde Balduzzi, Alexander Bucksch [Georgia Univ., USA], Daniel H. Chitwood [Donald Danforth Plant Science Center, USA])

  Plant morphology is inherently mathematical. The geometries of leaves and flowers and intricate topologies of the root have fascinated plant biologists and mathematicians alike. Beyond providing aesthetic inspiration, understanding plant morphology has become pressing in an era of climate change and a growing population. Gaining an understanding of how to modify plant architecture through molecular biology and breeding is critical to improving agriculture, and the monitoring of ecosystems and global vegetation is vital to modeling a future with fewer natural resources. In this review [45], we begin by summarizing the rich history and state of the art in quantifying the form of plants, mathematical models of patterning in plants, and how plant morphology manifests dynamically across disparate scales of biological organization. We then explore the fundamental challenges that remain unanswered concerning plant morphology, from the barriers preventing the prediction of phenotype from genotype to modeling the fluttering of leaves in a light breeze. We end with a discussion concerning the education of plant morphology synthesizing biological and mathematical approaches and ways to facilitate research advances through outreach, cross-disciplinary training, and open science.

6.1.2. Modeling the plant ontogenic program

Participants: Christophe Godin, Yann Guédon, Jean-Baptiste Durand, Pierre Fernique, Marc Labadie, Christophe Pradal, Jean Peyhardi.

This research theme is supported by one PhD program.

The remarkable organization of plants at macroscopic scales may be used to infer particular aspects of meristem functioning. The fact that plants are made up of the repetition of many similar components at different scales, and the presence of morphological gradients, e.g. [54], [70], [71], [67], provides macroscopic evidence for the existence of regularities and identities in processes that drive meristem activity at microscopic scales. Different concepts have been proposed to explain these specific organizations such as "morphogenetic program" [75], "age state" [66] or "physiological age" [56]. All these concepts state that meristem fate changes according to position within the plant structure and during its development. Even though these changes in meristem fate are specific to each species and lead to the differentiation of axes, general rules can be highlighted [66], [56]. Here we develop computational methods to decipher these rules.

- *Relating branching structure to the shoot properties.* (Jean Peyhardi, Yann Guédon, Evelyne Coste [AGAP, AFEF team], Catherine Trottier [I3M], Yves Caraglio [AMAP], Pierre-Eric Lauri [AGAP, AFEF team])

  Shoot branching structures often take the form of a succession of homogeneous branching zones and have been analyzed using segmentation models such as hidden semi-Markov chains. Axillary meristem fates are influenced by local properties of the parent shoot such as for instance its growth rate or local curvature. The objective of this work is to develop statistical models that generalize hidden semi-Markov chains with the capability to incorporate explanatory variables that vary along the parent shoot (e.g. leaf growth rate, leaf surface, internode length, local curvature of the parent shoot). More precisely, the simple multinomial distributions that represent the axillary productions observed in the different branching zones are replaced by multinomial generalized linear models (GLMs). Since the two classical categories of multinomial GLMs that correspond either to nominal or ordinal categorical response variables were not appropriate, we chose to develop a new family of multinomial GLMs called partitioned conditional GLMs [25] that enable to tackle hierarchically-structured categorical response variables. Typically, we need to distinguish different timing of branching events (e.g. immediate shoot, one-year-delayed shoot and latent bud), different categories of offspring shoots (e.g. among one-year-delayed shoots, vegetative short shoot, vegetative long shoot and flowering shoot) and to specialize the explanatory variables for certain categories of offspring shoots (e.g. the growth of the parent shoot influence the immediate offspring shoots but not the one-year-delayed offspring shoots). The resulting integrative models are called semi-Markov switching partitioned conditional GLMs and have been applied to apple and pear tree branching structures.

- *Genetic determinisms of the alternation of flowering in apple tree progenies.* (Jean-Baptiste Durand, Alix Allard [AGAP, AFEF team], Evelyne Costes [AGAP, AFEF team])

  A first study was published to characterize genetic determinisms of the alternation of flowering in apple tree progenies [64]. Data were collected at two scales: at whole tree scale (with annual time step) and a local scale (annual shoots, which correspond to portions of stems that were grown during the same year). Two replications of each genotype were available.

  Indices were proposed for early detection of alternation during the juvenile phase. They were based on a trend model and a quantification of the deviation amplitudes and dependency, with respect to the trend. This allowed early quantification of alternation from the yearly numbers of inflorescences at tree scale. Some quantitative trait loci (QTL) were found in relation with this indices.

  For better interpretation of the relationships of alternation at both scales, new models and indices were developed for sequences of flowering events at axis scale. New data sets where collected in other F1 progenies. Ancestral relationships between parents of different progenies were taken into account to enhance the power of QTL detection using Bayesian methods, and other QTL were found using these new indices.
- *Characterizing tree patchiness using a tree segmentation/clustering approach.* (Pierre Fernique, Anaëlle Dambreville, Jean-Baptiste Durand, Christophe Pradal, Yann Guédon, Frédéric Normand [CIRAD, HortSys, Réunion Island], Pierre-Eric Lauri [INRA, System]).

  Patchiness is characterized by clumps of homogeneous botanical entities (e.g. a clump of flowering growth units) within tree canopy. It is therefore assumed that there are subtrees within which the characteristics of the botanical entities follow the same or nearly the same distribution, and between which these characteristics have different distributions. The detection of such subtrees can thus be stated as tree-indexed data segmentation. We therefore transposed multiple change-point models to tree-indexed data. The output of the segmentation procedure is a partition of trees such that two non-adjacent subtrees can be very similar in terms of botanical entity characteristics. We thus incorporated a second stage of clustering of subtrees based on a mixture model in order to group non-adjacent similar subtrees. This statistical modeling framework was applied to young mango trees [32].
- *Simulating fruit tree phenology.* (A.S. Briand, Frédéric Boudon, Frédéric Normand [CIRAD, HortSys, Réunion Island], Anaëlle Dambreville, Jean-Baptiste Durand, Pierre Fernique, Yann Guédon, Christophe Pradal, Pierre-Eric Lauri [INRA, System])

  Mango is a tropical tree characterized by strong asynchronisms within and between trees. To study more precisely the interplay between the plant structural components, we built an integrative model to simulate the plant development based on the L-system formalism and GLM to model the dependencies between events. With such model, we showed the importance of architectural and temporal factors in the development of the units of the trees, see 1. The model also simulates the phenology of shoots and inflorescences. For this, the sizes of the different organs is modelled by statistical laws estimated from measurements that depends on their locations in the architecture. The growth speed of organs is modulated by the temperature. The model has been then coupled with an ecophysiological model of fruit growth [73], [74]. The global aim is to have a crop simulation model to predict fruit yield and quality on mango tree. An overview of this global model based on the coupling of different structural or ecophysiological sub-models has been also presented in the FSPMA conference [44].

  In the context of the PhD of S. Persello, we aim at extending this model with the effect of agricultural practices. For this, a number of experiment has been conducted this year with some mango trees being pruned with different intensity (global mass removed) and severity (depth of the removed elements). Analysis and characterization of the effect of pruning on the subsequent vegetative development of the tree in currently under investigation.

Figure 1. Simulation of the development of a mango tree over two cycles [58]. The first and last image corresponds to the end of the vegetative period of the 3rd and 5th growing cycle (June), respectively while the second and third images correspond to the flowering phase (August) of the 3rd and 4th cycles, respectively. The different colours of the inflorescences of the 3rd image show different developmental stages and the flowering asynchronism over the tree.

- *Characterizing the successive flowering phases of strawberry in relation to genetic determinants.* (Yann Guédon, Marc Labadie, Béatrice Denoyes [INRA, UMR BFP, Villenave d'Ornon], Justine Perrotte)

  Our aim was to characterize the phenology of perpetual flowering strawberry genotypes, which is of particular importance for better predicting fruit production. We applied multiple change-point models for the synchronous segmentation of the individuals of a given genotype in successive flowering phases [24]. We identified two groups of genotypes that differ by the intensity of the flowering at the end of the flowering period. Using a genetic approach, we identified a locus controlling the flowering intensity at the end of the flowering period that likely explain these two groups of genotypes. A multivariate generalization of the synchronous segmentation approach is developed in the context of Marc Labadie's PhD [50], the idea being to characterize not only the flowering pattern as in our first study but more generally the developmental pattern combining vegetative development, branching and flowering.

- *Self-nested structure of plants.*(Christophe Godin, Romain Azaïs, Farah Ben Naoum, Jean-Baptiste Durand, Alain Jean-Marie)

  In a previous work [6], we designed a method to compress tree structures and to quantify their degree of self-nestedness. This method is based on the detection of isomorphic subtrees in a given tree and on the construction of a DAG (Directed Acyclic Graph, equivalent to the original tree, where a given subtree class is represented only once (compression is based on the suppression of structural redundancies in the original tree). In the compressed graph, every node representing a particular subtree in the original tree has exactly the same height as its corresponding node in the original tree.

  The method proposed in [6] thus compresses a tree in width, but not in height. In a new work, we designed an extension of this compression method in which a tree is compressed in both width and height. The method is based on the detection of so-called *quasi-isomorphic paths* in a tree and on the compression of these paths in height. A paper describing the corresponding algorithms has been recently accepted in the Journal of Theoretical Biology [16].

