



IN PARTNERSHIP WITH:  
**CIRAD**

**INRA**

Activity Report 2015

## **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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# Project-Team VIRTUAL PLANTS

*Creation of the Project-Team: 2007 July 01*

## **Keywords:**

### **Computer Science and Digital Science:**

- 1.1.13. - Virtualization
- 1.1.4. - High performance computing
- 2.1.10. - Domain-specific languages
- 2.1.3. - Functional programming
- 2.1.9. - Dynamic languages
- 2.2.6. - Adaptive compilation
- 2.5. - Software engineering
- 3.1.1. - Modeling, representation
- 3.1.3. - Distributed data
- 3.1.8. - Big data (production, storage, transfer)
- 3.4.5. - Bayesian methods
- 5.1.1. - Engineering of interactive systems
- 5.2. - Data visualization
- 5.3.3. - Pattern recognition
- 5.3.4. - Registration
- 5.4.4. - 3D and spatio-temporal reconstruction
- 5.4.5. - Object tracking and motion analysis
- 5.5.1. - Geometrical modeling
- 5.9.2. - Estimation, modeling
- 6.1. - Mathematical Modeling
- 6.2.4. - Statistical methods
- 6.2.6. - Optimization
- 6.2.8. - Computational geometry and meshes
- 6.3. - Computation-data interaction
- 7.2. - Discrete mathematics, combinatorics
- 7.3. - Operations research, optimization, game theory
- 7.5. - Geometry
- 7.8. - Information theory
- 7.9. - Graph theory

### **Other Research Topics and Application Domains:**

- 1.1.10. - Mathematical biology
- 1.1.11. - Systems biology
- 1.1.2. - Molecular biology
- 1.1.3. - Cellular biology
- 1.1.4. - Developmental biology
- 2.6. - Biological and medical imaging
- 9.4.1. - Computer science

- 9.4.2. - Mathematics
- 9.4.5. - Data science
- 9.6. - Reproducibility
- 9.7.1. - Open access

## 1. Members

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### Visiting Scientists

Jean Louis Dinh [PhD student of the University of Nottingham]  
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### Administrative Assistant

Laurence Fontana

## 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. These 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

- *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 tis-sular 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 [17] and [22].
- *Scientific Workflows*: Analyzing biological data may involve very complex and interlinked steps where several tools are combined together. Scientific workflow systems have reached a level of maturity that makes them able to support the design and execution of such in-silico experiments, and thus making them increasingly popular in the bioinformatics community. However, in some emerging application domains such as system biology, developmental biology or ecology, the need for data analysis is combined with the need to model complex multi-scale biological systems, possibly involving multiple simulation steps. This requires the scientific workflow to deal with retro-action to understand and predict the relationships between structure and function of these complex systems. In collaboration with the Zenith EPI, we have proposed a conceptualisation of OpenAlea workflows [34] by introducing the concept of higher-order dataflows as a means to uniformly combine classical data analysis with modeling and simulation, in the context of plant phenotyping.
- *Mechanical model of meristem development*: The growth of plant tissues results from the growth of cells that are inflated by turgor pressure. In recent years, different bio-physical processes by which genes regulate locally the rate and the directions of cell growth have been identified. At tissue level, the growth of each region is mechanically constrained by the existence of neighboring regions. This creates stresses within the plant tissues, possibly with differential directional intensities, which in turn, can be sensed locally at the level of each individual cell by genes. Shapes thus results from the complex interplay between genes and growth, mediated by mechanics. In the recent years, we have been developing a model of growth of plant tissues that is able to represent this overall feedback mechanism [13]. This model is the first 3D approach of multicellular plant tissue development based on a tensorial representation of mechanical properties and stresses in cell walls. Its implementation relies on a coupling between OpenAlea and Sofa, two main software platforms for modeling in biology developed at Inria.

## 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, Guillaume Baty, Julien Coste, 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 studies plant morphogenesis at the scale of 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 enables the visualization, 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, Gregoire Malandain, Christophe Pradal, Christophe Godin.
- Contact: Christophe Godin
- URL: <https://gforge.inria.fr/projects/oalab>

## 5.3. TissueMeca

KEYWORDS: Bioinformatics - Biology - Mechanics - Morphogenesis

FUNCTIONAL DESCRIPTION

A mechanical model of growing tissue has been implemented using the open source software SOFA and OpenAlea. Using OpenAlea, a generic tissue representation can be defined with attributes giving structural, geometrical and physical parameters of the simulation. Then, based on SOFA and its modular approach, it is possible to combine different element types (triangle and edge elements), forces (elastic forces and turgor) and positional constraints within the same model to find the static elastic equilibrium, given a current configuration. The use of an implicit integration scheme makes it possible to achieve close-to interactive simulation of growth. The module implements also growth equations for the different cell walls after each elastic equilibrium step. Algorithms to simulate division and refinement of each element of the modelled tissue are also available.

- Participants: Frédéric Boudon, Olivier Ali, Jean-Philippe Bernard, Benjamin Gilles, Christophe Godin.
- Contact: Frédéric Boudon
- <https://gforge.inria.fr/projects/tissuemeca/>

## 5.4. PlantScan3D

KEYWORDS: Bioinformatics - Biology - Laser scanners - 3D Reconstruction

FUNCTIONAL DESCRIPTION

This software aims at semi-automatically reconstructing the 3D structures of plants from laser scans. For this, it encapsulates automatic reconstruction method developed by the Virtual Plants team (Preuksakarn et al., 2010) or by the literature (Vernoust and Lazarus, 2000). Once reconstructed the structure can be graphically edited by adding, deleting, repositioning or reorganizing segments in the structure. The original pointset can be processed with contraction operators to shift the points toward the center of the shape. Some post processing procedures are available to retrieve automatically botanical features such as divergence angle sequences.

- Participants: Frédéric Boudon, Chakkrit Preuksakarn, Christophe Godin
- Contact: Frédéric Boudon
- URL: <http://plantscan3d.gforge.inria.fr/>

## 5.5. 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 knowledge on the studied system, allows to constrain the segmentation and to track cells throughout time simultaneously. 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, Grégoire Malandain, Patrick Lemaire, Christophe Godin
- Contact: Christophe Godin
- URL: <https://gforge.inria.fr/projects/marsalt/>

## 5.6. Alep

KEYWORDS: Foliar Fungus, Pathogen, FSPM, Epidemics, Infectious Cycle, Modelling framework

LONG: Architecture & Leaf Pathogens

FUNCTIONAL DESCRIPTION

Alep is a FSPM library implemented in Python that adapts the concepts and tools of OpenAlea to pathosystem modelling. The key components of Alep are two abstract classes that represent Dispersal Units and Lesions of foliar fungi in a generic form. The equations in these classes are specified to model a given species of fungus. Alep also contains several generic functions to manipulate these objects and define their contract: functions of dispersal by rain and by wind, functions managing the growth and competition of several lesions on the same leaf. A particular pathosystem is modeled by assembling a coherent set of components via a plugin system. This strategy allows the composition of existing algorithms as well as the extension or the inclusion of new algorithms. Their assembly and scheduling of execution uses scientific workflows defined in OpenAlea. This way, models can run at different time and spatial scales.

- Participants: Guillaume Garin, Christophe Pradal, Christian Fournier, Vianey Houles, Corinne Robert, Bruno Andrieu
- Contact: Christophe Pradal
- URL: <https://gforge.inria.fr/projects/openaleapkg>

## 5.7. AutoWIG

KEYWORDS: Syntactic Analysis

FUNCTIONAL DESCRIPTION

The goal of AutoWIG (Automatic Wrapper and Interface Generator) is to provide an automatic approach for the process of Python interfacing of C++ libraries. This Python library relies on two main principles: i) automatic C++ code parsing using LLVM/clang, and ii) Python wrapper generation with C++ code introspection.

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

## 5.8. Phenomenal

KEYWORDS: Image Analysis

FUNCTIONAL DESCRIPTION

Phenomenal is a Python library that provides a set of algorithms to process images produced by image-based phenotyping platforms. The library contains algorithms for i) plant image segmentation, ii) 3D reconstruction of plant organs and plant canopies, iii) calculation of intercepted light and radiation use efficiency. All these algorithms are integrated in the OpenAlea platform.

- Participants: Simon Artzet, Jérôme Chopard, Michael Mielewczik, Nicolas Brichet, Christian Fournier, Christophe Pradal
- Contact: Christophe Pradal
- URL: <https://gforge.inria.fr/projects/phenomenal/>

## 5.9. Platforms

### 5.9.1. 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.).

### 5.9.2. 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 [76], [63]. 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.* (Chakkrit Preuksakarn, Mathilde Balduzzi, Frédéric Boudon, Christophe Godin, Pascal Ferraro [Labri, Bordeaux], Yassin Refahi )

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 [73]. Additionally, a number of automatic methods were proposed in the literature. The question of their comparison and relative accuracy is however critical for further exploitation in biological applications. To address such problem, we developed an evaluation pipeline that takes two plant structures as input and compares their organization using two indices of geometrical and structural similarities [55]. A first comparative evaluation of the different methods of the literature has been designed and conducted. A graphical editor has been developed and makes it possible to test the different methods and correct manually the reconstruction. A procedure to automatically determine phyllotactic angles from scans of small plants has been added to the reconstruction pipeline and has been tested on database of 150 scans of *Arabidopsis thaliana* with different genotypes. The editor has also been tested on apple trees and large African trees.

In the context of the PhD of M. Balduzzi, we also investigated the reconstruction of tree foliage from 3D scans. Such elements are crucial to study the interaction of the plant with its environment. However, laser scans contain outliers in the silhouette of the scans that make the meshing of the pointset extremely difficult. New generation of laser scanners provide intensity of the laser reflected on the surface of scanned objects. This intensity depends on the distance to the object, its optical property and the incidence angle. A first work on this topic showed that after correcting the distance effect, the incidence angle can be deduced from the intensity. From this result, we developed a reconstruction pipeline using the scan intensities and based on Shape-From-Shading. Outliers being along the edge of the surface point cloud, we chose to develop a propagation SFS method initialized with points of the scans with high quality. We proved that surface with constant intensity are necessarily surfaces of constant slope or sand-pile surfaces. Using this result, a propagation method along iso-intensity regions was developed. These surfaces can then be sampled to provide a smooth point set without outliers.

