



IN PARTNERSHIP WITH:

INRA

CIRAD

Activity Report 2013

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

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Creation of the Project-Team: 2007 July 01.

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2. Overall Objectives

2.1. Introduction

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.

2.2. Highlights of the Year

- Participation to the Functional-Structural Plant Model (FSPM) international conference. The FSPM conference is an important event for the plant modeling community. At this occasion, the team made several oral presentations:
 - reconstruction methods of branching systems and foliage from laser scanner data [30], [29], or of root systems from images [33]),
 - analysis methods for Mango tree phenology [32], ramification of apple trees [40], [34] or environmental effect on growth of forest trees[38])

- simulation (disease propagation on crops [36], [35] or fruit physiology [31]).
- Publication of a joint work with RDP at ENS-Lyon in the journal 'Nature'. In December 2013, a joint work on phyllotaxy with the RDP lab from ENS-Lyon was published online in the journal Nature [13]. Based on the analysis of phyllotaxis perturbations in mutants, this study sheds a new light on our interpretation of phyllotaxis, revisiting the standard model and suggesting that several fields based on auxin and cytokinin with different properties are required to provide robustness to phyllotaxis.

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.

3.3. OpenAlea: An open-software platform for plant modeling

OpenAlea is a component based, open-software platform for interdisciplinary research in plant modeling and simulation. This 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 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, LaBRI, Laboratory Jean Kuntzmann and ENS Lyon. The Virtual Plants team coordinates both development and modeling consortiums, 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.).

4. Software and Platforms

4.1. V-Plants

Participants: Frédéric Boudon, Christophe Godin [coordinator], Yann Guédon, Christophe Pradal [software architect], Jean-Baptiste Durand, Pascal Ferraro, Julien Coste, Guillaume Baty.

Computer algorithms and tools developed by the Virtual Plants team are integrated in a common software suite *V-Plants*, dedicated to the modeling and analysis of plant development at different scales (e.g. cellular tissue, whole plant, stand). The VPlants packages are integrated in OpenAlea as Python components. Several components are distributed and usable through the visual programming environment (see figure 1):

- Multi-scale geometric modeling and visualization. VPlants.PlantGL is a geometric library which provides a set of graphical tools and algorithms for 3D plant modeling at different scales [7]. It is used by many other components to represent the geometry of biological shapes from 3D meristems, plant architectures to plant populations. VPlants.PlantGL is built around a scene-graph data structure and provides efficient algorithms and original geometrical shapes (parametric surfaces, dedicated envelops), that are useful for plant modeling.
- Statistical sequence and tree analysis. Different statistical packages (i.e. VPlants.StafTool, VPlants.SequenceAnalysis, VPlants.TreeMatching and VPlants.TreeAnalysis) are now available in OpenAlea. They provide different models and algorithms for plant architecture analysis and simulation.
- Meristem functioning and development. A first set of components has been created in the last 4-years period to model meristem development in OpenAlea. These tools are currently being integrated thoroughly in the platform so that modelers and biologists can use them, and reuse components easily (for meristem 3D reconstruction, cell tracking, statistical analysis of tissues, creating and manipulating atlases, creating or loading models of growth that can further be run on digitized structures, etc).
- Standard data structure for plants. A new implementation of the MTG formalism for representing and manipulating multiscale plant architecture has been developed. It provides a central data-structure to represent plants in a generic way in OpenAlea. This implementation is available through the packages OpenAlea.MTG. These components make it possible to share plant representations between users and fosters the interoperability of new models.
- Simulation system. The study of plant development requires increasingly powerful modeling tools to help understand and simulate the growth and functioning of plants. In the last decade, the formalism of L-systems has emerged as a major paradigm for modeling plant development. Previous implementations of this formalism were made based on static languages, i.e. languages that require explicit definition of variable types before using them. These languages are often efficient but involve quite a lot of syntactic overhead, thus restricting the flexibility of use for modelers. We developed L-Py [2] an adaptation of L-systems to the Python language (basis of OpenAlea). Thanks to its dynamic typing property, syntax is simple, code execution is made easy and introspection property of the language makes it possible to parameterize and manipulate simply complex models. Independent L-systems can be composed to build-up more complex modular models. MTG structures (that are a common way to represent plants at several scales) can be translated back and forth into L-system data-structure and thus make it easy to reuse in L-systems tools for the analysis of plant architecture based on MTGs. Extensions to integrate multiscale dynamic models are currently being developed in collaboration with P. Prusinkiewicz and his team from the University of Calgary.