  The class of self-nested trees presents remarkable compression properties because of the systematic repetition of subtrees in their structure. In a collaboration with two other Inria project-teams (MISTIS and BIGS), studied methods to approximate a tree with a tree in the class of self-nested trees. We first provided a better combinatorial characterization of this specific family of trees. We then showed that self-nested trees may be considered as an approximation class of unordered trees. We finally compared our approximation algorithms with a competitive approach of the literature on a simulated dataset. [42]

6.1.3. Analyzing the influence of the environment on the plant ontogenic program

Participants: Jean-Baptiste Durand, Christian Fournier, Christophe Godin, Yann Guédon, Christophe Pradal, Jean Peyhardi, Pierre Fernique, Guillaume Garin.

This research theme is supported by three PhD programs.

The ontogenetic programme of a plant is actually sensitive to environmental changes. If, in particular cases, we can make the assumption that the environment is a fixed control variable (see section 6.1.2), in general the structure produced by meristem results from a tight interaction between the plant and its environment, throughout its lifetime. Based on observations, we thus aim to trace back to the different components of the growth (ontogenetic development and its modulation by the environment). This is made using two types of approaches. On the one hand, we develop a statistical approach in which stochastic models are augmented with additional time-varying explanatory variables that represent the environment variations. The design of estimation procedures for these models make it possible to separate the plant ontogenetic programme from its modulation by the environment. On the other hand, we build reactive models that make it possible to simulate in a mechanistic way the interaction between the plant development and its environment.

- *Investigating how architectural development interfere with epidemics and epidemic control.* (Christian Fournier, Corinne Robert [Ecosys, INRA], Guillaume Garin [ITK, Montpellier], Bruno Andrieu [Ecosys, INRA], Christophe Pradal)

  Sustainable agriculture requires the identification of new, environmentally responsible strategies of crop protection. Modelling of pathosystems can allow a better understanding of the major interactions inside these dynamic systems and lead to innovative protection strategies. In particular, functional–structural plant models (FSPMs) have been identified as a means to optimize the use of architecture-related traits. A current limitation lies in the inherent complexity of this type of modelling, and thus the purpose of this work is to provide a framework to both extend and simplify the modelling of pathosystems using FSPMs. Complex models are disassembled into separate *knowledge sources* originating from different specialist areas of expertise and these can be shared and reassembled into multidisciplinary models. This year, we worked on four application studies that used the framework. In the frame of the PhD of Guillaume Garin, we perform a validation of the wheat septoria model, an analysis of the influence of the wheat architecture on the competition between septoria and brown rust, and a sensitivity analysis of the response of the severity of septoria to architectural traits. In the frame of the Echap project, we use the wheat-septoria model to indentify optimal date of pesticide application. All these studies allows to populate the framework with consistent example of application, and lead to the development of operational modules that allows the fitting and validation of pathosystem models with experimental data.

- *Investigating how hydraulic structure interfere with gas-exchange dynamics of complex plants canopies under water deficit* (Christophe Pradal, Christian Fournier, Rami Albasha [LEPSE, Inra] and Eric Lebon [LEPSE, Inra])

  Individual leaves positioning within a plant canopy is a major determinant of the spatial distribution pattern of gas-exchange rates and energy budget within that canopy. Under water deficit, this distribution may be altered since soil drying affects stem hydraulic conductivity and, consequently, leaves stomatal conductance, suggesting that the hydraulic structure of the shoot may shape the intra-canopy variability of gas-exchange rates under water deficit. In this project, we design HydroShoot [30], a functional-structural plant model which allows simulating the hydraulic structure, energy budget and gas-exchange fluxes of complex plant canopies under water deficit. Model parameters are calibrated and validated using sapflow and entire plant gas exchange data collected in 2009 and 2012 from grapevine (Vitis vinifera L. cv. Syrah) experiments under three training systems (Lyre, GDC and VSP) having contrasted canopy structures. The model is then used to evaluate the role of the hydraulic structure in predicting the intra-canopy variability of temperature and intrinsic water use efficiency of trained grapevines. The resulting HydroShoot model allows to capture the effect of the different training systems on the spatial distribution of temperature and foliar photosynthesis within the canopy. We show that the intra-canopy variability of gas-exchange dynamics were mainly explained by the variability of local climate conditions, while the role of the hydraulic structure appeared only as secondary. Finally, the proposed HydroShoot model has been implemented for grapevine in the OpenAlea platform and will be extended to other plant architectural systems.

- *Eucalyptus development in response to different water stress and fertilization levels* (Yann Guédon, Charlène Arnaud (CIRAD AMAP and BioWooEB), Sylvie Sabatier (CIRAD AMAP)

  Eucalyptus grandis has been grown successfully in plantations in many tropical regions including southern Brazil. The objective of the PhD of Charlène Arnaud (CIRAD AMAP and BioWooEB) is to study the modulation of the development of Eucalyptus main stems in response to water stresses and different levels of potassium or sodium fertilization. Eucalyptus main stem is characterized by a two-scale growth pattern with (i) at coarse scale, roughly stationary growth phases with phase changes likely corresponding to cold seasons and (ii) at fine scale, more ore less systematic alternation of short and long internodes as a consequence of the phylotactic pattern. We thus developed specific multiple change-point models (piecewise 1st-order autoregressive models) for characterizing this two-scale growth pattern. The objective will be now to study the modulation of this pattern in response to different water stress and fertilization levels.

- *Quantifying the impact of water deficit on the production and flowering of apple trees* (Jean-Baptiste Durand, Benoit Pallas [AGAP, AFEF team], Evelyne Costes [AGAP, AFEF team])

  Water stress generates a number of physiological and morphological responses in plants that depend on the intensity and duration of stress as well as the plant species and development stage. In perennial plants, WS may affect plant development through cumulative effects that modify plant functions, architecture and production over time. Plant architecture depends on the fate of the terminal and axillary buds that can give rise, in the particular case of apple, to reproductive or vegetative growth units (GUs) of different lengths. In this study, the impact of long-term WS (7 years) on the fate of terminal and axillary buds was investigated in relation to flowering occurrence and production pattern (biennial vs regular) in the "Granny Smith" cultivar. It was observed that water stress decreased the total number of GUs per branch, regardless of their type. Conversely, water stress did not modify the timing of the two successive developmental phases characterized by the production of long and medium GUs and an alternation of floral GUs over time, respectively. The analysis of GU successions over time using a variable-order Markov chain that included both the effects of the previous flowering events and water treatment, revealed that water stress reduced the transition towards long and medium GUs and increased transition probabilities toward floral, short and dead GUs. Water stress also slightly increased the proportion of axillary floral GUs. The higher relative frequency of floral GUs compared with vegetative ones reduced the tendency to biennial bearing under water stress. The accelerated ontogenetic trend observed under water stress suggests lower vegetative growth that could, in turn, be beneficial to floral induction and fruit set [29], [37]. Ongoing work is conducted to determine the role of external (temperature and water stress) and internal (hormonal signalling, C source-sink relationships) factors in floral induction and consequently, in the regular or biennial behaviour in fruiting in apple trees. Particularly, its aim is to determine at which scale within the plant the production patterns are impacted by each factor. To analyse the carbon source-sink relationships from shoot to tree scales, this study is based on a set of genotypes displaying a large variability in flowering and production patterns.

6.2. Meristem functioning and development

In axis 2 work focuses on the creation of a *virtual meristem*, at cell resolution, able to integrate the recent results in developmental biology and to simulate the feedback loops between physiology and growth. The approach is subdivided into several sub-areas of research.

6.2.1. Data acquisition and design of meristem models

- *Improvement of the MARS-ALT pipeline robustness.*

  Meristem, laser microscopy, image reconstruction, cell segmentation, automatic lineaging
  Participants: Léo Guignard,, Christophe Godin, Christophe Pradal, Grégoire Malandain [Morpheme, Inria], Gaël Michelin [Morpheme, IPL Morphogenetics, Inria], Guillaume Baty, Sophie Ribes [IBC, UM], Jan Traas [RDP, ENS Lyon], Patrick Lemaire [CRBM, CNRS], Yassin Refahi [RDP, ENS-Lyon / Sainsbury Lab, Cambridge, UK].

  This research theme is supported by a PhD FRM grant, Jan Traas's ERC, Inria ADT programme and the Morphogenetics Inria Project Lab.

  The MARS-ALT (Multi-Angles Registration and Segmentation - Automatic Lineage Tracking) software pipeline [5] automatically performs a segmentation at cell resolution from 3D or 2D voxel images where the membranes/walls are marked (by a die for example) and makes it possible to follow the lineage of these cells through time.

  This year, the ALT tracking pipeline has been reformulated by using a generic cell modeling approach (enabling for example more than one cell division), and both stability and robustness were improved. The modeling approach is generic and can be used on other kind of data (nuclei, human cells, ...). Moreover, the architecture of the image processing components has been modified (plugin approach) and integrated with the TissueLab platform. The new segmentation-tracking library is called TimageTK will be released at the beginning of next year.

  We also finalize the development of a a new segmentation and tracking pipeline, ASTEC (Adaptive Segmentation and Tracking of Embryonic Cells). ASTEC is a one-pass algorithm (in contrast to MARS-ALT, that perform first the segmentation and then the tracking in two-passes) that is best suited for movies with numerous close time-points acquired at high spatio-temporal resolution. This pipeline takes advantage of information redundancy across the movies and biological knowledge on the segmented organism to constrain and improve the segmentation and the tracking. We used this one-pass algorithm to segment and track all cell shapes of a developing embryo of the marine invertebrate *Phallusia mammillata*. As a result we obtained the full track of the shapes of all the cells from the 64 cell stage up to the early tailbud stage (1030 cells undergoing 640 division events followed across 180 time-points through 6 hours of development imaged every 2 minutes, Figure 2).