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

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 analyses currently available are still very crude and need improvement and robustness to process huge amount of data. We are developing an integrated pipeline allowing assessment of growths of individual organs, of plant geometry, and of derived variables such as light interception. The pipeline currently consists of 2D image analysis workflows built with standard image libraries (OpenCV, Scikit.Image), algorithms for 3D reconstruction, segmentation and tracking of plant organs for maize (under development), and workflows for estimation of light interception by plants during their growth. A 3D FSPM model

for maize architectural development, is used to help segmenting plant images and to automate the mapping between segmented 3D objects and plant organs defined in the model.

- *Reconstruction of root structures.* (Julien Diener, Frédéric Boudon, Christophe Pradal, Christophe Godin, Philippe Nacry [BPMP, INRA], Christophe Périn [AGAP, CIRAD], Anne Dievart [AGAP, CIRAD], Xavier Draye [UCL, Belgium])

*This research theme is supported by the Agropolis through the Rhizopolis project and by NUMEV.*

Similarly to aerial part of plants, new needs for automatic digitizing of root systems emerge. Most existing methods focus only on semi-automatic approaches. This does not support the high-throughput capabilities of acquisition systems. In the context of the RhizoScan project, we previously designed a prototype of an automatic image analysis pipeline to extract root system architecture of branching systems grown in Petri boxes. This pipeline provides i) a set of model based image segmentation method, ii) the extraction of a graph representation of the root system, and iii) a method to identify the root axes organization. This year, we improved and extended the pipeline in the following way:

1. We integrated a validation step in the workflow based on the comparison method presented in [55].
  2. We developed a standard file format for root architecture (RSML) described in [19] during an international collaboration with the niversité Catholique de Louvain (Belgium), the CPIB of the University of Nottingham (UK), the University of Vienna (Austria), the Jülich research center (Germany) and INRA.
- *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 [75]. Previous studies demonstrated the possibility to create species-specific models of fruit structure with relatively low effort [57]. 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 [38]

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.

### 6.1.2. Modeling the plant ontogenic programme

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

*This research theme is supported by two PhD programmes.*

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. [52], [65], [66], [62], 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 programme" [71], "age state" [61] or "physiological age" [54]. 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 [61], [54]. 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, which was part of the PhD subject of Jean Peyhardi, 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 [72] 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], Jean Peyhardi, Baptiste Guitton [AGAP, AFEF team], Yan Holtz [AGAP, AFEF team] Catherine Trottier, Evelyne Costes [AGAP, AFEF team], Yann Guédon)

A first study was published to characterize genetic determinisms of the alternation of flowering in apple tree progenies [58]. Data were collected at two scales: at whole tree scale (with annual time step) and a local scale (annual shoot, which corresponds to portions of stem 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 were collected in other F1 progenies. Ancestral relationships between parents of different progenies were taken into account to enhance the power of QTL detection, and other QTL were found using these new indices.

- *Identifying and characterizing patterns in tree-structured data* (Pierre Fernique, Jean-Baptiste Durand, Yann Guédon).

In the context of Pierre Fernique's PhD (Montpellier 2 University and CIRAD), two complementary approaches were developed for analyzing patterns in tree-structured data:

- multitype branching processes relying on local dependency properties for analyzing motifs.
- multiple change-point models relying on long-term dependencies for segmenting trees in homogeneous zones.

In multitype branching processes, the plant development is viewed as a demographic process, a parent entity of a given type generating child entities of different types (e.g. vegetative and flowering entities). Formally, the botanical entity properties are summarized as a categorical state variable. The number of child entities in each state is modeled through discrete multivariate distributions. Model

selection procedures are necessary to specify parsimonious generation distributions. We developed an approach based on probabilistic graphical models to identify and exploit properties of conditional independence between numbers of children in different states, so as to simplify the specification of their joint distribution. The graph building stage was based on exploring the space of possible chain graph models, which required defining a notion of neighbourhood of these graphs [59]. To relax the strong constraints regarding dependencies induced by parametric distributions, mixture of graphical models were also considered [60]. Multitype branching processes were applied to the analysis of the patchiness pattern (consisting of canopies made of clumps of either vegetative or flowering growth units) in mango trees. To identify the clumps, a novel approach based on tree-segmentation was developed [35].

- *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 [AFEF team, AGAP])

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. 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. This structural and phenological model has been presented at the ISHS symposium on Montpellier [37].

This year, the model has been extended, during the internship of S. Persello to take into account fruiting probabilities and coupled with an ecophysiological model of fruit growth [68], [69]. 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 different ISHS symposia [40], [50]

- *Integrative developmental growth stages of shoots* (Anaëlle Dambreville, Yann Guédon, Pierre-Eric Lauri [AFEF team, AGAP], Frédéric Normand [CIRAD, HortSys, Réunion Island])

Plant growth, i.e. the increase of organ dimensions over time, and development, i.e. the change in plant structure, are often studied as two separate processes. However, there is structural and functional evidence that these two processes are strongly related. Our aim was to investigate the co-ordination between growth and development using mango trees, which have well-defined developmental stages. Developmental stages, determined in an expert way, and organ sizes, determined from objective measurements, were collected during the vegetative growth and flowering phases of two cultivars of mango. For a given cultivar and growth unit type (either vegetative or flowering), a multi-stage model based on absolute growth rate (AGR) sequences deduced from the measurements was first built, and then growth stages deduced from the model were compared with developmental stages. Strong matches were obtained between growth stages and developmental stages, leading to a consistent definition of integrative developmental growth stages [14]. The growth stages highlighted growth asynchronisms between two topologically connected organs, namely the vegetative axis and its leaves. Integrative developmental growth stages emphasize that developmental stages are closely related to organ growth rates and can be interpreted in terms of the possible physiological processes (hydraulics, biomechanics and carbohydrate partitioning) underlying these stages. We also explore growth stages deduced from relative growth rate (RGR) sequences applying the same methodology. AGR and RGR have different meanings regarding plant metabolism since AGR represents net sink strength whereas RGR represents net sink activity. For vegetative growth units, the match rates between RGR-based stages and developmental stages were rather similar to the match rates between AGR-based stages and developmental stages, because of the rich information provided by the four organs modeled (the axis and three selected leaves). The match rates were far lower for the inflorescences where only the main axis was modeled. This is related to the fact that, compared to AGRs,



RGRs amplify the variations at the beginning of growth of an organ while damping the variations at the end of growth.

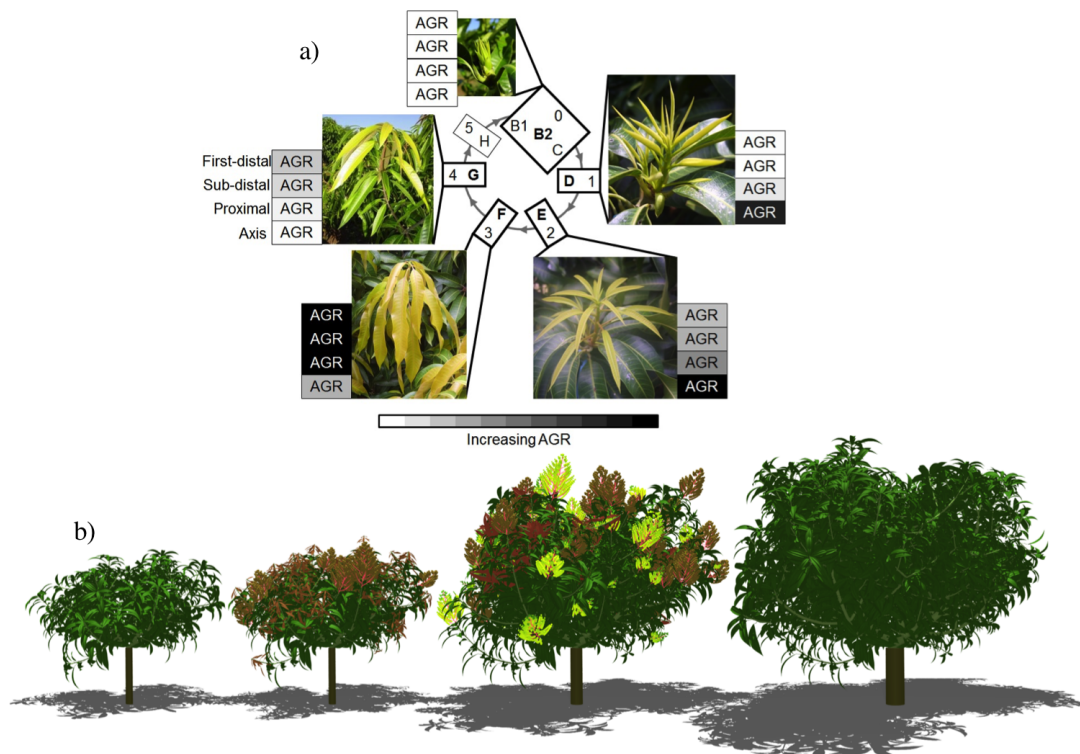


Figure 1. a) Correspondences between developmental stages of mango growth units determined from morphological observations in an expert way (inside the central circle) and growth stages obtained using segmentation models (outside the circle) [14]. Main developmental stages in bold are illustrated by the photographs. Variations in absolute growth rate for axis and leaves are illustrated using a white to black scale. b) Simulation of the development of a mango tree over two cycles [37]. 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 successive flowering phases 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. 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, 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 [7], 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 [7] 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 (To appear).

### 6.1.3. Analyzing the influence of the environment on the plant ontogenic programme

**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.

- *Influence of environmental conditions and horticultural practices on the branching and axillary flowering structures of fruit tree shoots.* (Yann Guédon, Evelyne Costes [AFEF Team, AGAP], Ted DeJong [UC Davis], Claudia Negron [UC Davis]).

In the context of a collaboration with Claudia Negron and Ted DeJong, we studied the influence of water availability and pruning practices [21] on the branching and axillary flowering structures of different categories of almond shoots. Stochastic models (hidden semi-Markov chains) were built for the branching and axillary flowering structures of different categories of almond shoots corresponding to different genetic backgrounds, levels of irrigation and pruning practices.

- *Analyzing growth components in trees.* (Yann Guédon, Yves Caraglio [AMAP], Olivier Taugourdeau [AMAP])

We identified robust indicators that summarize the respective importance of ontogeny and environmental constraints (mainly related to light environment) in forest tree development [26]. In this context, tree growth data correspond to the retrospective measurement of annual shoot characteristics (e.g. length, number of branches) along the main stem. We applied segmentation models to identify tree growth phases. These segmentation models, which are hidden semi-Markov chains, were compared with simple hidden Markov chains that correspond to the environment-driven development assumption. This statistical modelling approach was applied to both evergreen (Corsican pine and silver fir) and deciduous (sessile oak and Persian walnut) tree species growing in contrasted conditions ranging from managed forest stands to unmanaged understoreys. Growth phase duration distributions estimated within these segmentation models characterize the respective importance of ontogeny and environmental constraints in tree development at the population scale and have very

contrasted characteristics in terms of shape and relative dispersion between ontogeny-driven and environment-driven tree development. These characteristics may change over tree life, reflecting changes in tree competition. Growth phase duration distributions summarize the joint trajectory of tree ontogeny and environment without requiring tree growth follow-up data for their estimation.