4.2. OpenAlea

Participants: Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal [coordinator], Christian Fournier, Julien Coste.

This research theme is supported by the Inria ADT Grant OpenAlea 2.0 and by an Agropolis RTRA Grant named OpenAlea.

OpenAlea[8] is an open source and collaborative software project primarily dedicated to the plant research community. It is designed as a component framework to dynamically glue together models from different plant research labs, and to enhance re-usability of existing models in the plant research community.

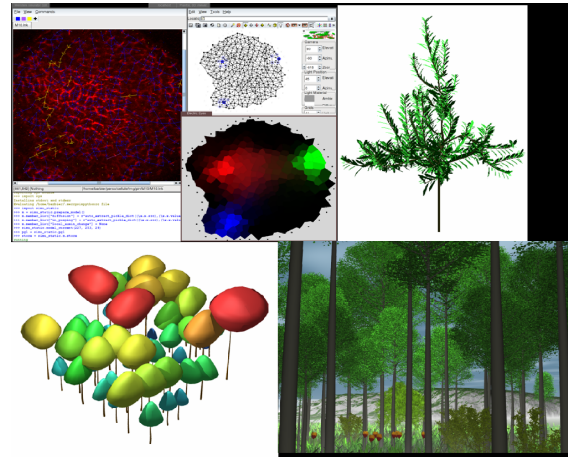


Figure 1. V-Plants components of the OpenAlea platform: simulating plant processes at different scales. Top Left: Reconstruction of a virtual meristem, analysis and simulation of the auxin fluxes inside the meristem. Top Right: Reconstruction of a virtual apple tree from digitized data. Bottom: Simulation of an ecosystem (A beech "Fagus Sylvatica L." trees forest) with a multi level approaches. On the left, explicit representation of the crown volumes that serves as input to generate the detailed representation, on the right.

The architecture of OpenAlea is based on a component architecture. It provides a set of standard components (OpenAlea.Stdlib), a package manager to dynamically add and retrieve new components, and a port graph data-structure to compose models by interconnecting components into a data-flow.

Visualea provides a visual programming environment, used by scientists to build new model interactively by connecting available components together through an easy-to-use graphical user interface.

In 2013, the following progresses were accomplished:

1. Development and extension of OpenAlea and Visualea:

- The standard library of components has been extended with useful scientific packages such as a flexible data plotting package (Openalea.Pylab), 2D and 3D image manipulation (Openalea.Image) and linear algebra operations (Openalea.Numpy).
- Several models of computation have been implemented on the data-flow data-structure to enable discrete event simulation and control flow inside OpenAlea.

2. Animation and diffusion

- A scientific board has been defined to manage the development and diffusion of OpenAlea. It is composed by 12 scientists.
- StandAlone binary installers have been released on Windows and Mac to ease the installation of a large number of packages without relying on a web server. A Ubuntu repository has been set up on Launchpad.
- The OpenAlea project is hosted at the Inria gforge (link <http://openalea.gforge.inria.fr>). The web site is visited by more than 370 unique visitor each month; 650000 web pages have been visited and the different available components of OpenAlea have been downloaded more than 540,000 times during the last two years. OpenAlea is the first project at Inria Gforge in term of number of downloads and of page views.

4.3. Alinea

Participants: Christian Fournier, Christophe Pradal, Frédéric Boudon.

Other participants : Bruno Andrieu, Michael Chelle, Gaëtan Louarn, Benoit de Solan, Mariem Abichou, Liqi Han, Elmer Ccopa-Rivera, Frédéric Baret, Rafaële Casa, Guillaume Garin, Corinne Robert, Sébastien Saint-Jean, Didier Combes, Camille Chambon, Romain Barillot, Jean-Christophe Soulie, Delphine Luquet.