  Based on this quantitative digital representation, we systematically identified cell fate specification events up to the late gastrula stage. Computational simulations revealed that remarkably simple rules integrating measured cell-cell contact areas with spatio-temporal expression data for extracellular signalling molecules are sufficient to explain most early cell inductions. This work suggests that in embryos developing with stereotyped cell shapes and positions (like *Phallusia mammillata* embryos), the genomic constraints for precise gene expression levels are relaxed, thereby allowing rapid genome evolution.

- *Creating mesh representation of cellular structures.*
  Participants: Guillaume Cerutti, Sophie Ribes, Christophe Godin, Géraldine Brunoud [RDP, ENS], Carlos Galvan-Ampudia [RDP, ENS], Teva Vernoux [RDP, ENS], Yassin Refahi [RDP, ENS, Sainsbury Lab].

  This research theme is supported the HFSP project Biosensors.

  To produce a more efficient data structure accounting for the geometry of cellular tissues, we studied the problem of reconstructing a mesh representation of cells in a complex, multi-layered tissue structure, based either on membrane/wall images segmented using MARS or on nuclei images of shoot apical meristems. The construction of such mesh structures for plant tissues is currently a missing step in the existing image analysis pipelines.

  We developed tools to reconstruct a 3D cell complex representing the tissue, based on the dual simplicial complex of cell adjacencies. This set of tetrahedra is optimized from a reasonable initial

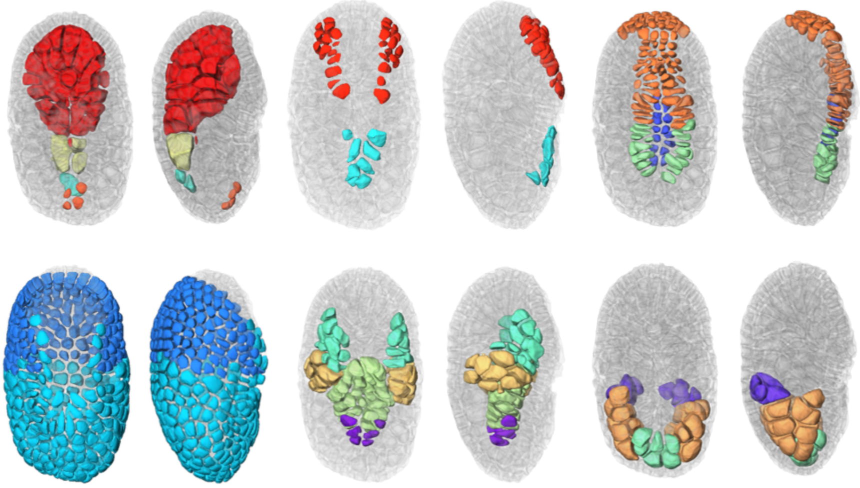

Figure 2. 3D projection of the segmented embryo at the early tailbud stage. The cells are colored by tissue type. The cells are slightly roded to allow their distinction. The other cells of the embryo are in transparent grey. The doral and lateral sides are shown.

guess to match the adjacencies in the tissue, which proved to produce a very faithful reconstruction [62]. We also developed a set of methods to triangulate such reconstructions, and enhance the quality of triangular mesh representations of plant tissue, simultaneously along several criteria [61].

These tools are integrated in the DRACO-STEM computational pipeline released as an independent package to enable biomechanical simulations on real-world data.

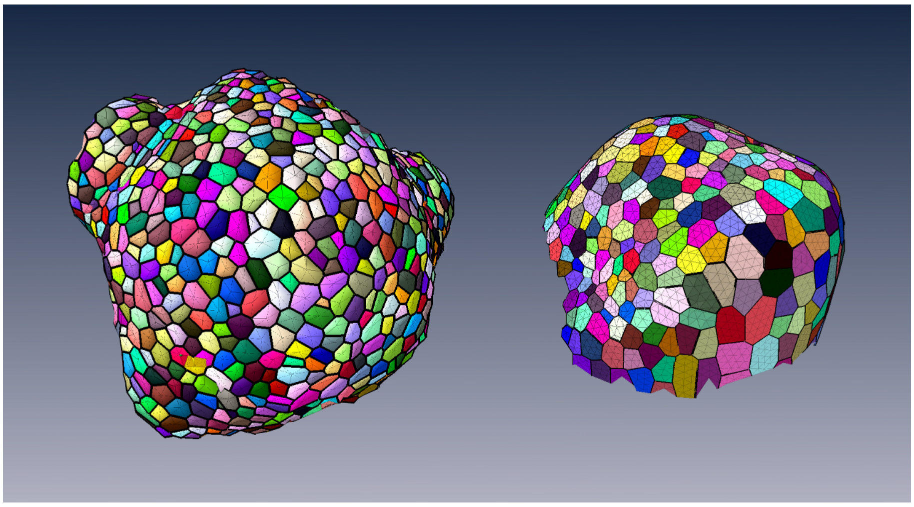

Figure 3. Triangular mesh representations of shoot apical meristem and flower meristem tissues obtained from MARS segmentations

- *Design of 3D digital atlases of tissue development.*
  Participants: Sophie Ribes, Yassin Refahi [RDP, ENS, Sainsbury Lab], Guillaume Cerutti, Christophe Godin, Christophe Pradal, Christophe Pradal, Frédéric Boudon, Gregoire Malandain [RDP, ENS], Gaël Michelin [RDP, ENS], Jan Traas [RDP, ENS], Teva Vernoux [RDP, ENS], Patrick Lemaire [CRBM, CNRS].

  This research theme is supported the Inria Project Lab Morphogenetics, the ADT Mars-Alt and the HFSP project Biosensors.

  To organize the various genetic, physiological, physical, temporal and positional informations, we build a spatialized and dynamic database [72]. This database makes it possible to store all the collected information on a virtual 3D structure representing a typical organ. Each piece of information has to be located spatially and temporally in the database. Tools to visually retrieve and manipulate the information, quantitatively through space and time are being developed. For this, the 3D structure of a typical organ has been created at the different stages of development of the flower bud. This virtual structure contains spatial and temporal information on mean cell numbers, cell size, cell lineages, possible cell polarization (transporters, microtubules), and gene expression patterns. Such 3D digital atlas is mainly descriptive. However, like for classical databases, specific tools make it possible to explore the digital atlas according to main index keys, in particular spatial and temporal keys. Both a dedicated language and a 3D user interface are being designed to investigate and query the 3D virtual atlas. Current developments of this tool consist in using directly the segmented images produced from laser microscopy to build the atlas. To better represent the development of a biological population, a method to compute an "average" structure is being investigated.

6.2.2. Shape analysis of meristems

Participants: Jonathan Legrand, Guillaume Cerutti, Pierre Fernique, Frédéric Boudon, Yann Guédon, Christophe Godin, Pradeep Das [RDP, ENS], Arezki Boudaoud [RDP, ENS].

The MARS-ALT pipeline provides rich spatio-temporal data sets for analyzing the development of meristems, since it allows to performs 3D cell-segmentation and to compute cell-lineage. This enable the extraction and study of spatio-temporal properties of a tissue at cellular scale. To facilitate the analysis and to structure the obtained data have implemented a dedicated temporal graph structure. In this graph, vertex are cells and edges are spatial or temporal relationships, thus proposing a natural representation of the growing tissue. Various variables can be attached either to the vertices (e.g. cell volume, inertia axes) or the edges (e.g. wall surface, distance between cell centroids). This graph may be augmented by new variables resulting from various spatial or temporal filtering (e.g. cell volumetric growth). Looking at homogeneous regions in the variable space, cellular patterns can be identified, by clustering methods for instance.

Considering the highly-structured nature of our data (time and space structuring) and the potential diversity and heterogeneity of possible cell descriptors, we developed two complementary approaches:

- A first one that favours the spatial structuring: In this approach, the cell neighbourhood and the cell descriptors are jointly taken into account in a clustering approach whose objective is to identify a small number of clusters corresponding to well-defined cell identities. Once the cells have been labelled using the clustering algorithm, cell generation distributions may be estimated on the basis of the labelled lineage trees.
- A second one that favours the temporal structuring: In this approach, the data of interest are lineage forest and the only spatial structuring taken into account corresponds to siblings with respect to a given parent cell. In a first step, cell identities are inferred on the basis of the cell descriptors taking into account lineage relationships using hidden Markov tree models and the spatial regions that emerge from the cell identity labelling are then characterized. This second approach is supported by the fact that cell topology is only affected by division which makes highly relevant the local spatial information taken into account in this approach.

6.2.3. Mechanical models of plant tissues

Participants: Jean-Philippe Bernard, Olivier Ali, Christophe Godin, Benjamin Gilles, Frédéric Boudon, Ibrahim Cheddadi, Jan Traas [ENS-Lyon], Olivier Hamant [ENS-Lyon], Arezki Boudaoud [ENS-Lyon].

This research theme is supported by the Inria Project Lab Morphogenetics and Jan Traas's ERC.