- *Analyzing fruit tree phenology in various climatic conditions* Yann Guédon, Jean-Michel Legave [AFEF team, AGAP], Gustavo Malagui [Universidade Tecnológica Federal do Paraná]

The responses of flowering phenology to temperature increases in temperate fruit trees have rarely been investigated in contrasting climatic regions. This is an appropriate framework for highlighting varying responses to diverse warming contexts, which would potentially combine chill accumulation declines and heat accumulation increases. To examine this issue, a data set was constituted in apple tree from flowering dates collected for two phenological stages of three cultivars in seven climate-contrasting temperate regions of Western Europe and in three mild regions, one in Northern Morocco and two in Southern Brazil. Multiple change-point models were applied to flowering date series, as well as to corresponding series of mean temperature during two successive periods, respectively determining for the fulfillment of chill and heat requirements. A new overview in space and time of flowering date changes was provided in apple tree highlighting not only flowering date advances as in previous studies but also stationary flowering date series [18]. At global scale, differentiated flowering time patterns result from varying interactions between contrasting thermal determinisms of flowering dates and contrasting warming contexts. This may explain flowering date advances in most of European regions and in Morocco vs. stationary flowering date series in the Brazilian regions. A notable exception in Europe was found in the French Mediterranean region where the flowering date series was stationary. While the flowering duration series were stationary whatever the region, the flowering durations were far longer in mild regions compared to temperate regions. Our findings suggest a new warming vulnerability in temperate Mediterranean regions, which could shift towards responding more to chill decline and consequently experience late and extended flowering under future warming scenarios.

- *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 Echapp project, we use the wheat-septoria model to identify 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.

## 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], 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 [6] automatically performs a segmentation at cell resolution from 3D or 2D voxel images where the membranes/walls are marked (by a dye 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, ...). These trials will be conducted during the year. Moreover, the architecture of the image processing components has been modified (plugin approach) and integrated with the TissueLab platform. Some visualization tools have been improved, and the platform includes a module allowing an interaction with data (Alizon Konig, master internship). This point enables an efficient creation of gold standard to validate segmentation results.

This year, we also finalize the development of 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.

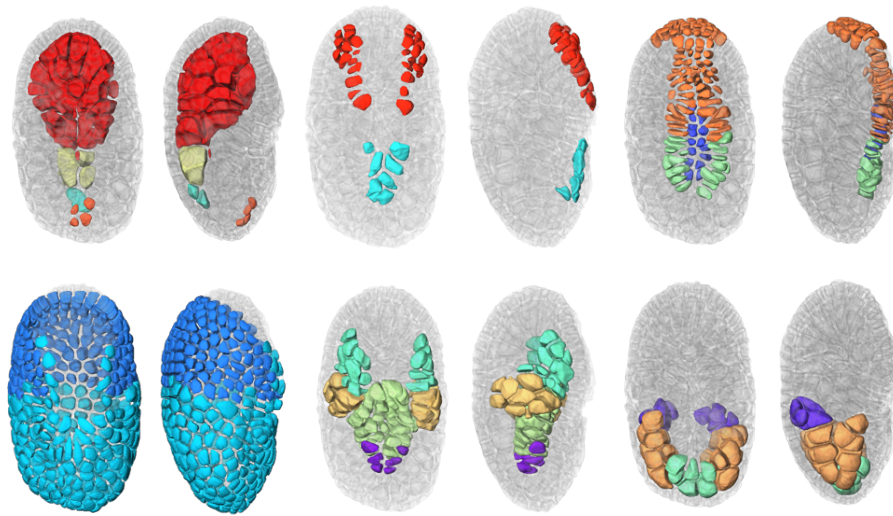


Figure 2. 3D projection of the segmented embryo at the early tailbud stage. The cells are colored by tissue type. The cells are slightly eroded to allow their distinction. The other cells of the embryo are in transparent grey. The dorsal and lateral sides are shown.

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 guess to match the adjacencies in the tissue, which proved to produce a very faithful reconstruction[39]. 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 [28].

These tools can produce light discrete representations of the cell interfaces that enables fast visualization, information projection, and quantitative analysis of the tissue, and have given way to some of the first biomechanical simulations on real-world data.

- *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], Guillaume Baty, Jan Traas [RDP, ENS], Teva Vernoux [RDP, ENS], Patrick Lemaire [CRBM, CNRS], Françoise Monéger [RDP, ENS].

*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 [67]. 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



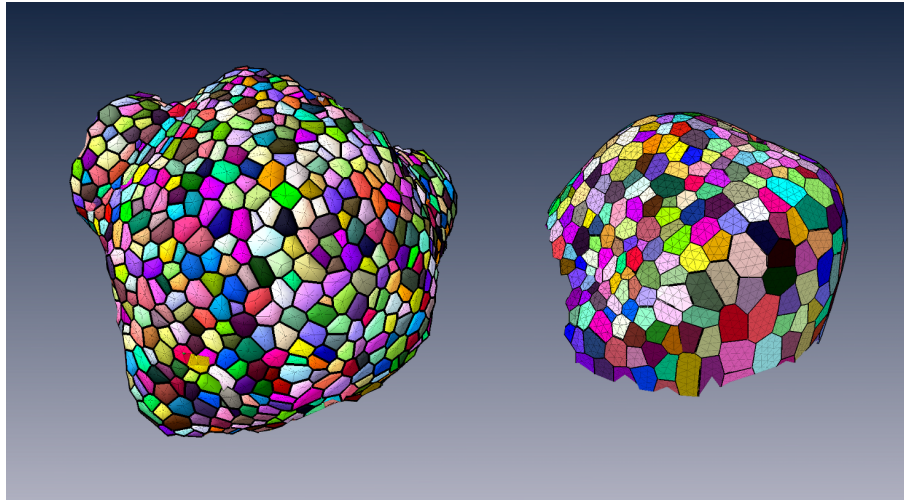


Figure 3. Triangular mesh representations of shoot apical meristem and flower meristem tissues obtained from MARS segmentations

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 investigated.

### 6.2.2. Shape analysis of meristems

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

At cellular resolution, we studied the organization of cells in the meristems. The MARS-ALT pipeline provides rich spatio-temporal data sets for analyzing the development of meristems. A first step consisted of designing a dedicated graph structure for efficiently representing the spatial (adjacency between cells) and temporal (cell division) relationships between cells. 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 value space, cellular patterns can be identified.

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 are 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 the Jan Traas's ERC.*

The rigid cell walls that surround plant cells are the main load-bearing structures in plant tissues. These walls are submitted to stresses due to cell turgor pressure. Above some threshold, these stresses cause deformation in the cell walls and triggers wall **irreversible expansion** (*synthesis*). Shape changes of plant tissues are therefore tightly related to the turgidity of cells and to the mechanical state and the molecular composition of the underlying cell walls. We developed a conceptual and numerical framework to model the mechanical structure of cell walls and their deformation by turgor pressure in 3-dimensions. This framework was used to study the interplay between post-transcriptional regulation, biochemistry, and mechanics within growing plant tissues. This work has been published this year in Plos Computational Biology [13].

In this first step, all mechanical and structural quantities are defined at the tissular scale. This is made possible by abstracting the connection between the actual molecular composition of the walls and the various signalling cascade at play during growth. To extend this approach, we also started to develop a mechanobiological approach relating the irreversible expansion of the walls to molecular mechanisms happening within them, based on the thermodynamical equilibrium of the pectin-based matrix within the wall. We propose that at the molecular scale expansion of this matrix is based on the adsorption of newly synthesized pectin molecules. This adsorption mechanism is regulated by the mechanical stresses applied on the wall. We show that this mechanism belongs to a class of biochemical / biomechanical processes commonly appearing in the dynamics of supra-molecular load-bearing structures: the force-driven polymerization processes. A preliminary version of these ideas (the 1D case) is currently under review in Trends In Plants Sciences.

We also considered to extend the original modeling approach to situations where entire organ dynamics should be modeled over large time lapse (several days) (PhD work of Jean-Philippe Bernard). In our first approach, the mechanical model relies on a finite element method (FEM) to describe the deformation of the tissue. In FEM, the tissue is represented by a mesh. The positions of the vertices at each time step are estimated from a linear system. If the tissue is big or if the mesh is fine, the linear system can be large and thus leads to computational overheads. An alternative way to classical FEM is to use a meshless method where the deformation of the tissue can be characterized by a linear combination of deformations of a finite and small set of frames. Because shape functions are no longer defined on each element but on the whole tissue, they have to be updated at each growth step by estimating a new rest configuration. With meshless method, the discretization of the system can be dynamically updated parsimoniously according to the precision required to model the emergence of shapes. With an uniform distribution of the frames within the volume, our method still leads to computational overheads. However, since the meristem initiates a branching structure at a macroscopic scale, we combined our mechanical model at tissular resolution with classical method used to generate branching structures at macroscopic scales. For this, we use the information of the plant branching structure to distribute the frames along the plant's axes. This allows us to use curvilinear shape functions while describing the branching structure growth using L-systems. This multi-scale framework allows us to define developmental rules which can initiate new organs at the surface of the meristematic dome by softening locally the meristem dome and thus creating new growing initia. First very encouraging results were obtained this year that demonstrate the feasibility of the approach.

### 6.2.4. Gene regulatory networks: Design of a genetic model of inflorescence development.

**Participants:** Eugenio Azpeitia, Christophe Godin, François Parcy, Etienne Farcot.

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

Modeling gene activities within cells is of primary importance since cell identities correspond to stable combination of gene expression.

We studied the regulatory network that controls the flowering transition during morphogenesis. To overcome the network complexity and integrate this regulation during ontogenesis, we have developed a first model of the control of floral initiation by genes, and in particular the situation of cauliflower mutants, in which the meristem repeatedly fails in making a complete transition to the flower. Three different network models were done and validated. A first Boolean version, a second fuzzy logic and an ODEs models were studied. The models are able to correctly recover the gene steady states observed in the meristems during the flower transitions, the gene transitions and the mutant effects. Importantly, the model is able to explain the cauliflower mutants. This work couples models at different scales, since the gene regulatory network is used as a decision module in an L-system model of the inflorescence architecture. This mixed model has led us to make different hypotheses about gene interactions and hormonal regulation. First predictions about gene actors controlling the passage to flower could be verified. Some links between gene regulation and plant growth have been identified. These links can be experimentally tested which could lead to a first integrated picture of flower development.