The Alinea software suite is distributed as a meta-package of the OpenAlea Platform. It is produced by a consortium of modelers from INRA , and consists of various ecophysiological and biophysical models of simulation (radiative transfer, interaction between plant and pest, circulation of hydric fluxes, and dispersion). The project is supported by 5 INRA teams and the Inria Virtual Plants project. This project has been homologated as strategic resource for INRA, and is integrated in the CATI IUMA (Centre Automatisé de Traitement de l'Information, : Informatisation et Utilisation des Modèles dédiés aux Agro-Ecosystemes). The five following components are distributed with the OpenAlea platform:

- Alinea.Adel is a module to simulate the 3D architectural development of gramineous crops. In 2013, a new parameterisation procedure was developed for wheat, that allows to use the model for the simulation of agronomic experiments with a minimal set of measurements [28].
- Alinea.Alep is a generic model developed in 2013 to simulate pathosystems from the scale of leaf to the scale of the canopy
- Alinea.Caribu is a modeling suite for lighting 3D virtual scenes, especially designed for the illumination of virtual plant canopies such as virtual crop fields. It uses a special algorithm, the nested radiosity, that allows for a precise estimation of light absorption at the level of small canopy elements.
- Alinea.pyRATP allows to simulate the light interception, photosynthesis and transpiration of a plant canopy.
- Alinea.TopVine is a component to reconstruct grapevine canopy structure. Other components are in developmental state and will be released after publication by their authors.

5. New Results

5.1. Analysis of structures resulting from meristem activity

5.1.1. Acquisition and design of plant geometry

Participants: Chakkrit Preuksakarn [Univ Kasertsart, Thailand], Mathilde Balduzzi, Frédéric Boudon, Christophe Pradal, Christophe Godin, Christian Fournier.

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 [59], [53]. 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 pictures, laser scanner, video and direct sketching.

- *Reconstruction of plant architecture from 3D laser scanner data.* (Chakkrit Preuksakarn, Mathilde Balduzzi, Frédéric Boudon, Christophe Godin, Pascal Ferraro [Labri, Bordeaux])

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 branching system, a number of automatic methods were proposed in the literature to reconstruct plausible branching structures from laser scanner data. The question of their assessment and accuracy is however critical for further exploitation in biological applications. For this, we developed an evaluation pipeline to assess reconstructions accuracy. A laser scan database on which experts built reference reconstructions is used as a basis of the evaluation. The pipeline is given two structures and compares both their elements and their organization. Similar elements are identified based on geometric criteria using an optimization algorithm. The organization of these elements is then compared and their similarity quantified. Two indices of geometrical and structural similarities are defined, and automatic reconstructions can thus be compared to reference structures to assess their accuracy. The method is successful at capturing the variation of similarities between two structures as different levels of noise are introduced. A first comparative evaluation of the different methods of the literature has been designed and conducted. This work has been presented at the FSPM conference and submitted at *Annals of Botany* for its special issue.



Figure 2. Reconstruction of a cherry tree. Left: photograph of the original tree. Right: 3D reconstruction from a laser scan rendered and integrated on the same background.

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 on the silhouette of the scans that make the meshing of the pointset difficult. New generation of laser scanners provide intensity of the laser reflected on the surface of scanned objects. This intensity depends of 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 approaches. This work has also been presented at the FSPM conference.

- *Reconstruction from video.* (Frédéric Boudon, Jerome Guenard [IRIT, Toulouse], Geraldine Morin [IRIT, Toulouse], Pierre Gurdjos [IRIT, Toulouse], Vincent Charvillat [IRIT, Toulouse])

Even if mature computer vision techniques allow the reconstruction of challenging 3D objects from images, due to high complexity of plant topology, dedicated methods for generating 3D plant models must be devised. In collaboration with our colleagues from IRIT, Toulouse, we developed an analysis-by-synthesis method which generates 3D models of a plant from both images and a priori knowledge of the plant species.

Our method is based on a skeletonisation algorithm which allows to generate a possible skeleton from a foliage segmentation. Then, a 3D generative model, based on a parametric model of branching systems that takes into account botanical knowledge is built. This method extends previous works by constraining the resulting skeleton to follow hierarchical organization of natural branching structure.