During the previous years, we set up a mechanical model of a growing *shoot apical meristem* (the specific tissue at the very tip of plants where stem cells are active and produce new organs such as branches, leafs and flowers). The aim of this project is to provide a computational framework for simulating growth of multicellular plant tissue. This framework integrates a theoretical description of the major biophysical processes at stake. A first version of the model, based on a static description of the tissues rheological properties, has been published last year [57].

This year, we used this model in close collaboration with biologists to investigate the coupling between growth and cell wall remodeling required in early stages of organogenesis. Our simulations pointed out that cell wall remodelling and growth initiation have to be co-regulated in order to initiate young organs formation. Biologists unraveled a biochemical signaling pathway that could explain this synergy. This joint work has been submitted to a high factor Biology journal.

In parallel, we also improved the underlying biophysical theory. One important aspect of the problem is the multiscale interconnections between mechanical forces generated at the scale of the whole tissue and the molecular response to these forces at the subcellular level. To tackle this issue, we established a parcimonous molecular description of the cell wall (one of the main organelle involded in growth) attesting for its biochemical behavior under mechanical loading. This description has been formalized as a unidimensional toy-model. With this toy-model we exposed how large-scale behavior of an expanding cell wall could be controlled by the biochemical behavior of a limited set of molecular actors. This work has been published [14].

Additionally, we started to work on the integration of a feedback loop between mechanical stresses and growth (PhD work of Hadrien Oliveri started in Oct. 2015). A close study of this feedback mechanism made us refine several aspects of our modelling approach. On the molecular scale, we introduced a tensor formalism to quantify cell polarity, based on the description of its cortical microtubule network. Microtubules being stress-sensitive, we described this feedback loop through the coupling between this polarity tensor and the mechanical stress field. In parallel, through a parcimonous model of microtubule-guided cell wall turnover, we derived an expression of the stiffness tensor as a function of cell polarity. This enabled us to relate subcellular stress-induced dynamics of microtubules to the evolution of large scale rheological properties of the tissue. We also started to work on the numerical implementation of this feedback mechanism. FEM-based simulations have been carried out on simple structures as proof of concept. By doing so we assessed the numerical valididy of our resolution scheme along with the relevance of our biophysical description.

6.2.4. *Mechanical modelling of embryo morphogenesis.*

Participants: Bruno Leggio, Emmanuel Faure, Patrick Lemaire [CRBM, CNRS], Christophe Godin.

A work on data analysis and modelling of morphogenesis and development in embryos of ascidians has been started this year. It comprises two main branches: starting from segmented data at cellular resolution, global and local symmetries of embryo development were analyzed. An analysis in terms of entropy of conserved embryonic properties was developed in order to characterise different stages of development as well as different tissues.

In parallel, a mechanical and topological analysis of cell-cell interactions was carried out. This lead us to develop a new and original physical model of cleavage-plane determination in different tissues, with the goal of understanding the role of purely mechanical interactions in shaping ascidian embryos.

6.2.5. *Modelling the influence of dimerisation sequence dissimilarities on the auxin signalling network*

Participants: Jonathan Legrand, Yann Guédon, Jean-Benoist Léger [INRA, MIA, Paris], Stéphane Robin [INRA, MIA, Paris], Teva Vernoux [ENS-Lyon].

Auxin is a major phytohormone involved in many developmental processes by controlling gene expression through a network of transcriptional regulators. In *Arabidopsis thaliana*, the auxin signalling network is made of 52 potentially interacting transcriptional regulators, activating or repressing gene expression. All the possible interactions were tested in two-way yeast-2-hybrid experiments. Our objective was to characterise this auxin signalling network and to quantify the influence of the dimerisation sequence dissimilarities on the interaction between transcriptional regulators [20]. We applied model-based graph clustering methods relying on connectivity profiles between transcriptional regulators. Incorporating dimerisation sequence dissimilarities as explanatory variables, we modelled their influence on the auxin network topology using mixture of linear models for random graphs. Our results provide evidence that the network can be simplified into four groups, three of them being closely related to biological groups. We found that these groups behave differently, depending on their dimerisation sequence dissimilarities, and that the two dimerisation sub-domains might play different roles. We propose here the first pipeline of statistical methods combining yeast-2-hybrid data and protein sequence dissimilarities for analysing protein-protein interactions. We unveil using this pipeline of analysis the transcriptional regulator interaction modes.

6.2.6. *Model integration*

Participants: Frédéric Boudon, Christophe Godin, Guillaume Cerutti, Jean-Louis Dinh, Eugenio Azpeitia, Jan Traas.

This research theme is supported by the Morphogenetics Inria Project Lab.

One key aspect of our approach is the development of a computer platform dedicated to programming virtual tissue development, TissueLab. This platform, based on *OpenAlea*, will be used to carry out integration of the different models developed in this research axis. In the past year, progress has been made in defining a generic tissue data structure that would be visualized, manipulated and updated through this platform. Currently, robust geometric operations such as division are implemented and tested. Moreover, a redesign of the structure based on more elaborated formalisms such as combinatorial maps is being investigated. A 2D version is being developed in the context of Jean-Louis's Dinh PhD thesis, and will be described in a forthcoming book chapter.

6.3. Multi-scale models and analysis: from cells to plant architecture (and back)

6.3.1. Modeling water transport in roots

Participants: Mikaël Lucas [IRD], Christophe Pradal, Christophe Godin, Yann Boursiac [BPMP], Christophe Maurel [BPMP].

This research theme is supported by the ANR project HydroRoot.

A model of Arabidopsis thaliana root hydraulics at the cellular level was developed in the OpenAlea modeling platform. The model relies on the integration throughout root architecture of elementary hydraulic components. Each component integrates local radial and axial water flows. Axial hydraulic conductivity is calculated according to Poiseuille's law, based on local size of xylem vessels. Radial hydraulic conductivity is determined in part by aquaporin activity and was set constant throughout root architecture in the first model versions. In its current state, the model is parameterized using architectural, tissular and physiological data that were experimentally determined in the Aquaporin group at UMR BPMP. The architectural reconstruction of the root system is based on a tridimensional multi-scale tree graph (MTG). The current model is capable of predicting the water flow that is transported by a root system in the standard experimental conditions used in the Aquaporin group. This model was used to perform sensitivity analyses and determine the respective contributions to root hydraulic dynamics of various biological parameters (axial and radial hydraulic conductivites, root architecture). One major finding is that the root hydraulic conductivity (Lpr) computed from the model is highly dependent on root architecture. This is due to the limiting role of axial (xylem) conductance, one feature that had been neglected in previous representations of root water transport. The radial hydraulic conductivity may primarily be limiting in conditions of Lpr inhibition, since its increase from values in control roots has marginal effects on Lpr. A new set of experimental data including root diameter repartitions in wild-type plants, and xylem vessel diameters in mutants with altered xylem morphology (irx3, esk1) will be used to challenge the model. Root cell hydraulic conductivities will also be measured in these and aquaporin mutant phenotypes. Our aim is to check whether, based on anatomical and morphological data, the model can properly predict the radial hydraulic conductivity of these genotypes.

As the simulations may be time consuming and results sometimes difficult to interpret on complex branching systems, we started to investigate new methods to compute efficiently hydraulic conductivities and corresponding flows on complex root systems using architecture compression technics developed in the 1st axis of the project. First results show that very efficient computations of complex hydraulic architectures can be derived from the use of these compression techniques on idealized root architectures. These encouraging results provide a new abstraction that will be used in combination with the detailed modeling approach described above to break down the complexity of the analysis these huge branching systems.

6.3.2. Mechanical modeling of fruit growth

Participants: Ibrahim Cheddadi [Inra, Avignon], Mik Cieslak [U. Calgary], Frédéric Boudon, Valentina Baldazzi [Inra, Avignon], Nadia Bertin [Inra, Avignon], Michel Genard [Inra, Avignon], Christophe Godin.

This research theme is supported by the Agropolis project MecaFruit3D.

Fruits and plants in general are large scale hydraulic systems in which growth is closely linked to water fluxes: thanks to osmotic pressure difference, the cells are able to absorb water from their environment and therefore increase their volume; as the cells are bounded by rigid walls, this results in both hydrostatic pressure (the so-called turgor pressure) in the cell and tension in the cell walls; above a threshold, synthesis of new cell wall material occurs and relaxes the tension. This process allows cells to grow, and along with cell division, is responsible for plant growth. In fruits, phloem and xylem vascular networks provide the water fluxes necessary for growth, while the osmotic pressure is mainly regulated by sugar intake from the phloem. The goal of this project is to combine a description of water and sugar fluxes at the fruit scale (see section 4) with a modelling of growth at cell level, as described above.

As a first step in this direction, we have developed a bidimensional multicellular model that couples, on the one hand, water fluxes between cells (symplastic pathway) and between cells and intercellular space (apoplastic pathway), and on the other hand, mechanical properties of the cell walls and mechanical equilibrium of this complex system. Existing multicellular models for plant growth overlook this coupling. From a mathematical point of view, it corresponds to a coupling between (1) the ordinary differential equations that describe fluxes and cell walls properties and (2) the highly non linear system of equations that describes the mechanical equilibrium of the cell walls.

We have developed a numerical method for this coupled system, that allows to simulate in a reasonable amount of time a hundred of connected cells. Numerical simulations exhibit a highly non linear behaviour with respect to the governing parameters. Thanks to the detailed analysis of a simplified setup, we have identified two clearly distinct growth regimes: one regime that allows large growth heterogeneities by amplifying the effect of differences between cells, and conversely another regime that smoothes differences out and yields a homogeneous growth. On the biological level, the first regime is well adapted to morphogenesis, whereas the second one is well adapted to homothetic growth after the differentiated tissues have been created. A publication of these completely new results is in preparation.