Finally, given that the cauliflower have different morphologies (i.e. regular and romanesco cauliflower morphologies) we explored the effect of changes in the L-system parameter values over the cauliflower morphology. Interestingly, we discovered by exploring the model that variations in the regulation of some phyllotactic parameters can produce the different cauliflower morphologies and explain other reported differences among them. Predictions were made using the model and experimental validations of this hypothesis are currently being tested. All our results could provide a comprehensive understanding of how genes and plant architecture are linked in a dynamical way.

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

**Participants:** Jonathan Legrand, Yann Guédon, 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. 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 proposed the first pipeline of statistical methods combining yeast-2-hybrid data and protein sequence dissimilarities for analyzing 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 Baty, Guillaume Cerutti, Jean-Louis Dinh, Jan Traas.

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

Our approach consists of building a programmable tissue which is able to accept different modeling components. This includes a central data structure representing the tissue in either 2-D or 3-D, which is able to grow in time, models of gene activity and regulation, models of signal exchange (physical and chemical) between cells and models of cell cycle (which includes cell division). An introduction to the modeling of some main components of such integrated system was published as a book chapter in the series of Ecole de Physique des Houches [43]. For each modeling component, one or several approaches are investigated in depth, possibly at different temporal and spatial scales, using the data available from the partners (imaging, gene networks, and expression patterns). Approaches are compared and assessed on the same data. The objective of each sub-model component will be to provide plugin components, corresponding to simplified versions of their models



if necessary, that can be injected in the programmable tissue platform. This work is developed in collaboration with the RDP group at ENS-Lyon [70] and the CPIB group in Nottingham, UK [53].

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 could be used in 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 conductivities, root architecture). One major finding is that the root hydraulic conductivity ( $L_{pr}$ ) 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  $L_{pr}$  inhibition, since its increase from values in control roots has marginal effects on  $L_{pr}$ . 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. The non linear system of equations (2) is the bottleneck to reach a higher number of cells; in order to overcome this, we plan to use the framework developed for the mechanical modelling of meristems (see section 6.2.3) and adapt it to this system. This will also allow to address tridimensional tissues.

Numerical simulations exhibit a highly non linear behaviour with respect to the governing parameters. 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 plan to compare this model to experimental results of the tomato fruit at the tissue level. In the longer term, a continuous version of this multicellular model could be an interesting way to build a model at the fruit scale.

### 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 platforms are emerging with associated image analysis toolbox (e.g. Smart-Root, RhizoScan) and the high-level analysis these complex phenotyping data requires new computational investigation methods.

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 using piecewise heteroscedastic linear models. To this end, we introduced a new slope heuristic for the selection of the number of zones in cell length series [29] [36].
2. individual root scale to analyze the dynamics of lateral root elongation. We investigated the use of 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 branching structure.

This pipeline of analysis methods will be applied to different species (maize, millet and *arabidopsis*) and for different biological objectives (study of genetic diversity for 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 one PhD programme and 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 controlling the vegetative development in *Arabidopsis thaliana*.

The changes in leaf size and shape during ontogeny associated with the heteroblastic development is a composite trait for which extensive spatio-

temporal data can be acquired using phenotyping platforms such as PHENOPSIS. 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 *Arabidopsis* rosette using various traits and minimum a priori assumptions. 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 showed that the degree of covering of the leaf abaxial surface with trichomes is not sufficient 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 led 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 [74], [64], [2], 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. A paper describing this model has been submitted recently for publication.

### 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 is currently being 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 disciplines, independently of their biological application.

### 6.4.1. *Scientific workflows*

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

#### 6.4.1.1. *OpenAlea scientific workflows*

Analyzing biological data may involve very complex and interlinked steps where several tools are combined together. Scientific workflow systems have reached a level of maturity that makes them able to support the design and execution of such in-silico experiments, and thus making them increasingly popular in the bioinformatics community (e.g. to annotate genomes, assemble NGS data, ...). However, in some emerging application domains such as system biology, developmental biology or ecology, the need for data analysis is combined with the need to model complex multi-scale biological systems, possibly involving multiple simulation steps. This requires the scientific workflow to deal with retro-action to understand and predict the relationships between structure and function of these complex systems. In collaboration with the Zenith EPI, we have proposed a conceptualisation of OpenAlea workflows [34] by introducing the concept of higher-order dataflows as a means to uniformly combine classical data analysis with modeling and simulation. Ongoing work include deploying OpenAlea workflows on a Grid technology using the SciFloware middleware in close collaboration with Zenith within IBC and INRA Phenome projects.

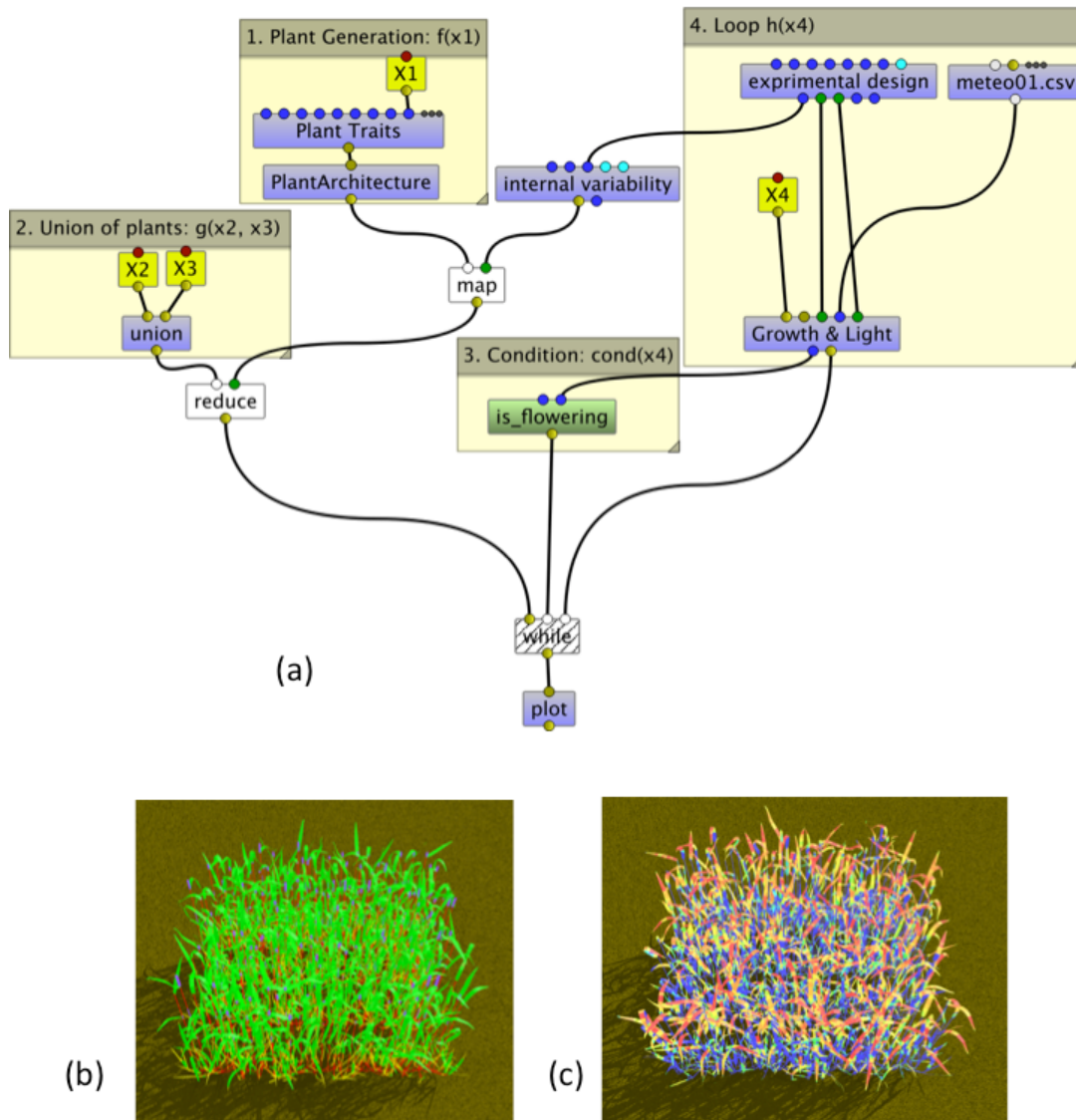


Figure 4. (a) OpenAlea workflow [34] for simulating Maize and Wheat crop performance based on phenotypic and environment data, and two image outputs (b and c). Colors represent the organ's type in (b) and the amount of intercepted light in (c).



#### 6.4.1.2. Querying Scientific workflows repositories

Several workflow systems have developed scientific workflow repositories (e.g., repositories of Galaxy workflows at IBC, or repositories of OpenAlea workflows). Such repositories have grown to sizes that call for advanced methods to support workflow discovery, in particular for similarity search. Effective similarity search requires both high quality algorithms for the comparison of scientific workflows and efficient strategies for indexing, searching, and ranking of search results. Yet, the graph structure of scientific workflows poses severe challenges at each of these steps. We present a complete system for effective and efficient similarity search in scientific workflow repositories, based on the Layer Decomposition approach to scientific workflow comparison. Layer Decomposition specifically accounts for the directed dataflow underlying scientific workflows and, compared to other state-of-the-art methods, delivers best results for similarity search at comparably low runtimes. Stacking Layer Decomposition with even faster, structure-agnostic approaches allows us to use proven, off-the-shelf tools for workflow indexing to further reduce runtimes and scale similarity search to sizes of current repositories [25]. Very efficient and powerful ranking methods have been used in this work. We based our choice on the large scale study of algorithms for rank aggregation with ties we performed [56].

#### 6.4.2. Statistical modeling

**Participants:** Yann Guédon, Jean Peyhardi.

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 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 [17] and [22].

#### 6.4.3. Lossy compression of tree structures

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

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 accepted at DCC'2016 [46] 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 [7] 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. The redaction of an article is currently in progress.

## 7. Bilateral Contracts and Grants with Industry

### 7.1. Bilateral Contracts with Industry

Guillaume Garin has been funded by ITK.