3D models are then generated. A reprojection of the models can be compared with the original image to assess the visual accuracy of the reconstruction. We optimise the parameter values of the generative model based on the reprojection criterion. Realistic results are obtained on different species of plants, in particular vineyards. This work has been presented at the ISVC conference and published in LNCS [46].

- *Reconstruction of virtual fruits from pictures.* (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 Fruit3D.

The aim of this work is to provide methods for generating fruit structure that can be integrated with models of fruit function and used to investigate such effects. To this end, we have developed a modeling pipeline in the OpenAlea platform that involves two steps: (1) generating a 3D volumetric mesh representation of the entire fruit, and (2) generating a complex network of vasculature that is embedded within this mesh. To create the 3D volumetric mesh, we use reconstruction algorithms from the 3D mesh generation package of the Computational Geometry Algorithms Library (CGAL). To generate the pattern of vasculature within this volumetric mesh, we use a Space Colonisation Algorithm that populates the volume of the fruit by simulating competition for space of the vasculature. We have applied our modeling pipeline to generate the internal and external geometry of a cherry tomato fruit using Magnetic Resonance Imaging data as input. These studies demonstrate the possibility to create species-specific models of fruit structure with relatively low effort [31]. These volumetric meshes are then combined with models of function to form integrative computational fruit models, which will help to investigate the effects of fruit structure on quality (see section 5.3.2).

- *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])

Similarly to aerial part of plants, some needs for reconstruction procedure of root systems emerges. Most existing methods focus only on semi-automatic approaches. This does not support the high-throughput capabilities of acquisition systems. Within the Rhizopolis project (Agropolis foundation), we have designed an automatic analysis pipeline to extract root system architecture from images. This pipeline provides i) a model based segmentation method of the scanned image content (Petri plate, seeds, leaves and root pixels), ii) the extraction of a graph representation of the root system, and iii) a novel method to identifying the root axes organization.

5.1.2. Modeling the plant ontogenic programme

Participants: Christophe Godin, Yann Guédon, Evelyne Costes, Jean-Baptiste Durand, Anaëlle Ambreville, Pierre Fernique, Christophe Pradal, Jean Peyhardi, Catherine Trottier, Yassin Refahi, Etienne Farcot.

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. [48], [54], [55], [52], 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" [57], "age state" [51] or "physiological age" [50]. 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 [51], [50]. Here we develop computational methods to decipher these rules.

- *Relating branching structure to the shoot properties* (Jean Peyhardi, Yann Guédon, Evelyne Coste, Catherine Trottier, 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 is 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. maximum growth rate of the leaf, surface of the leaf, length of the internode, 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 multi-step multinomial GLMs that enable to tackle partially ordered categorical response variables. Typically, we need to distinguish different timing of branching (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 multi-step multinomial GLMs and are applied to different data sets corresponding mainly to fruit tree branching structures.

- *Genetic determinisms of the alternation of flowering in apple tree progenies.* (Jean-Baptiste Durand, Jean Peyhardi, Baptiste Guitton [AGAP, AFEF team], Yan Holtz [AGAP, AFEF team] Catherine Trottier, Evelyne Costes, Yann Guédon)

A first study was performed to characterize genetic determinisms of the alternation of flowering in apple tree progenies [34], [17]. Data were collected at two scales: at whole tree scale (with annual time step) and a local scale (annual shoot or AS, which is the 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 allows to quantify alternation from the yearly numbers of inflorescences at tree scale.

However, phenotyping subsamples of AS sequences is more realistic in the framework of genotype selection. To model alternation of flowering at AS scale, a second-order Markov tree model was built. Its transition probabilities were modeled as generalized linear mixed models, to incorporate the effects of genotypes, year and memory of flowering for the Markovian part, with interactions between these components. Asynchronism of flowering at AS scale was also assessed using an entropy-based criterion.

This work started during the PhD's work of Baptiste Guitton. It was then extended in 2012 by Yan Holtz during this Master 2 internship, supervised by Evelyne Costes and Jean-Baptiste Durand. New progenies were considered, as well as the performance of approximating the descriptors at whole tree scale with those at AS scale. These descriptors allowed the identification of QTL zones involved in the control of flowering in apple trees.