We have developpeed a collaboration with biophysicists in RDP laboratory in Lyon (Arezki Boudaoud and Yuchen Long) in order to compare the results of this model to experiments at the microscopic scale of the meristem. A publication is in preparation.

In the longer term, we plan extend this model to the larger scale of tissues and organs in order to model fruit growth.

6.3.3. Analyzing root growth and branching

Participants: Beatriz Moreno Ortega, Sixtine Passot, Yann Guédon, Laurent Laplaze [IRD, DIADE], Mikaël Lucas [IRD, DIADE], Bertrand Muller [INRA, LEPSE].

This research theme is supported by two PhD programmes.

New 2D and 3D root phenotyping plateforms are emerging with associated image analysis toolbox (e.g. SmartRoot, RhizoScan) and the identification of developmental patterns within these complex phenotyping data requires new approaches. Here, we aim at developing a pipeline of methods for analyzing root systems at three scales:

1. tissular scale to identify and characterize the division, elongation and mature zones along a root apex using piecewise heteroscedastic linear models for segmenting epidermal cell length profiles [35].
2. individual root scale to analyze the dynamics of lateral root elongation. We in particular applied semi-Markov switching linear models for classifying roots on the basis of the identification of phases within growth rate profiles,
3. root system scale to analyze the primary root branching structure.

This pipeline of analysis methods was applied to different species (maize, Pearl millet [23]) with contrasting biological objectives (study of genetic diversity for Pearl millet and of metabolic and hormonal controls of morphogenesis for maize).

6.3.4. Analyzing shoot and leaf elongation

Participants: Maryline Lièvre, Yann Guédon, Leo Guignard, Christine Granier [INRA, LEPSE].

This research theme is supported by the labex Agro project "Integrated model of plant organ growth".

This study is based on the observation that there is a lack of methods enabling the integrated analysis of the processes controling the vegetative development in *Arabidopsis thaliana*.

The change in leaf size and shape during ontogeny associated with heteroblastic development is a composite trait for which extensive spatio-temporal data can be acquired using phenotyping platforms. However, only part of the information contained in such data is exploited, and developmental phases are usually defined using a selected organ trait. We introduced new methods for identifying developmental phases in the *Arabidopsis* rosette using various traits and minimum a priori assumptions [21]. A first pipeline of analysis was developed combining image analysis and statistical models to integrate morphological, shape, dimensional and expansion dynamics traits for the successive leaves of the *Arabidopsis* rosette. Dedicated segmentation models called semi-Markov switching models were built for selected genotypes in order to identify rosette developmental phases. Four successive developmental phases referred to as seedling, juvenile, transition and adult were identified for the different genotypes. We show that the degree of covering of the leaf abaxial surface with trichomes is insufficient to define these developmental phases. Using our pipeline of analysis, we were able to identify the supplementary seedling phase and to uncover the structuring role of various leaf traits. This enabled us to compare on a more objective basis the vegetative development of *Arabidopsis* mutants.

We developed a second pipeline of analysis methods combining a semi-automatic method for segmenting leaf epidermis images based on the ilastik software, and the analysis of the obtained cell areas using a gamma or inverse Gaussian mixture models whose component parameters are tied by a scaling rule. These mixture models allowed us to estimate the distribution of the number of endocycles. We highlighted in this way that the mean number of endocycles changes drastically with leaf rank. We extended the inference approach to take into account not only complete cell areas but also censored cell areas (corresponding to cells that intercept the edges of the images). We also investigated possible temporal interpretations of endoreduplication using stochastic processes.

6.3.5. A stochastic model of phyllotaxis

Participants: Yassin Refahi, Christophe Godin, Etienne Farcot, Teva Vernoux [RDP, ENS].

This research theme has been supported by IBC and the Inria Project Lab Morphogenetics.

The geometric arrangement of lateral organs along plant stems, named phyllotaxis, shows a variety of striking patterns with remarkable regularities and symmetries. This has interested biologists, physicists, mathematicians and computer scientists for decades. These studies have lead to a commonly accepted standard interpretation of phyllotaxis that postulates that organs inhibit the formation of new organs in their vicinity. At a molecular scale, these inhibitory fields have been shown to result from the spatio-temporal distribution of the plant hormone auxin. This model theoretically explains a large part of the diversity of phyllotactic patterns observed in plants.

Recently, our colleagues from ENS-Lyon observed intriguing perturbation in *arabidopsis* mutants. These perturbations were also present, to a lesser extent in the wild type. In a series of works [79], [69], [1], we could show that these perturbations patterns in both wild-type and mutant plants could be explained by permutations in the order of insertion along the stem of 2 or 3 consecutive organs. After closer inspection, we realized that the mutated gene encodes a protein diffusing from the organs and creating a field around the organs that regulates the plastochron. We could demonstrate that in the mutant, the absence of this field leads to co-initiations and subsequently to the observed permutations.

To proceed further and find a mechanistic interpretation of this phenomenon, we developed a stochastic extension of the standard model of phyllotaxis. We first analyzed the properties of the inhibitory fields created by the existing primordia on the initiation of new primordia, and concluded that the angular positions of organs are very robust to perturbations while plastochrons may be dramatically affected. This suggested that there exists a strong decoupling between space and time in the patterning process. To account for this observation, we modeled the perception of the initiation signal by cells using stochastic processes coupled with the intensity of inhibitory fields and showed that the observed permutation patterns emerge spontaneously from this purely local processes. This model recapitulates accurately the classical phyllotactic patterns and, in addition, produces realistic pattern disorders at higher organization levels as a result of stochasticity in signal perception. We show that these subtle disorders surprisingly reveal key information on the functioning of the developmental system and can therefore be regarded as *biological watermarks* of the system. In genetically or environmentally modified plants, these biological watermarks inform us on the molecular mechanisms that have been affected in the experiment. Our theoretical analysis allows us to predict the specific pattern variations that would arise from perturbations of the signaling pathways involved in lateral inhibition signaling at the shoot apex [27].

6.3.6. The role of auxin and sugar in rose bud outgrowth control

Participants: Jessica Bertheloot [INRA, Angers], Frédéric Boudon, Christophe Godin.

Auxin in the stem is known to be a key regulator of apical dominance. Over the last decades, many studies have been undertaken to understand its action mode, which is indirect because auxin in the main stem does not enter into the bud. Recently, apical dominance over basal buds in pea has been related to low sugar availability caused by high sugar demand of growing apical organs. Auxin and sugar are two signals regulating the entrance of bud into sustained growth in opposite ways. In the last year, it has also been demonstrated that sugar effect on bud outgrowth was preceded by a modification of the hormonal levels involved in bud outgrowth, which suggests that auxin and sugar pathways do interact in a non- trivial way. However, auxin and sugar effects have been studied separately until now. In this work, we investigate what is the combined effect of sugar and auxin on bud outgrowth, and how they integrate to regulate bud entrance into sustained growth. For this, a series of experiments has been carried out on a single-node cuttings of Rosa hybrida grown in vitro in which different combinations of sugar and auxin levels have been tested. A model of the regulatory networks controlling stem-bud molecular interaction has been developed.

6.4. Generic methodological results

In the context of our research work on biological questions, we develop concepts and tools in mathematics, statistics and computer science. This paragraph is intended to put emphasis on the most important results obtained by the team during the current year in these disciplins, independently of their biological application.

6.4.1. OpenAlea scientific workflows and grid computing

Participants: Christophe Pradal, Sarah Cohen-Boulakia, Christian Fournier, Didier Parigot [Inria, Zenith], Patrick Valduriez [Inria, Zenith].

Plant phenotyping consists in the observation of physical and biochemical traits of plant genotypes in response to environmental conditions. Challenges, in particular in context of climate change and food security, are numerous. High-throughput platforms have been introduced to observe the dynamic growth of a large number of plants in different environmental conditions. Instead of considering a few genotypes at a time (as it is the case when phenomic traits are measured manually), such platforms make it possible to use completely new kinds of approaches. However, the data sets produced by such widely instrumented platforms are huge, constantly augmenting and produced by increasingly complex experiments, reaching a point where distributed computation is mandatory to extract knowledge from data. We design the infrastructure InfraPhenoGrid [26] to efficiently manage data sets produced by the PhenoArch plant phenomics platform in the context of the French Phenome Project. Our solution consists in deploying *OpenAlea* scientific workflows on a Grid using a middleware, SciFloware, to pilot workflow executions. Our approach is user-friendly in the sense that despite the intrinsic complexity of the infrastructure, running scientific workflows and understanding results obtained (using provenance information) is kept as simple as possible for end-users.

6.4.2. Reproductibility in Scientific workflows

Participants: Christophe Pradal, Sarah Cohen-Boulakia, Jerome Chopard.

With the development of new experimental technologies, biologists are faced with an avalanche of data to be computationally analyzed for scientific advancements and discoveries to emerge. Faced with the complexity of analysis pipelines, the large number of computational tools, and the enormous amount of data to manage, there is compelling evidence that many if not most scientific discoveries will not stand the test of time: increasing the reproducibility of computed results is of paramount importance. In the context of the project 8.2.5.4, we study how scientific workflows can help to improve the reproducibility of computational experiment in the domain of life science. We characterize and define the criteria that need to be catered for by *reproducibility-friendly* scientific workflow systems, and use such criteria to place several representative and widely used workflow systems and companion tools within such a framework.