## 8. Partnerships and Cooperations

### 8.1. Regional Initiatives

#### 8.1.1. Agropolis computational plant seminar

**Participants:** Yann Guédon, Thierry Fourcaud [CIRAD, AMAP], Christine Granier [INRA, LEPSE], Soazig Guyomarc'H [Montpellier 2 University, DIADE], Laurent Laplaze [IRD, DIADE].

Funding: Agropolis foundation (Contractor for Virtual Plants: CIRAD. From 2013 to 2016)

In the context of the creation of a world-level pole on plant science in the region Languedoc-Roussillon, we created a monthly seminar on plant modeling and its applications. The seminar is organized by Yann Guédon, Thierry Fourcaud (CIRAD, AMAP), Christine Granier (INRA, LESPE), Soazig Guyomarc'h (Montpellier 2 University, DIADE) and Laurent Laplaze (IRD, DIADE) with the support of Agropolis International and Agropolis Foundation. In 2015, we organized a two-day workshop devoted to the modeling of plant development from the cellular to the organ scale.

### 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;

### 8.1.4. *SegmentationEvaluation*

**Participants:** Sophie Ribes, Benjamin Gilles [LIRMM], Guillaume Baty, Alizon Konig, Guillaume Cerutti.

Funding: IBC (Contractor for Virtual Plants: UM, 2015)

The goal of this project is to develop a framework allowing a robust validation for image segmentation. Segmentation is an ill-posed problem, and conventional validation approaches are corrupted by both intra and inter observer variabilities. We plan to develop: efficient tools allowing a creation of gold standard segmentation data (Alizon Konig, master internship under the supervision of Sophie Ribes); robust metrics to quantify differences between ground truth and algorithmic results.

Partners: ICAR, LIRMM, Montpellier.

## 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, 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 developing a software framework dedicated to the analysis of high throughput phenotyping data and models. It will be 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 light-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 in 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. MARS-ALT 2.0

**Participants:** Guillaume Baty, Christophe Pradal, Christophe Godin.

Funding: Inria ADT (Contractors for Virtual Plants: Inria from 2013 to 2015)

The goal of this project is to integrate in a single software platform all the software tools and algorithms that have been developed in various projects about meristem modeling in our teams. More precisely, we aim at building 3D models of meristem development at cellular resolution based on images obtained with confocal or multiphoton microscopy. This set of components will be used by biologists and modelers making it possible to build such meristem structures, to explore and to program them. This platform is embedded in the OpenAlea framework and is based on the imaging components of the platform MedInria. Asclepios, RDP ENS-Lyon/INRA, PHIV CIRAD

#### 8.2.5.2. 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.

#### 8.2.5.3. Echap

**Participants:** Christophe Pradal, Christian Fournier, Corinne Robert [INRA, EGC].

Funding: ONEMA (Contractor for Virtual Plants: INRA, From 2012 to 2014)

The objective of the ECHAP project is to reduce the frequency of treatments and the doses of pesticides applied on crops by taking advantage of natural mechanisms of disease escape related to crop architecture and by optimizing interception of pesticides by plant canopies. It focuses on the development of an integrative, yet modular, modeling tool on the OpenAlea platform that couples wheat architectural development, the interception and fate of fungicides and the dynamics of a pathogen. Various scenarios combining climate x architecture x fungicide treatment will be simulated to identify and propose efficient strategies of pesticide applications. Partners: UMR EGC (Paris-Grignon), UMR LEPSE (Montpellier), ARVALIS (Institut du végétal, France), ALTERRA (Research Institute for the Green World, The Netherlands), ADAS Intitute (UK), CNRS, and IRSTEA .

#### 8.2.5.4. Morphogenetics

**Participants:** Christophe Godin, Frédéric Boudon, Christophe Pradal, Grégoire Malandain, François Faure, Jan Traas, François Parcy, Arezki Boudaoud, Teva Vernoux.

Funding: Inria Project Lab (From 2013 to 2016)

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).

#### 8.2.5.5. *Rose*

**Participants:** Christophe Godin, Frédéric Boudon, Christophe Pradal.

Funding: INRA - Projet de Pari Scientifique (From 2012 to 2015)

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

## 8.3. International Initiatives

### 8.3.1. ANR-DFG

#### 8.3.1.1. *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)

### 8.3.2. Inria International Partners

#### 8.3.2.1. *Informal International Partners*

An important collaboration with the CIRAD research unit HortSys at the Reunion island and in particular Frédéric Normand has been established for several years. The topic of the collaboration is the study of the phenology of mango tree. Three members of the team have been visiting our collaborators during the year. This is a tripartite collaboration that also involves Pierre-Eric Lauri of the AGAP/AFEF team.

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 [21]. 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.

#### 8.3.2.2. *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 best characterized 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. International Research Visitors

### 8.4.1. *Visits of International Scientists*

The team received several visitors from foreign research groups in 2015:

- Farah Ben Naoum, from Sidi Bel Abbes University, Algeria, visited the team last summer for 1 month.
- Yoan Coudert, from University of Cambridge, UK, visited the team for 3 months.
- David Ford, from University of Washington, USA, visited the team for 1 week.
- Winfried Kurth of the University of Goettingen, Germany, visited the team for 1 week in June.
- Dennis Shasha, from Courant Institute of Mathematics, New York University, in the context of an Inria international chair, visited the team during its stay.
- Julia Pulwiczki, PhD student of the University of Calgary visited the team 2 weeks in May-June.

### 8.4.2. *Visits to International Teams*

#### 8.4.2.1. *Research stays abroad*

- Frédéric Boudon visited Frédéric Normand of the UR Hortsys at the CIRAD La Réunion two weeks in April.
- Christophe Pradal visited Frédéric Normand of the UR Hortsys and Ian Bally and Paula Ibell of the University of Queensland at the CIRAD La Réunion two weeks in May.
- Christophe Pradal visited Professor Kurth of the University of Goettingen, Germany one week in November.

## 9. Dissemination

### 9.1. Promoting Scientific Activities

#### 9.1.1. Scientific events organisation

##### 9.1.1.1. General chair, scientific chair

- Christophe Godin was Session chair and organizer of the e-session "from plant cells to plant fields" (<http://cs-dc-15.org/e-tracks/organisms>) at the World e-Conference on Complex Systems, Tempe Arizona, Sept 30 - Oct 1 2015, and was a session chair at the International Conference on Arabidopsis Research (ICAR), Paris, France 5-9 July;

#### 9.1.2. Scientific events selection

##### 9.1.2.1. Member of the conference program committees

- Christophe Godin is a member of the FSPM International Conference Board.
- Frédéric Boudon was member of the program committee of the Xe ISHS International Symposium on modelling in Fruit Research and Orchard Management.
- Yann Guédon was member of the program committee of the 47<sup>m</sup>e journées de statistique de la SFdS.
- S. Cohen-Boulakia has been members of the following program committees: ACM SIGMOD conf 2015, 2016, IEEE Int. Conf. on Data Engineering (ICDE) 2015, BPM 2015 (Business Process Management), ICDT workshop on Algorithms and Systems for MapReduce and Beyond (BeyondMR) 2015.

##### 9.1.2.2. Reviewer

- Frédéric Boudon was referee for papers submitted to the SIGGRAPH and Eurographics conferences and of the Journée Française d'Informatique Graphique (AFIG).

#### 9.1.3. Journal

##### 9.1.3.1. Member of the editorial boards

- Christophe Godin is an associate editor of the Journal *Frontiers in Plant Science*.
- S. Cohen-Boulakia is member of the editorial board of the *Journal of Data Semantics* (Springer).

##### 9.1.3.2. Reviewer - Reviewing activities

- Christophe Godin was referee for papers submitted to *Frontiers in Plant Science*
- Frédéric Boudon was referee for papers submitted to *Computer Graphics Forum*, *Computer and Electronics in Agriculture*, *Sensors*, *Remote Sensing and Environment*, *Robotics and Autonomous Systems*.
- Yann Guédon was referee for papers submitted to *Computational Intelligence and Neuroscience*, *Frontiers in Plant Science* and *PLoS ONE*.
- Christian Fournier was referee for papers submitted to *Computer and Electronics in Agriculture*

#### 9.1.4. Invited talks

- C. Godin gave invited talks at: "CompSysBio: Advanced lecture course on computational systems biology", Aussois, France (April); Embo Practical Course on "In vivo Plant Imaging" Heidelberg, Germany (March); International Conference on Arabidopsis Research (ICAR);
- S. Cohen-Boulakia gave invited tutorials at the « DigiCosme Spring School 2015 on Data Management » (Saclay, May 2015) and at the summer school « Cumulo-Numbio : Cloud computing for the life sciences » (Aussois, June 2015).

- C. Pradal gave an invited talk at the "Nimbios Morphological Plant Models Workshop" (Knoxville, Tennessee, USA, September 2015) and at the "8th plenary meeting of the European TTO Circle" during the Expo Milan 2015 (Milano, Italy, June 2015).

### 9.1.5. Scientific expertise

- Christophe Godin was the external member of the mentoring and review committee of James Locke's group at the Sainsbury Laboratory, University of Cambridge. He is also a member of the Scientific Committee of INRA Environment/Agronomy department. Christophe Godin also participated in a concours for several CR2 positions at INRA, a concours of Professor in computer science at the University of Montpellier, to 2 thesis committee, to 2 PhD defences (1 as Jury president) and 2 HDR defences as a reviewer.
- Christophe Pradal is a member of the INRA expert scientific commissions (CSS Ecophysiologie, génétique et biologie intégrative des plantes) that assesses INRA individual researcher activities. He is also a member of the HCERES expert scientific commissions that assesses national research organisations.
- Christian Fournier is a member of of the INRA engineer evaluation commission (CEI Méthodes Pour la Recherche : Biologie végétale / Domaine Informatique, bio-informatique, statistiques et calcul scientifique) that assesses INRA individual engineer activities.

### 9.1.6. Research administration

- Christophe Godin is a member of the "bureau of comité des projets" at Inria Sophia-Antipolis Méditerranée research center. He is also a member of the Scientific board of the modeling axis of Labex NUMEV and a member of the direction board of the institut de biologie computationnelle de Montpellier (IBC) and the scientific co-coordinator with Patrick Lemaire of IBC 4th research axis on imaging and omics data.

## 9.2. Teaching - Supervision - Juries

### 9.2.1. Teaching

Master in Life Sciences "IMaLis" of ENS Paris. Christophe Godin co-organizes with Patrick Lemaire of a 35 hours module on Plant and animal morphogenesis.