As a perspective of this work, patterns in the production of children ASs (numbers of flowering and vegetative children) depending on the type of the parent AS must be analyzed using branching processes and different types of Markov trees, in the context of Pierre Fernique's PhD Thesis (see next item in Section 5.1.2).

- *Modeling branching patterns in fruit tree shoots through the characterization of their demographic properties* (Pierre Fernique, Jean-Baptiste Durand, Yann Guédon).

To test the effect of some properties of a given parent shoot on the properties of its children shoots, statistical models based on multitype branching processes were developed. This kind of dependence between parent and children shoots is frequently at stake in fruit trees, for which the number of

flowering or vegetative children of a parent shoot depends on its nature, with potential interactions with other factors. Thus, controlling demographic patterns of the shoots (through varietal selection or crop management strategies) is expected to bring substantial improvements in the quantity and quality of yields.

Formally, the shoot properties are summed up using the notion of shoot state. The number of children shoots in each state is modeled through discrete multivariate distributions. Model selection procedures are necessary to specify parsimonious 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. A parametric distribution was associated with each graph. It was obtained by combining families of univariate and multivariate distributions or regression models, and their mixtures. These families were chosen by selection model procedures among different parametric families [45], [32].

This work was carried out in the context of Pierre Fernique's first year of PhD (Montpellier 2 University and CIRAD). It was applied to model dependencies between short or long, vegetative or flowering shoots in apple trees. The results highlighted contrasted patterns related to the parent shoot state, with interpretation in terms of alternation of flowering (see previous item in Section 5.1.2). It was also applied to the analysis of the connections between cyclic growth and flowering of mango trees (see next item in Section 5.1.2). This work will be continued during Pierre Fernique's PhD thesis, with extensions to other fruit tree species and other parametric discrete multivariate families of distributions, including covariates and mixed effects.

- *Analyzing fruit tree phenology* (Anaëlle Dambreville, Jean-Baptiste Durand, Pierre Fernique, Yann Guédon, Christophe Pradal, Pierre-Eric Lauri [AFEF team, AGAP], Frédéric Normand, Catherine Trottier)

Mango is a tropical tree characterized by strong asynchronisms within and between trees. Causation networks explaining the vegetative and reproductive growths within and between growing cycles were studied on the basis of generalized linear models [16]. We highlighted in this way marked interplays between structural and temporal components of tree structure development at three scales. At growth unit scale, a growth unit which appeared early in the growing cycle had higher rate of burst compared to late appeared growth units. At growing cycle scale, a flowering growth unit delayed its future vegetative growth compared to a vegetative growth unit. At tree scale, a fruiting tree delayed further vegetative growth and flowering compared to a non-fruiting tree. These results evidenced that tree phenology is strongly affected by structural components and not only by the environment.

To study more precisely the interplays between all these structural components, we started during the internship of A. Jestin to build an integrative model to simulate the development of mango tree based on the L-system formalism and GLM to model the dependencies between events.

We are also investigating jointly structure development and phenology of mango, and characterizing the specific spatio-temporal patterns leading to patches of vegetative or flowering growth units. Our approach is based on statistical models for trees; particularly hidden Markov tree models and multitype branching processes [32].

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

Growth and development are often studied as two separated processes. Our aim is to investigate the coordination between growth and development in mango shoots. We considered three types of organ, namely the shoot axis, its attached leaves and the inflorescence. Two types of data were collected during the shoot and inflorescence follow-up: developmental stages determined in an expert way and organs sizes determined from measurements. To give an integrative view of the shoot and inflorescence growth and development, we adopted the following strategy. For a

given cultivar, we first built a multi-state model on the basis of absolute growth rate sequences deduced from the measurements. Using these models, we computed growth stages. These growth stages highlighted growth asynchronisms between two topologically-connected organs: the axis and its leaves. Then, we compared these growth stages with the developmental ones and we obtained strong matches between them. The integrated developmental growth stages emphasized that the developmental stages are markedly related to growth rates and can be interpreted in terms of physiological (hydraulics, carbohydrates partitioning) and developmental (organs preformation versus neoformation) processes.

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

In a previous work [5], 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, 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. This method thus compresses a tree in width, but not in height. In this 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 is being written.