6.4.3. Statistical modeling

Participants: Yann Guédon, Jean Peyhardi, Jean-Baptiste Durand Peyhardi, Catherine Trottier [IMAG, Montpellier].

We develop statistical models and methods for identifying and characterizing developmental patterns in plant phenotyping data. Phenotyping data are very diverse ranging from the tissular to the whole plant scale but are often highly structured in space, time and scale. Problems of interest deal with the definition of new family of statistical models specifically adapted to plant phenotyping data and the design of new methods of inference concerning both model structure, model parameters and latent structure. This is illustrated this year by [18] and [25].

6.4.4. Lossy compression of tree structures

Participants: Christophe Godin, Romain Azaïs, Jean-Baptiste Durand, Alain Jean-Marie.

In in [6], we defined the degree of self-nestedness of a tree as the edit-distance between the considered tree structure and its nearest embedded self-nested version. Indeed, finding the nearest self-nested tree of a structure without more assumptions is conjectured to be an NP-complete or NP-hard problem. We thus introduced a lossy compression method that consists in computing in polynomial time for trees with bounded outdegree the reduction of a self-nested tree that closely approximates the initial tree. This approximation relies on an indel edit distance that allows (recursive) insertion and deletion of leaf vertices only. We showed in a conference paper presented at DCC'2016 [55] with a simulated dataset that the error rate of this lossy compression method is always better than the loss based on the nearest embedded self-nestedness tree [6] while the compression rates are equivalent. This procedure is also a keystone in our new topological clustering algorithm for trees. In addition, we obtained new theoretical results on the combinatorics of self-nested structures and their ability to approximate complex trees in a costless manner [42].

6.4.5. Version climber

Participants: Christophe Padal, Dennis Shasha, Sarah Cohen-Boulakia, Patrick Valduriez.

Imagine you are a data scientist (as many of us are/have become). Systems you build typically require many data sources and many packages (machine learning/data mining, data management, and visualization) to run. Your working configuration will consist of a set of packages each at a particular version. You want to update some packages (software or data) to their most recent possible version, but you want your system to run after the upgrades, thus perhaps entailing changes to the versions of other packages.

One approach is to hope the latest versions of all packages work. If that fails, the fallback is manual trial and error, but that quickly ends in frustration.

We advocate a provenance-style approach in which tools like *ptrace* and *reprozip*, combine to enable us to identify version combinations of different packages. Then other tools like *pip* and *VirtualEnv* enable us to fetch particular versions of packages and try them in a sandbox-like environment.

Because the space of versions to explore grows exponentially with the number of packages, we have developed a memorizing algorithm that avoids exponential search while still finding an optimum version combination.

Experimental results have been tested (with full reproducibility) on well known packages used in data science to illustrate the effectiveness of our approach as well as life science computational experiment.

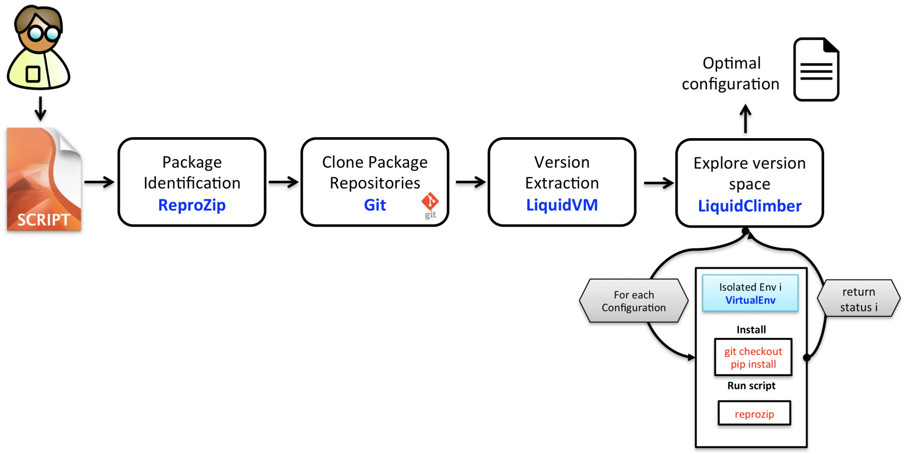

Figure 4. The steps of the operational subsystem: capture the execution of the initial configuration, liquify, fetch versions from git/svn etc., then deploy as directed by VersionClimber.

7. Bilateral Contracts and Grants with Industry

7.1. Bilateral Contracts with Industry

Guillaume Garin has been funded by itk (http://www.itk.fr/en/). With itk, a generic model of plant pathosystem was developed in the OpenAlea platform and illustrated on Vine and Wheat.

8. Partnerships and Cooperations

8.1. Regional Initiatives

8.1.1. New pearl

Participants: Sixtine Passot, Yann Guédon, Soazig Guyomarc'h [Montpellier University, DIADE], Laurent Laplaze [IRD, DIADE].

Funding: Labex Agro (Contractor for Virtual Plants: CIRAD, from 2014 to 2017)

Pearl millet is an orphan crop regarding research effort despite its key role for food safety in Sub-Saharan Africa. The objective of the New Pearl project is to develop basic biological knowledges concerning Pearl millet development and genetic diversity. We are more specifically involved in the study of the root system development and the genetic diversity on the basis of root phenotypic traits.

8.1.2. MecaFruit3D

Participants: Mik Cieslak, Frédéric Boudon, Christophe Godin, Nadia Bertin [PSH, Avignon].

Funding: Labex Agro (Contractor for Virtual Plants: INRA, from 2013 to 2016)

The fruit cuticle plays a major role in fruit development and shelf-life. It is involved in water losses, cracking, and protection against stress, and thus it may have major economic impacts. Objectives of the project are to better understand the multiple roles of the fruit cuticle in the control of fleshy fruit growth and quality.

The multicellular model for fruit growth that we develop (see section 6.3.2) will be used to study qualitatively the impact of the cuticle mechanical properties.

Partners: PSH, INRA, Avignon; LCVN, IES, Université Sud de France, Montpellier.

8.1.3. Integrated model of plant organ growth

Participants: Yann Guédon, Christine Granier [INRA, LEPSE], Garance Koch [INRA, LEPSE], Nadia Bertin [INRA, PSH], Valentina Baldazzi [INRA, PSH].

Funding: Labex Agro (Contractor for Virtual Plants: CIRAD. From 2015 to 2018)

The objective of this project is to develop a generic model which will predict interactions among the main processes controlling the development of source and sink organs in tomato, i.e. cell division, cell expansion and endoreduplication in relation to carbon and water fluxes under fluctuating environment. To achieve this objective we will i) capitalize on expertise, multi-scale phenotyping tools and genetic resources already compiled on the fruit model tomato and the model plant *Arabidopsis thaliana*; ii) perform new experiments to collect phenotyping data currently missing in this field, especially concerning the early phase of fruit and leaf development in tomato and the interactions between genes and environment; iii) develop a process-based model of organ growth which will integrate knowledge collected at the different scales.

Partners: PSH, INRA, Avignon; LEPSE, INRA, Montpellier, Biologie du fruit et Pathologie INRA, Bordeaux;

8.2. National Initiatives

8.2.1. HydroRoot

Participants: Mikaël Lucas [IRD], Christophe Pradal, Christophe Godin, Yann Boursiac [BPMP], Christophe Maurel [BPMP].

Funding: ANR (Contractor for Virtual Plants: Cirad, From 2012 to 2016)
The HydroRoot project proposes a unique combination of approaches in the model plant Arabidopsis thaliana to enhance our fundamental knowledge of root water transport. Accurate biophysical measurements and mathematical modeling are used, in support of reverse and quantitative genetics approaches, to produce an integrated view of root hydraulics. The HydroRoot project will address as yet unknown facets of root water transport. It will lead to an integrated view of root hydraulics that considers both tissue hydraulics and root architecture and explains how these components are controlled at the molecular level by physiological and/or environmental cues. Because of its strong physiological and genetic background, this research may also directly impact on breeding programs, for production of crops with optimised water usage and stress responses.

8.2.2. Phenome

Participants: Christian Fournier, Christophe Pradal, Yann Guédon, Sarah Cohen-Boulakia, Simon Artzet, Jerome Chopard, Patrick Valduriez.

Funding: ANR-Investissement d'avenir (Contractor for Virtual Plants: INRA, From 2015 to 2018)
The goal of Phenome is to provide France with an up-to-date, versatile, high- throughput infrastructure and suite of methods allowing characterisation of panels of genotypes of different species under climate change scenarios. We are involved in the methodological part of the project, that aims at developping a software framework dedicated to the analysis of high throughput phenotyping data and models. It will based on the OpenAlea platform that provides methods and softwares for the modelling of plants, together with a user-friendly interface for the design and execution of scientific workflows. We also develop the InfraPhenoGrid infrastructure that allows high throughput computation and recording of provenance during the execution of Workflows.

8.2.3. DigEM

Participants: Christophe Godin, Grégoire Malandain, Patrick Lemaire.