Master Plant Ecophysiology, Christian Fournier, Introduction to architectural plant modelling, 4h, M1, Montpellier University

Master Computer Science: Frédéric Boudon (resp.), Christophe Godin, Christophe Pradal, Benjamin Gilles [ICAR, LIRMM] and David Vanderhaege and Loïc Barthe [IRIT, Toulouse], Computer graphics, 45h, M2, University Montpellier, France.

Master Biostatistics : University Montpellier.

Yann Guédon teaches the stochastic modeling course (<http://www.agro-montpellier.fr/um2/um1/masterbiostatistique>). This involves 21h of M2 classes.

Master of bioinformatic and biomathematics (University Cheikh AntaDiop, Dakar, Sénégal). Christophe Godin and Yann Guédon participated to the module iPlant (M2 - 12h).

Master of Biology Fonctionnelle. Christophe Godin gave a class of Master 2 on 'Phyllotaxis' in the at the University of Montpellier 2 (M2 - 4h).

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

### 9.2.2. Supervision

- PhD : Léo Guignard, "*Segmentation, visualization and mechanical modeling of embryonic development in the ascidian*", Montpellier University, 9 Dec. 2015, C. Godin, P. Lemaire.

- PhD : Guillaume Garin, "*Développement d'un cadre générique de modélisation du couple plante – agent pathogène dans OpenAlea et d'une méthodologie de transfert vers un Outil d'Aide à la Décision*", 11 Dec. 2015, ANRT Ciffre ITK, C. Robert, B. Andrieu, C. Pradal, C. Fournier.
- PhD in progress : Jean-Philippe Bernard, "*Adaptive mechanical model of early flower development based on 4D imaging*", Montpellier University, C. Godin, B. Gilles.
- PhD in progress : Beatriz Moreno Ortega, "*Analysis and modeling of metabolic and hormonal controls of lateral root growth during their ontogeny. Application to the impact of water stress on the root architecture*", Montpellier SupAgro, B. Muller, Y. Guédon.
- PhD in progress : Sixtine Passot, "*Adaptation of millet root architecture : Phenotyping and spatio-temporal analysis of growing root systems*", Montpellier University, L. Laplaze, Y. Guédon.
- 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 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, Y. Guédon.
- PhD in progress : Adama Ndour, "*Role of root architecture of pearl millet for tolerance to water stress*", Montpellier University, L. Laplaze, M. Lucas, C. Pradal.

### 9.2.3. Juries

- S. Cohen-Boulakia has been reviewer and member of the defense committee for the two following PhD thesis: Francois Moreews (U. Rennes 1), Mouhamadou Ba (INSA Rennes)

## 9.3. Popularization

- Christophe Godin and Frédéric Boudon presented the Secret Code of Flowers in the context of an Inria initiative at the Science Festival in October.
- Christophe Godin gave several classes at Lycée Pompidou, Castelnau Le Lez, at Terminal level and gave a "Café-in" seminar on "Comment les plantes font-elles des mathématiques ?"

# 10. Bibliography

## Major publications by the team in recent years

- [1] P. BARBIER DE REUILLE, I. BOHN-COURSEAU, K. LJUNG, H. MORIN, N. CARRARO, C. GODIN, J. TRAAS. *Computer simulations reveal novel properties of the cell-cell signaling network at the shoot apex in Arabidopsis*, in "PNAS", 2006, vol. 103, pp. 1627-1632, <http://www-sop.inria.fr/virtualplants/Publications/2006/BBLMCGT06>
- [2] F. BESNARD, Y. REFAHI, V. MORIN, B. MARTEAUX, G. BRUNOUD, P. CHAMBRIER, F. ROZIER, V. MIRABET, J. LEGRAND, S. LAINÉ, E. THÉVENON, E. FARCOT, C. CELLIER, P. DAS, A. BISHOPP, R. DUMAS, F. PARCY, Y. HELARIUTTA, A. BOUDAUD, C. GODIN, J. TRAAS, Y. GUÉDON, T. VERNOUX. *Cytokinin signalling inhibitory fields provide robustness to phyllotaxis*, in "Nature", 2014, vol. 505, n° 7483, pp. 417-421 [DOI : 10.1038/NATURE12791], <https://hal.inria.fr/hal-00926908>
- [3] F. BOUDON, J. CHOPARD, O. ALI, B. GILLES, O. HAMANT, A. BOUDAUD, 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° 1, pp. 1-16 [DOI : 10.1371/JOURNAL.PCBI.1003950], <https://hal.archives-ouvertes.fr/hal-01142486>



- [4] F. BOUDON, C. PRADAL, T. COKELAER, P. PRUSINKIEWICZ, C. GODIN. *L-Py: an L-system simulation framework for modeling plant architecture development based on a dynamic language*, in "Frontiers in plant science", May 2012, vol. 3, n<sup>o</sup> 76 [DOI : 10.3389/FPLS.2012.00076], <http://hal.inria.fr/cirad-00703085>
- [5] F. CHAUBERT-PEREIRA, Y. GUÉDON, C. LAVERGNE, C. TROTTIER. *Markov and semi-Markov switching linear mixed models used to identify forest tree growth components*, in "Biometrics", sept 2010, vol. 66, n<sup>o</sup> 3, pp. 753–762, <http://www-sop.inria.fr/virtualplants/Publications/2010/CGLT10>
- [6] R. FERNANDEZ, P. DAS, V. MIRABET, E. MOSCARDI, J. TRAAS, J.-L. VERDEIL, G. MALANDAIN, C. GODIN. *Imaging plant growth in 4D: robust tissue reconstruction and lineaging at cell resolution*, in "Nature Methods", jul 2010, vol. 7, pp. 547–553, <http://www-sop.inria.fr/virtualplants/Publications/2010/FDMMTVMG10>
- [7] C. GODIN, P. FERRARO. *Quantifying the degree of self-nestedness of trees: application to the structural analysis of plants*, in "IEEE/ACM Transactions in Computational Biology and Bioinformatics", 2010, vol. 7, pp. 688–703, <http://www-sop.inria.fr/virtualplants/Publications/2010/GF10>
- [8] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *A new specification of generalized linear models for categorical responses*, in "Biometrika", 2015, vol. 102, n<sup>o</sup> 4, pp. 889–906 [DOI : 10.1093/BIOMET/ASV042], <https://hal.inria.fr/hal-01240023>
- [9] C. PRADAL, S. DUFOUR-KOWALSKI, F. BOUDON, C. FOURNIER, C. GODIN. *OpenAlea: A visual programming and component-based software platform for plant modeling*, in "Functional Plant Biology", 2008, vol. 35, n<sup>o</sup> 9 & 10, pp. 751–760, <http://www-sop.inria.fr/virtualplants/Publications/2008/PDBFG08a>
- [10] T. VERNOUX, G. BRUNOUD, E. FARCOT, V. MORIN, H. VAN DEN DAELE, J. LEGRAND, M. OLIVA, P. DAS, A. LARRIEU, D. WELLS, Y. GUÉDON, L. ARMITAGE, F. PICARD, S. GUYOMARC'H, C. CELLIER, G. PARRY, R. KOUMPROGLOU, J. DOONAN, M. ESTELLE, C. GODIN, S. KEPINSKI, M. J. BENNETT, L. DE VEYLDER, J. TRAAS. *The auxin signalling network translates dynamic input into robust patterning at the shoot apex*, in "Molecular Systems Biology", 2011, vol. 7, n<sup>o</sup> 508, <http://www-sop.inria.fr/virtualplants/Publications/2011/VBFMVLODLWGAPGCPKDEG>

## Publications of the year

### Doctoral Dissertations and Habilitation Theses

- [11] S. COHEN-BOULAKIA. *Data Integration in the Life Sciences: Scientific Workflows, Provenance, and Ranking*, Université Paris-Sud, June 2015, Habilitation à diriger des recherches, <https://hal.archives-ouvertes.fr/tel-01245229>

### Articles in International Peer-Reviewed Journals

- [12] J.-P. BERNARD, E. FRENOD, A. ROUSSEAU. *Paralic confinement computations in coastal environment with interlocked areas*, in "Discrete and Continuous Dynamical Systems - Series S", February 2015, vol. 8, n<sup>o</sup> 1, pp. 45-54 [DOI : 10.3934/DCDSS.2015.8.45], <https://hal.archives-ouvertes.fr/hal-00833340>
- [13] F. BOUDON, J. CHOPARD, O. ALI, B. GILLES, O. HAMANT, A. BOUDAOU, 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<sup>o</sup> 1, pp. 1-16 [DOI : 10.1371/JOURNAL.PCBI.1003950], <https://hal.archives-ouvertes.fr/hal-01142486>