We are currently studying how to generalize the previous approach using stochastic trees. The idea is to generalize the previously defined equivalence relation so that equivalent trees are identical in distribution now and are no longer strictly isomorphic. Algorithms to estimate the different distributions from tree samples rely on combinatorics arguments that are used to estimate the probability that an observed tree is produced by a particular stochastic tree model for which a conjecture has been proposed (still to be demonstrated). The asymptotic analysis of similar compression rates on ordered tree-graphs has been carried out by Flajolet et al. (1990) for different types of distributions (uniform, multi-type branching processes). The work is developed in the context of the Post-doc of Romain Azais.

5.1.3. Analyzing the influence of the environment on the plant ontogenic programme

Participants: Frédéric Boudon, Jean-Baptiste Durand, Christophe Godin, Yann Guédon, Jean Peyhardi, Pierre Fernique, Maryline Lièvre, Christine Granier, Evelyne Costes, Pascal Ferraro, Catherine Trotter.

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 5.1.2), 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 environment 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 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])

In a forest ecology context, we identified robust indicators that summarize the balance between tree ontogeny and environmental constraints (mainly related to light environment). In this context, tree growth data typically correspond to the retrospective measurement of annual shoot characteristics (e.g. length, number of branches) along the main stem. We applied segmentation models (hidden Markov and semi-Markov chains) that enable to identify tree growth phases. This statistical modeling approach was applied to both deciduous (sessile oak and Persian walnut) and evergreen (Corsican pine and silver fir) tree species growing in contrasted conditions ranging from managed forest stands to unmanaged understoreys. The growth phase duration distributions estimated within these segmentation models characterize the balance between tree ontogeny and the environmental constraints in tree development at the population scale. These distributions had very contrasted characteristics in terms of shape and relative dispersion between ontogeny-driven and environment-driven tree development. The characteristics of growth phase duration distributions may change over tree life reflecting changes in tree competition.

- *Investigating how architectural development interfer with epidemics and epidemic control* (Christian Fournier, Corinne Robert [EGC], Guillaume Garin [ITK], Bruno Andrieu [EGC], Christophe Pradal)

Recent considerations towards sustainable agriculture require identifying new natural strategies of crop protection. In this perspective, a better identification of major interactions inside pathosystems between the plants, the pathogens and their environment is crucial. These multiscale biological systems are complex: multiple relationships stand out with various dynamics and at various locations in the canopy, related to its architectural development. The purpose of this research is to provide a framework to study the influence of architectural development on pathosystems with modeling. A first generic framework was designed and implemented in the platform OpenAlea [36]. It allows implementing pathogens of different kind using the same concepts, and a re-use of plant models available in Openalea, thus simplifying the development of pathosystem models based on 3D plants models. A second action was to develop a modular integrated model coupling architectural canopy development, disease dynamics, pesticide application, pesticide decay and effect of pesticide on disease dynamics [35]. This model is currently being assessed against data for validation, and aim at designing new strategies that reduce pesticide applications by increasing natural resistance linked to canopy architecture.

5.2. 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.

5.2.1. Data acquisition and design of meristem models

Participants: Frédéric Boudon, Christophe Godin, Christophe Pradal, Léo Guignard, Vincent Mirabet [RDP, ENS], Jan Traas, Grégoire Malandain, Jean-Luc Verdeil [PHIV, AGAP].

This research theme is supported by the iSam and Morphogenetics projects.

- *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, Guillaume Baty, Jan Traas, Patrick Lemaire, Pradeep Das [RDP, ENS], Yassin Refahi [RDP, ENS].