Funding: ANR (Contractor for Virtual Plants: Inria, From 2015 to 2019)
In this project, we will use advanced ligh-sheet imaging of live embryos to quantitatively describe embryonic morphogenesis in ascidians, a class of animals that undergo very rapid genomic divergence, yet show an extraordinary stasis of embryonic morphologies, based on invariant early cell lineages shared by all studied species. The global aims of the proposal, which will bridge micro- and macroevolutionary scales of analysis, are: i) to provide a global systems-level description at cellular resolution of an animal embryonic program; ii) to use this description to characterize intra-specific and inter-specific patterns of morphogenetic variations; iii) to analyze possible molecular mechanisms explaining the unusual robustness of this program to environmental and genetic perturbations. To achieve these aims, we will combine advanced live light-sheet microscopy, computational biology, functional gene assays and evolutionary approaches.

8.2.4. Leaf Serration

Participants: Christophe Godin, Eugenio Azpeitia.

Funding: ANR (Contractor for Virtual Plants: Inria, From 2014 to 2019)
Leaf growth and development result from the coordination in time and space of cellular divisions and cellular expansion, and expansion of certain plant cells reaches up to one thousand times their size when living the meristem. Transcription factors belonging to the CUP-SHAPED COTYLEDON (CUC) genes and homeodomain genes of the KNOTTED-LIKE (KNOXI) family were shown to be essential for the control of leaf size and shape. In addition, the phytohormone auxin is a critical regulator of growth and development, involved in the regulation and coordination of cell division and cell expansion. The mechanisms of auxin signalling are based on a complex set of co-receptors exhibiting high to low affinity for auxin and an even more complex modular network of transcriptional repressors and activators tightly controlling the expression of a large set of genes.

The SERRATIONS project is based on recent data relative to key transcription factors regulating leaf morphogenesis and advanced knowledge on the generic signalling mechanisms of the phytohormone auxin that plays a critical role in the control and coordination of cellular responses sustaining leaf size and shape. The goal of the project is to identify auxin signalling modules involved in leaf morphogenesis and to integrate these data in mathematical modelling to provide new insights into complex regulatory networks acting on leaf morphogenesis and to further test model-derived hypotheses.

8.2.5. Other national grants

8.2.5.1. SCOOP

Participants: Pierre Fernique, Yann Guédon, Christophe Pradal, Christophe Godin, Frédéric Boudon, Jean-Baptiste Durand.

Funding: Inria ADT (Contractors for Virtual Plants: Inria from 2014 to 2016)
The goal of this project is to improve the software quality and the dissemination of Vplants components for plant phenotyping. Virtual Plants team has played a pioneering role in the development of methods for analyzing plant development that take account of the complexity of plant architecture. Numerous software components has been developed for more than 20 years and a profound re- engineering is now necessary to facilitate the collaborations with biologist and agronomists of CIRAD, INRA and IRD and to help the dissemination of ours methods in the scientific community.

8.2.5.2. Morphogenetics

Participants: Christophe Godin, Frédéric Boudon, Olivier Ali, Jean Phillipe Bernard, Hadrien Oliveri, Christophe Pradal, Guillaume Cerutti, Grégoire Malandain, François Faure, Jan Traas, François Parcy, Arezki Boudaoud, Teva Vernoux.

Funding: Inria Project Lab (From 2013 to 2017)

Morphogenetics is an Inria transversal project gathering 3 Inria teams and two Inra teams. It aimed at understanding how flower shape and architecture are controlled by genes during development. Using quantitative live-imaging analysis at cellular resolution we will determine how specific gene functions affect both growth patterns and the expression of other key regulators. The results generated from these experiments will be integrated in a specially designed database (3D Atlas) and used as direct input to new predictive computational models for morphogenesis and gene regulation. Model predictions will then be further tested through subsequent rounds of experimental perturbation and analysis. A particular emphasis will be put on the modeling of mechanics in tissues for which different approaches will be developed.

Partners: RDP ENS-Lyon; Imagine Inria Team (Grenoble); Morpheme Inria Team (Sophia-Antipolis), UMR PCV (Grenoble).

8.2.5.3. Rose

Participants: Christophe Godin, Frédéric Boudon.

Funding: INRA - PhD project (From 2016 to 2019)
In this project we want to quantify and understand how sugars interfere with hormonal signals (auxin, cytokinins) to regulate lateral bud outgrowth of aerial stems of roses. Experiments will be made on Rose stems to test different levels of sugar conditions and hormonal concentrations on bud outgrowth. An extension of the recently published hormonal model of apical dominance will be made to take into account the role of carbon as a signaling molecule.

Partners: UMR SAGAH, Angers

8.2.5.4. ReProVirtuFlow

Participants: Christophe Pradal, Sarah Cohen-Boulakia, Jerome Chopard.

In the life science domain, scientists are facing the deluge and the size of available data, the composition of a myriad of existing tools, and the complexity of computational experiment. In this context, reproducing an experiment is particularly difficult, as evidenced by numerous recent studies. The aim of this GDR CNRS project is to make a complete review of existing approaches in this field, considering in priority as elements of solution: (i) scientific worklfows, (ii) data provenance, and (iii) virtual machines. This project brings together experts in data bases, algorithms and virtual environments, working in the domain of life science.

Funding: GDR - CNRS

8.3. European Initiatives

8.3.1. Collaborations with Major European Organizations

8.3.1.1. Hook

Participants: Christophe Godin, Olivier Ali.

A new collaboration started with the University of Umeä (Sweden) on the modeling of the apical hook in the hypocotyl of *Arabidopsis thaliana*. The question we want to answer is what regulates the opening dynamics of the apical hook at the tip of the hypocotyl and how. For this, a multidisciplinary approach, combining 3D laser imaging, molecular biology, genetics and modeling will be developed by the partners.

Partners: University of Umeä, RDP ENS-Lyon.

8.4. International Initiatives

8.4.1. ANR-DFG

8.4.1.1. AlternApp

Participants: Yann Guédon, Maryam Aliee.

Funding: ANR-DFG (Contractor for Virtual Plants: INRA, From 2015 to 2019)

The aim of the AlternApp project is to investigate functional hypotheses on the genetic and environmental control of floral induction in apple tree progenies. Two segregating populations will be studied in two different environmental conditions for floral induction and bearing behavior, in order to identify genomic regions associated with regular phenotypes. The specific contribution of the team will be to develop statistical methods to quantify phenotype and genotype, as well as years and climatic effects on alternation. Transcriptome of varieties contrasted in their bearing behavior and artificially set into high or low cropping conditions will be explored by New Generation Sequencing Technology (NGS) to identify new candidate genes and allelic variations of interest. By this project, new results are expected on floral induction in apple tree in relation to their alternate bearing behavior and more applied results linked to the discovery of allelic variation in key genes that could be used in breeding programs.

Partners: AFEF INRA team (Montpellier), PIAF INRA team (Clermont-Ferrand), JKI (Dresden, Germany), UHOH (Hohenheim, Germany), Foundation E. Mach (San Michele all'Adige, Italy)

8.4.2. Inria International Partners

8.4.2.1. BioSensors

Participants: Guillaume Cerutti, Sophie Ribes, Frédéric Boudon, Christophe Godin, Teva Vernoux [ENS-Lyon], Géraldine Brunoud [ENS-Lyon], Carlos Galvan-Ampudia [ENS-Lyon].

Funding: Human Frontiers - HFSP (From 2014 to 2017)
We propose to elucidate the basis for positional information by hormones during plant morphogenesis. While it is known that cell fate decisions require simultaneous input from multiple hormones, to-date a precise understanding of how these signals are coordinated and act together to drive morphogenesis does not exist. Our limited mechanistic understanding is largely due to the difficulty to quantify the distribution of these small molecules in space and time. To explore this fundamental question, we will exploit recent advances in synthetic biology to engineer an RNA-based biosensor platform applicable to a broad range of small molecules and in particular to hormones. Using live-imaging technologies, we will use the sensors to obtain quantitative dynamic 3D maps of hormone distributions and relate these maps to the spatio-temporal distribution of cell identities, both during normal morphogenesis and upon perturbations of hormone levels. This analysis will be done on the shoot apical meristem, one of the bestcharacterized developmental systems in higher plants. In this context, mathematical approaches will be essential to analyze and establish a predictive model for how multiple hormones influence cell fate in a spatio-temporal manner.

8.4.2.2. Informal International Partners

An important collaboration with the CIRAD research unit HortSys at the Reunion island and in particular Frédéric Normand, Yann Guédon, Pierre Fernique and Christophe Pradal has been established for several years. The topic of the collaboration is the study of the phenology of mango tree. This is a tripartite collaboration that also involves Pierre-Eric Lauri of the System research unit (INRA, Montpellier).

We have for several years a strong partnership with Ted de Jong group at UC Davis concerning the influence of various agronomic practices (water stress, pruning) on fruit tree branching and production. This is a tripartite collaboration that also involves Evelyne Costes of the AGAP/AFEF team.

A collaboration in plant phenotyping with the CSIRO and the INRA/Lepse team has been established for several years. The topic of the collaboration is to develop a full pipeline using OpenAlea 2.0 on plant phenotyping platforms. This is a joint collaboration with UMR LEPSE in Montpellier (François Tardieu).

A collaboration started in the last two years with the group of Henrik Jönsson of the Sainsbury Lab, Cambridge, UK. The collaboration is related to several modeling projects in the context of shoot apical and flower meristems development, with a particular focus on the use of quantitative 3D reconstructions of meristem structures. Yassin Refahi from the Sainsbury Lab is regularly paying visits to Montpellier. The Virtual Plants team is also regularly invited to Cambridge.