- [14] A. DAMBREVILLE, P.-É. LAURI, F. NORMAND, Y. GUÉDON. *Analysing growth and development of plants jointly using developmental growth stages*, in "Annals of Botany", 2015, vol. 115, n<sup>o</sup> 1, 13 p. [DOI : 10.1093/AOB/MCU227], <https://hal.inria.fr/hal-01100553>
- [15] J.-B. DURAND, Y. GUÉDON. *Localizing the latent structure canonical uncertainty: entropy profiles for hidden Markov models*, in "Statistics and Computing", 2016, vol. 26, n<sup>o</sup> 1, pp. 549-567 [DOI : 10.1007/s11222-014-9494-9], <https://hal.inria.fr/hal-01090836>
- [16] M. GRAND-BROCHIER, A. VACAVANT, G. CERUTTI, C. KURTZ, J. WEBER, L. TOUGNE. *Tree leaves extraction in natural images: Comparative study of pre-processing tools and segmentation methods*, in "IEEE Transactions on Image Processing", 2015, vol. 24, n<sup>o</sup> 5, pp. 1549-1560 [DOI : 10.1109/TIP.2015.2400214], <https://hal.archives-ouvertes.fr/hal-01176699>
- [17] Y. GUÉDON. *Segmentation uncertainty in multiple change-point models*, in "Statistics and Computing", 2015, vol. 25, n<sup>o</sup> 2, pp. 303 - 320 [DOI : 10.1007/s11222-013-9433-1], <https://hal.inria.fr/hal-01117013>
- [18] J.-M. LEGAVE, Y. GUÉDON, G. MALAGI, A. EL YAACOUBI, M. BONHOMME. *Differentiated Responses of Apple Tree Floral Phenology to Global Warming in Contrasting Climatic Regions*, in "Frontiers in Plant Science", December 2015, vol. 6, n<sup>o</sup> 1054, 13 p. [DOI : 10.3389/FPLS.2015.01054], <https://hal.inria.fr/hal-01244070>
- [19] G. LOBET, M. P. POUND, J. DIENER, C. PRADAL, X. DRAYE, C. GODIN, M. JAVAUX, D. LEITNER, F. MEUNIER, P. NACRY, T. P. PRIDMORE, A. SCHNEPF. *Root System Markup Language: toward a unified root architecture description language*, in "Plant Physiology", January 2015, vol. 167, n<sup>o</sup> 3, pp. 617-627 [DOI : 10.1104/PP.114.253625], <https://hal.archives-ouvertes.fr/hal-01113767>
- [20] E. MARZA, S. TAOUJI, K. BARROSO, A.-A. RAYMOND, L. GUIGNARD, M. BONNEU, N. PALLARES-LUPON, J.-W. DUPUY, M. E. FERNANDEZ-ZAPICO, J. ROSENBAUM, F. PALLADINO, D. DUPUY, E. CHEVET. *Genome-wide screen identifies a novel p97/CDC-48-dependent pathway regulating ER-stress-induced gene transcription*, in "EMBO Reports", 2015, vol. 16, n<sup>o</sup> 3, pp. 332-340 [DOI : 10.15252/EMBR.201439123], <https://hal-univ-rennes1.archives-ouvertes.fr/hal-01163728>
- [21] C. NEGRÓN, L. CONTADOR, B. D. LAMPINEN, S. G. METCALF, Y. GUÉDON, E. COSTES, T. M. DEJONG. *How different pruning severities alter shoot structure: a modelling approach in young 'Nonpareil' almond trees*, in "Functional Plant Biology", 2015, vol. 42, n<sup>o</sup> 3, pp. 325-335 [DOI : 10.1071/FP14025], <https://hal.inria.fr/hal-01120092>
- [22] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *A new specification of generalized linear models for categorical responses*, in "Biometrika", 2015, vol. 102, n<sup>o</sup> 4, pp. 889-906 [DOI : 10.1093/BIOMET/ASV042], <https://hal.inria.fr/hal-01240023>
- [23] A. RAVASIO, I. CHEDDADI, T. CHEN, T. PEREIRA, H. T. ONG, C. BERTOCCHI, A. BRUGUES, A. JACINTO, A. J. KABLA, Y. TOYAMA, X. TREPAT, N. GOV, L. NEVES DE ALMEIDA, B. LADOUX. *Gap geometry dictates epithelial closure efficiency*, in "Nature Communications", July 2015, vol. 6 [DOI : 10.1038/NCOMMS8683], <https://hal.archives-ouvertes.fr/hal-01245750>
- [24] A. RODRIGUEZ, L. TORRES, U. JUAREZ, D. SOSA, E. AZPEITIA, B. GARCIA-DE TERESA, E. CORTES, R. ORTIZ, A. M. SALAZAR, P. OSTROSKY-WEGMAN, L. MENDOZA, S. FRIAS. *Fanconi anemia cells with unrepaired DNA damage activate components of the checkpoint recovery process*, in "Theoretical Biology and

Medical Modelling", 2015, vol. 12, n<sup>o</sup> 1, 19 p. [DOI : 10.1186/s12976-015-0011-4], <https://hal.inria.fr/hal-01217314>

- [25] J. STARLINGER, S. COHEN-BOULAKIA, S. KHANNA, S. DAVIDSON, U. LESER. *Effective and Efficient Similarity Search in Scientific Workflow Repositories*, in "Future Generation Computer Systems", September 2015, 79 p. [DOI : 10.1016/J.FUTURE.2015.06.012], <https://hal.archives-ouvertes.fr/hal-01170597>
- [26] O. TAUGOURDEAU, Y. CARAGLIO, S. SABATIER, Y. GUÉDON. *Characterizing the respective importance of ontogeny and environmental constraints in forest tree development using growth phase duration distributions*, in "Ecological Modelling", 2015, vol. 300, pp. 61 - 72 [DOI : 10.1016/J.ECOLMODEL.2014.12.022], <https://hal.inria.fr/hal-01110350>

### Invited Conferences

- [27] C. PRADAL. *Multiscale topological and geometrical representation of plant architecture*, in "NimBIOS: Morphological Plant Models", Knoxville, United States, Alexander Bucksch and Dan Chitwood, September 2015, <https://hal.inria.fr/hal-01245386>

### International Conferences with Proceedings

- [28] G. CERUTTI, C. GODIN. *Meshing Meristems - An Iterative Mesh Optimization Method for Modeling Plant Tissue at Cell Resolution*, in "BIOIMAGING", Lisbonne, Portugal, January 2015, <https://hal.archives-ouvertes.fr/hal-01100808>
- [29] Y. GUÉDON. *Slope heuristics for multiple change-point models*, in "30th International Workshop on Statistical Modelling (IWSM 2015)", Linz, Austria, H. FRIEDL, H. WAGNER (editors), Statistical Modelling Society, July 2015, <https://hal.inria.fr/hal-01240037>
- [30] G. MICHELIN, L. GUIGNARD, U.-M. FIUZA, P. LEMAIRE, C. GODIN, G. MALANDAIN. *Cell Pairings for Ascidian Embryo Registration*, in "ISBI - International Symposium on Biomedical Imaging", New York, United States, April 2015 [DOI : 10.1109/ISBI.2015.7163872], <https://hal.inria.fr/hal-01113166>
- [31] G. MICHELIN, Y. REFAHI, R. WIGHTMAN, H. JÖNSSON, J. J. TRAAS, C. GODIN, G. MALANDAIN. *Spatio-temporal registration of 3D microscopy image sequences of Arabidopsis floral meristems*, in "ISBI - International Symposium on Biomedical Imaging", Prague, Czech Republic, April 2016 [DOI : 10.1109/ISBI.2015.7163872], <https://hal.inria.fr/hal-01251151>
- [32] J. PEYHARDI. *New qualitative choice models incorporating individual and choice characteristics*, in "30th International Workshop on Statistical Modelling (IWSM 2015)", Linz, Austria, H. FRIEDL, H. WAGNER (editors), Statistical Modelling Society, July 2015, vol. 1, pp. 319-323, <https://hal.inria.fr/hal-01242841>
- [33] J. PEYHARDI. *Nouveaux modèles de choix qualitatifs prenant en compte des caractéristiques individuelles et des caractéristiques de choix*, in "47èmes Journées de Statistique", Lille, France, Société Française de Statistique, June 2015, <https://hal.inria.fr/hal-01242827>
- [34] C. PRADAL, C. FOURNIER, P. VALDURIEZ, S. COHEN-BOULAKIA. *OpenAlea: Scientific Workflows Combining Data Analysis and Simulation*, in "SSDBM 2015: 27th International Conference on Scientific and Statistical Database Management", San Diego, United States, June 2015 [DOI : 10.1145/2791347.2791365], <https://hal.archives-ouvertes.fr/hal-01166298>

### National Conferences with Proceedings

- [35] P. FERNIQUE, J.-B. DURAND, Y. GUÉDON. *Détection de motifs disruptifs au sein de plantes : une approche de quotientement/classification d'arborescences*, in "47èmes Journées de Statistique", Lille, France, Société Française de Statistique, June 2015, <https://hal.inria.fr/hal-01240305>
- [36] Y. GUÉDON. *Heuristique de pente pour les modèles de détection de ruptures multiples*, in "47èmes Journées de Statistique", Lille, France, Société Française de Statistique, June 2015, <https://hal.inria.fr/hal-01240298>

### Conferences without Proceedings

- [37] F. BOUDON, A. JESTIN, A.-S. BRIAND, P. FERNIQUE, P.-E. LAURI, A. DAMBREVILLE, Y. GUÉDON, I. GRECHI, F. NORMAND. *The Role of Structural and Temporal Factors in the Architectural Development of the Mango Tree: Evidences from Simulation*, in "International Symposium on Modelling in Fruit Research and Orchard Management", Montpellier, France, June 2015, <https://hal.inria.fr/hal-01237402>
- [38] I. CHEDDADI, C. GODIN, F. BOUDON, V. BALDAZZI, M. M. GÉNARD, N. BERTIN. *Toward a mechanical model of 3D fruit development*, in "International Symposium on Modelling in Fruit Research and Orchard Management", Montpellier, France, June 2015, <https://hal.inria.fr/hal-01237387>
- [39] G. CERUTTI, S. RIBES, C. GODIN, C. GALVAN AMPUDIA, T. VERNOUX. *3D Tessellation of Plant Tissue A dual optimization approach to cell-level meristem reconstruction from microscopy images*, in "International Conference on 3D Vision", Lyon, France, October 2015 [DOI : 10.1109/3DV.2015.57], <https://hal.archives-ouvertes.fr/hal-01246580>
- [40] I. GRECHI, F. BOUDON, M. LÉCHAUDEL, F. NORMAND. *A crop simulation model to predict fruit yield and quality on mango tree: overview, progresses and perspectives*, in "International Mango Symposium", Darwin, Australia, September 2015, <https://hal.inria.fr/hal-01237410>
- [41] S. PASSOT, F. GNACKO, J. ATKINSON, B. ATKINSON, M. LUCAS, S. GUYOMARC'H, F. BOUDON, M. COUDERC, L. ZEKRAOUI, C. STURROCK, N. KANE, C. T. HASH, P. GANTET, M. J. BENNETT, D. WELLS, Y. Y. VIGOUROUX, Y. GUÉDON, L. LAPLAZE. *Exploring root development and architecture in one of the most heat and drought tolerant cereals, pearl millet*, in "Plant Phenotyping Symposium", Barcelone, Spain, November 2015, <https://hal.inria.fr/hal-01237385>
- [42] F. REYES, B. PALLAS, C. PRADAL, E. COSTES. *A Multi-Scale Model to explore Carbon Allocation in Plants*, in "International Symposium on Modelling in Fruit Research and Orchard Management", Montpellier, France, June 2015, <https://hal.inria.fr/hal-01245366>

### Scientific Books (or Scientific Book chapters)

- [43] C. GODIN, E. AZPEITIA, E. FARCOT. *An introduction to modelling flower primordium initiation*, in "From Molecules to Living Organisms: An Interplay Between Biology and Physics", Lecture Notes of the Les Houches School of Physics, December 2015, vol. 102, <https://hal.inria.fr/hal-01254880>

### Research Reports

- [44] C. ROBERT, C. C. FOURNIER, C. BEDOS, D. GOUACHE, B. B. PERRIOT. *ECHAP « L'architecture des couverts végétaux : un levier pour réduire l'utilisation des fongicides ? »*, INRA, January 2015, n<sup>o</sup> 1879/10, 43 p. , <https://hal.inria.fr/hal-01253658>