8.5. International Research Visitors

8.5.1. Visits of International Scientists

Julia Pulwicki from the University of Calgary, Canada, spent 10 days at our lab in May to study the opportunity to define a post-doctoral project for her and to set up the basis of a joint scientific project. This project has lead us to submit to the Inria post-doctoral programme a project on that was accepted. Julia arrived for a 12 month post-doctoral project in November.

In this study, we want to formalize the analogy between the development of shapes in biology and the feedback between mass and space curvature in general relativity. Our aim is to propose a quantitative approach of such a vision by developing a mathematical and computational framework combining formalisms from non-euclidean geometry developed in general relativity and models of signal propagation and gene regulation in plant tissues.

8.5.1.1. Research Stays Abroad

In the context of the project on mango modelling and the PhD of S. Persello, F. Boudon is currently positioned in the Reunion island in the Hortsys unit for one year. He develops there a project on Mango modelling in collaboration with F. Normand.

9. Dissemination

9.1. Promoting Scientific Activities

9.1.1. Scientific Events Organisation

9.1.1.1. Member of the Organizing Committees

Yann Guédon was member of the organizing committee of the 48ème journées de statistique de la SFdS.

9.1.2. Scientific Events Selection

9.1.2.1. Member of the Conference Program Committees

Christophe Godin and Yann Guédon were members of the program committee of the IEEE International Conference on Functional-Structural Plant Growth Modeling, Simulation, Visualization and Applications (FSPMA 2016).

9.1.2.2. Reviewer

Frédéric Boudon was referee for papers submitted to Eurographics and Siggraph Asia and was a rewiever and a member of the jury for best paper of the Journée Francaise d'Informatique Graphique (jFIG).

9.1.3. Journal

9.1.3.1. Member of the Editorial Boards

Christophe Godin is a member of the Editorial Board of Frontiers in Plant Sciences. He was also a guest editor for PLoS Computational Biology,

9.1.3.2. Reviewer - Reviewing Activities

- Yann Guédon was referee for papers submitted to Functional Ecology and Journal of Internet Services and Applications.
- Christophe Godin reviewed papers for several journals in plant sciences and modelling.

9.1.4. Invited Talks

- C. Godin gave invited talks at RDP-ENS-Lyon research unit in Lyon (January), at the African Institute for Mathematical Sciences (AIMS), Dakar, Senegal, (February), at the University of Lund, Sweden (June), at the Journées scientifiques Inria, Rennes, (June), at the European Conference on Computational Biology and Bioinformatics, The Hague, The Netherlands (September), Inria/Inra joint meeting programme, Aix-en-Provence, (October), at CRBM research unit in Montpellier (October), BPMP research unit in Montpellier (December), and a plenary talk at the International workshop on multiscale modeling of complex systems in plant and developmental biology, U. Riverside, USA (December).
- F. Boudon gave invited talks at the workshop "Tree data and modelling", Tampere, Finland (June), in the AGAP scientific seminar and at the journée AGAP.
- Y Guédon gave an invited talk at the AGAP scientific seminar.
- C. Pradal gave invited talk at the "Agricultural Model Exchange Initiative" in Bologna, Italy (June), at the workshop "Multi-scale Plant Modeling" at the Pacific Northwest National Laboratory, USA (August), and at the workshop SUCCES, in Paris (November).

9.1.5. Leadership within the Scientific Community

- Christophe Godin is member of the Board of the Functional Structural Plant Models series of conferences.
- Christophe Godin is co-coordinator with Patrick Lemaire of the 4th Research Axis on Imaging in Biology and Modeling of the Institute for Computational Biology (IBC) of Montpellier.
- Christophe Godin spent 3 days at the African Institute for Mathematical Sciences (AIMS) to study potential future collaborations between Inria and AIMS in Dakar.

9.1.6. Scientific Expertise

- Christophe Godin is a member of the International Scientific Advisory Committee of the new Plant Phenotyping and Imaging Research Centre (P2IRC), Saskatchewan, Canada.
- Christophe Godin is a member of the Review and Mentoring committee of James Lock's group in Sainsbury Lab, Cambridge, UK.
- Christophe Godin is a member of the scientific councils of the Environnement-Agronomie department (up to August 2016) and of the Biologie et Amélioration des Plantes Department at Inra (Starting September 2016).

9.1.7. Research Administration

- Christophe Godin is a member of the project committee board at Sophia-antipolis Mediterrannée Reacher Center
- Christophe Godin is also part of the steering board of the Institute for Computational Biology (IBC) of Montpellier.

9.2. Teaching - Supervision - Juries

9.2.1. Teaching

Master Computer Science: Frédéric Boudon, Guillaume Cerutti, Christophe Godin, Christophe Pradal and David Vanderhaege and Loïc Barthe [IRIT, Toulouse], Computer graphics, 45h, M2, University Montpellier, France.

Master Computer Science: Christophe Godin, Frédéric Boudon, Computational and Discrete Geometry and graphics, 15h, M1, University Montpellier, France.

Master Functional Plant Biology: Christophe Godin, Introduction to plant modeling, 25h, M2, University Montpellier, France.

Master Life Sciences (IMaLiS): module co-organized by Patrick Lemaire and Christophe Godin, Animal and Vegetal Morphogenesis, 6 days, 4 h + TD supervision every afternoon, ENS Paris, Montpellier, France.

Master Functional Plant Biology: Christophe Godin, Phyllotaxis class in a module on Mathematical modeling in biology, 4h, M2, University Montpellier, France.

Master Functional Bioinformatics: Christophe Godin and Patrick Lemaire (Coordination O. Radulescu), Modeling in biology, 5h, M2, University Montpellier, France.

Master Biostatistics: Yann Guédon and Pierre Fernique, Stochastic processes, 32h, M2, University Montpellier, France.

Master Bioinformatique - Biomathématiques: Christophe Godin, iPlant, Modeling organ development, 4h, M2, Cheikh Anta Diop University (UCAD), Dakar, Senegal.

Master Plant Breeding: Christophe Pradal, Plant modelling, 4h, M2, Project CultiVar, University Montpellier, France.

Engineering Degree: SupAgro Montpellier. Christophe Pradal and Christian Fournier. "Introduction to modelling" (1st year, 12h).

9.2.2. Supervision

- PhD in progress : Anne Schneider, *"Modeling branching in Roses"*, Angers University, Jessica Bertheloo, C. Godin, F. Boudon.
- PhD in progress : Hadrien Oliveri, *"Mechanical modeling of organ growth"*, Montpellier University, C. Godin, J traas and O. Ali.
- PhD in progress : Jean-Louis Dinh, *"Coupling flux and growth models in plant development"*, Nottingham University, C. Hodgman, C. Godin.
- PhD in progress : Jean-Philippe Bernard, *"Meshless methods for organ development"*, Montpellier University, C. Godin, B. Gilles.
- PhD in progress : Severine Persello, *"Structural-Functional modeling of yield and fruit quality build-up of the mango, and integration of the effects of cultural practices"*, Montpellier University, F. Normand, I. Grechi, F. Boudon.
- PhD : Beatriz Moreno-Ortega, Developmental instability in lateral roots of maize: a multi-scale analysis, Montpellier SupAgro, December 12th 2016, Betrand Muller, Yann Guédon.
- PhD : Sixtine Passot, Exploring pearl millet root system and its outcome for drought tolerance, Montpellier University, September 30th 2016, Laurent Laplaze, Yann Guédon.
- PhD in progress : Marc Labadie, Study of the alternation between vegetative and floral development in strawberry: spatio-temporal architecture and analysis of key flowering genes, Bordeaux University, Béatrice Denoyes, Yann Guédon.

9.2.3. Juries

- Christophe Godin was the Opponent of Beruz Bozorg, June, University of Lund, Sweden, a member of the PhD Jury of Gaël Michelin, October University Cote d'Azur, Président of the PhD Jury of Sam Caullodin, December ENS-Lyon. He also participated in the PhD committees of Adrien Corot (AgroparisTech), Léo Serra (AgroParisTech) and Mathilde Dumond (ENS-Lyon).
- Yann Guédon was referee of Philippe Cuvillier PhD: On temporal coherency of probabilistic models for audio-to-score alignment, Pierre and Marie Curie University, Paris, December 15th 2016, Arshia Cont (supervisor).

9.3. Popularization

- Olivier Ali is a member of the writing committee of the newsletter of the Sophia-Antipolis Méditerrannée Inria Centre.
- High School: Christophe Godin gives regular 2h classes at Lycée Pompidou (Montpellier) and in other Lycées.
- Christophe Godin gave two invited seminars in the context of the Maths Week (March), at the Lycée International de Valbonne, France.
- Christophe Godin gave an interview to the European Journal Labtimes about their paper published in eLife: Alejandrolvido (2016). Green noise. Labtimes 5, 34–35.

10. Bibliography

Major publications by the team in recent years

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[2] F. Boudon, J. Chopard, O. Ali, B. Gilles, O. Hamant, A. Boudaoud, J. Traas, C. Godin. *A Computational Framework for 3D Mechanical Modeling of Plant Morphogenesis with Cellular Resolution*, in "PLoS Computational Biology", January 2015, vol. 11, n^{o} 1, pp. 1-16 [*DOI :* 10.1371/JOURNAL.PCBI.1003950], https://hal.archives-ouvertes.fr/hal-01142486

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