## Scientific Popularization

- [45] C. GODIN. *L'importance capitale du travail de fournis des chercheurs*, in "1024 – Bulletin de la société informatique de France", January 2016, n<sup>o</sup> 5, 10 p. , <https://hal.inria.fr/hal-01256863>

## Other Publications

- [46] R. AZAÏS, J.-B. DURAND, C. GODIN. *Lossy compression of unordered rooted trees*, December 2015, working paper or preprint, <https://hal.archives-ouvertes.fr/hal-01236088>
- [47] A. BARBIERI, J. PEYHARDI, C. LAVERGNE, T. CONROY, S. GOURGOU, C. MOLLEVI. *Selection of item response theory models for the longitudinal analysis of health-related quality of life in cancer clinical trials*, December 2015, working paper or preprint, <https://hal.archives-ouvertes.fr/hal-01246368>
- [48] B. BRANCOTTE, B. RANCE, A. DENISE, S. COHEN-BOULAKIA. *Interrogation de bases de données biologiques publiques par reformulation de requêtes et classement des résultats avec ConQuR-Bio*, July 2015, JOBIM (Journées Ouvertes Biologie Informatique Mathématiques), Poster, <https://hal.archives-ouvertes.fr/hal-01167840>
- [49] C. FOURNIER, S. ARTZET, J. CHOPARD, M. MIELEWCZIK, N. BRICHET, L. CABRERA, X. SIRAUT, S. COHEN-BOULAKIA, C. PRADAL. *Phenomenal: a software framework for model-assisted analysis of high throughput plant phenotyping data*, September 2015, IAMPS 2015 (International Workshop on Image Analysis Methods for the Plant Sciences), Poster, <https://hal.inria.fr/hal-01253627>
- [50] I. GRECHI, F. BOUDON, M. LÉCHAUDEL, T. NORDEY, M. GÉNARD, F. NORMAND. *Modelling fruit yield and quality on the Mango tree: Recent progresses and future steps*, June 2015, International Symposium on Modelling in Fruit Research and Orchard Management, Poster, <http://hal.univ-reunion.fr/hal-01193184>
- [51] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *Partitioned conditional generalized linear models for categorical data*, January 2015, 25 pages, 13 figures, <https://hal.inria.fr/hal-01101036>

## References in notes

- [52] A. ARBER. *Natural philosophy of plant form*, University Press, Cambridge, 1950
- [53] L. BAND, J. FOZARD, C. GODIN, O. JENSEN, T. PRIDMORE, M. BENNETT, J. KING. *Multiscale systems analysis of root growth and development: modeling beyond the network and cellular scales*, in "The Plant Cell", 2012, <http://www-sop.inria.fr/virtualplants/Publications/2012/BFGJPBK12>
- [54] D. BARTHELEMY, Y. CARAGLIO, E. COSTES. *Architecture, gradients morphogntiques et âge physiologique chez les vgtaux*, in "Modélisation et Simulation de l'Architecture des Végétaux", J. BOUCHON, P. DE REFFYE, D. BARTHELEMY (editors), INRA, 1997, pp. 89-136
- [55] F. BOUDON, C. PREUKSAKARN, P. FERRARO, J. DIENER, P. NACRY, E. NIKINMAA, C. GODIN. *Quantitative assessment of automatic reconstructions of branching systems obtained from laser scanning*, in "Annals of Botany", April 2014, epub ahead of print [DOI : 10.1093/AOB/MCU062], <https://hal.archives-ouvertes.fr/hal-01064917>

- [56] B. BRANCOTTE, B. YANG, G. BLIN, S. COHEN-BOULAKIA, A. DENISE, S. HAMEL. *Rank aggregation with ties: Experiments and Analysis*, in "Proceedings of the VLDB Endowment (PVLDB)", August 2015, 2051, <https://hal.archives-ouvertes.fr/hal-01165336>
- [57] M. CIESLAK, M. GÉNARD, F. BOUDON, V. BALDAZZI, C. GODIN, N. BERTIN. *Integrating architecture and physiological perspectives in fruit development*, in "7th International Conference on Functional-Structural Plant Models", Saariselkä, Finland, R. SIEVÄNEN, E. NIKINMAA, C. GODIN, A. LINTUNEN, P. NYGREN (editors), June 2013, pp. 127-130, ISBN 978-951-651-408-9, <http://hal.inria.fr/hal-00850801>
- [58] J.-B. DURAND, B. GUITTON, J. PEYHARDI, Y. HOLTZ, Y. GUÉDON, C. TROTTIER, E. COSTES. *New insights for estimating the genetic value of F1 apple progenies for irregular bearing during the first years of tree production*, in "Journal of Experimental Botany", November 2013, vol. 64, n<sup>o</sup> 16, pp. 5099-5113 [DOI : 10.1093/jxb/ert297], <http://hal.inria.fr/hal-00845353>
- [59] P. FERNIQUE, J.-B. DURAND, Y. GUÉDON. *Estimation of Discrete Partially Directed Acyclic Graphical Models in Multitype Branching Processes*, in "COMPSTAT 2014, 21st International Conference on Computational Statistics", Geneva, Switzerland, Proceedings of COMPSTAT 2014, 21st International Conference on Computational Statistics, The International Association for Statistical Computing (IASC), August 2014, <https://hal.inria.fr/hal-01084524>
- [60] P. FERNIQUE, J.-B. DURAND, Y. GUÉDON. *Modèles graphiques paramétriques pour la modélisation des lois de génération dans des processus de branchement multitypes*, in "46èmes Journées de Statistique", Rennes, France, June 2014, <https://hal.inria.fr/hal-01058313>
- [61] L. E. GATSUK, O. V. SMIRNOVA, L. I. VORONTZOVA, L. B. ZAUGOLNOVA, L.A. ZHUKOVA. *Age states of plants of various growth forms: a review*, in "Journal of Ecology", 1980, vol. 68, pp. 675-696
- [62] C. GODIN, Y. CARAGLIO. *A multiscale model of plant topological structures*, in "Journal of Theoretical Biology", 1998, vol. 191, pp. 1-46, <http://www-sop.inria.fr/virtualplants/Publications/1998/GC98>
- [63] C. GODIN, E. COSTES, H. SINOQUET. *A method for describing plant architecture which integrates topology and geometry*, in "Annals of Botany", 1999, vol. 84, pp. 343-357
- [64] Y. GUÉDON, Y. REFAHI, F. BESNARD, E. FARCOT, C. GODIN, T. VERNOUX. *Pattern identification and characterization reveal permutations of organs as a key genetically controlled property of post-meristematic phyllotaxis*, in "Journal of Theoretical Biology", 2013 [DOI : 10.1016/j.jtbi.2013.07.026], <http://hal.inria.fr/hal-00859831>
- [65] F. HALLÉ, R. A. A. OLDEMAN, P. B. TOMLINSON. *Tropical trees and forests. An architectural analysis*, Springer-Verlag, New-York, 1978
- [66] J. L. HARPER, B. R. ROSEN, J. WHITE. *The growth and form of modular organisms*, The Royal Society, London, UK, 1986
- [67] C. LA ROTA, J. CHOPARD, P. DAS, S. PAINDAVOINE, F. ROZIER, E. FARCOT, C. GODIN, J. TRAAS, F. MONÉGER. *A data-driven integrative model of sepal primordium polarity in Arabidopsis*, in "The Plant cell", December 2011, vol. 23, n<sup>o</sup> 12, pp. 4318-4333



- [68] M. LÉCHAUDEL, M. GÉNARD, F. LESCOURRET, L. URBAN, M. JANNOYER. *Modeling effects of weather and source–sink relationships on mango fruit growth*, in "Tree Physiology", 2005, vol. 25, n<sup>o</sup> 5, pp. 583-597 [DOI : 10.1093/TREEPHYS/25.5.583], <http://treephys.oxfordjournals.org/content/25/5/583.abstract>
- [69] M. LÉCHAUDEL, G. VERCAMBRE, F. LESCOURRET, F. NORMAND, M. GÉNARD. *An analysis of elastic and plastic fruit growth of mango in response to various assimilate supplies*, in "Tree Physiology", 2007, vol. 27, n<sup>o</sup> 2, pp. 219-230 [DOI : 10.1093/TREEPHYS/27.2.219], <http://treephys.oxfordjournals.org/content/27/2/219.abstract>
- [70] J. MURRAY, A. JONES, C. GODIN, J. TRAAS. *Systems analysis of shoot apical meristem growth and development: integrating hormonal and mechanical signaling*, in "The Plant Cell", 2012, <http://www.sop.inria.fr/virtualplants/Publications/2012/MJGT12>
- [71] R. NOZERAN. *Integration of organismal development*, in "Positional controls in plant development", P. BARLOW, D. CARR (editors), 1984, pp. 375-401
- [72] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *Partitioned conditional generalized linear models for categorical data*, in "29th International Workshop on Statistical Modelling (IWSM 2014)", Göttingen, Germany, Statistical Modelling Society, July 2014, vol. 1, <https://hal.inria.fr/hal-01084505>
- [73] C. PREUKSAKARN, F. BOUDON, P. FERRARO, J.-B. DURAND, E. NIKINMAA, C. GODIN. *Reconstructing Plant Architecture from 3D Laser scanner data*, in "6th International Workshop on Functional-Structural Plant Models", Davis, United States, September 2010, pp. 12–17, <https://hal.archives-ouvertes.fr/hal-00490064>
- [74] Y. REFAHI, E. FARCOT, Y. GUÉDON, F. BESNARD, T. VERNOUX, C. GODIN. *A Combinatorial Model of Phyllotaxis Perturbations in Arabidopsis thaliana*, in "22nd Annual Symposium on Combinatorial Pattern Matching, Palermo, Italy", Palermo, Italy, Lecture Notes in Computer Science - LNCS, 2011, vol. 6661, pp. 323–335, <https://hal.inria.fr/hal-00828852>
- [75] A. RUNIONS, M. FUHRER, B. LANE, P. FEDERL, A.-G. ROLLAND-LAGAN, P. PRUSINKIEWICZ. *Modeling and Visualization of Leaf Venation Patterns*, in "ACM Transaction on Graphics", July 2005, vol. 24, n<sup>o</sup> 3, pp. 702–711, <http://doi.acm.org/10.1145/1073204.1073251>
- [76] H. SINOQUET, P. RIVET, C. GODIN. *Assessment of the three-dimensional architecture of walnut trees using digitizing*, in "Silva Fennica", 1997, vol. 3, pp. 265–273