The MARS-ALT (Multi-Angles Registration and Segmentation - Automatic Lineage Tracking) software pipeline 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 [4]. A new version of this pipeline is currently being developed. MARS-ALT Version 2 is based on the same algorithms and methods and is intended to improve the overall robustness of the pipeline (protocol, noise in the input image) and automate completely the process. To test the new pipeline, we use different acquisition protocols and different organisms (floral and apical meristems and the early stages of development of a marine animal *Phallusia mammillata*). The segmentation is corrected a posteriori to deal with imaging artifacts due to uncertainties of acquisition. The image data set on which we develop the methods consists of :

- *Arabidopsis thaliana* shoot apical meristem and primordia with around 6000 cells. The organ is captured from three different angles every 4 hours during 2 or 3 days with a confocal microscope (Collaboration Sainsbury lab, Cambridge)
- *Arabidopsis thaliana* flower meristems with around 2000 cells. The organ is also captured from three different angles with a confocal microscope (Collaboration RDP Lyon and Sainsbury lab)
- *Phallusia mammillata* and *Ciona intestinalis* embryos with from 32 cells to around 1000 cells. The organism is captured from four different angles every minute during 2 to 3 hours with a SPIM (Single Plane Illumination Microscope) (Collaboration CRBM Montpellier / EMBL Heidelberg). This work is developed in the context of the PhD work of Léo Guignard.

The pipeline provides as an output segmented images on which metrics for each cells can be extracted such as volume, principal components, convex hull and more. A new non-linear registration algorithm developed by G. Malandain (MORPHEME team, Inria Sophia-Antipolis) is now available and will lead to an improvement of ALT algorithm. Redesign and improvement of the lineage tracking pipeline will be the next step.

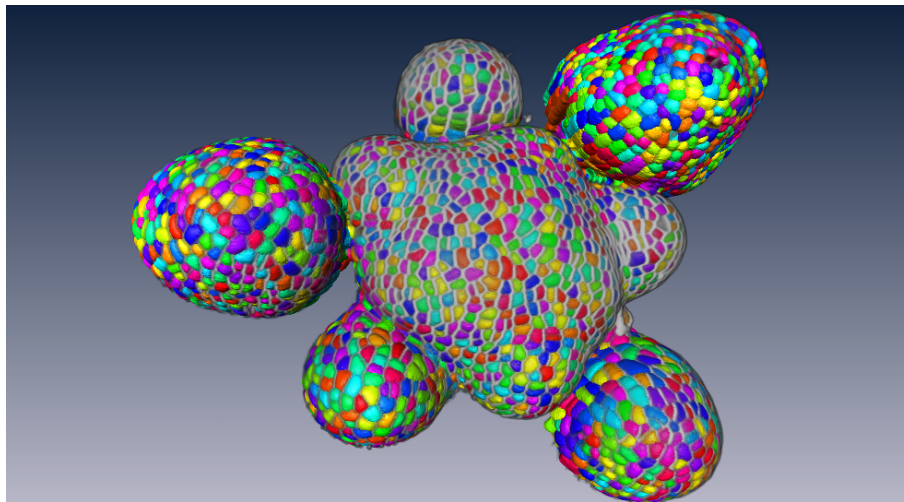


Figure 3. Superimposition of an automatic cell segmentation of an arabidopsis flower meristem using the new MARS pipeline with the original confocal image stack where the membranes are marked.

- *Design of 3D virtual atlases for specifying gene expression patterns* (Yassin Refahi, Christophe Godin, Jan Traas, Patrick Lemaire, Grégoire Malandain, Françoise Monéger [RDP, ENS])

This research theme is supported the ANR GeneShape and iSam projects.

To organize the various genetic, physiological, physical, temporal and positional informations, we build a spatialized and dynamic database. 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 virtual atlas is mainly descriptive. However, like for classical databases, specific tools make it possible to explore the virtual atlas according to main index keys, in particular spatial and temporal keys. Both a dedicated language and a 3D user interface are being designed to investigate and query the 3D virtual atlas.

A prototype version of the 3D virtual atlas was built 2 years ago [6]. Further developments of this tool will rely on the segmented images produced from microscopy, as presented in the previous section. In particular, a common underlying data structure has to be developed transversally to these two scientific developments. The definition of this data structure has been initiated last year through several team meetings, and should lead to a revised implementation next year.

5.2.2. Shape analysis of meristems

(Jonathan Legrand, Frédéric Boudon, Christophe Godin, Yann Guedon, Pradeep Das [ENS Lyon])

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 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). We are now designing models and algorithms for finding patterns in time courses of meristems. In particular, we are investigating spectral clustering methods in order to define homogeneous regions in terms of cell identities in the context of the PhD Work of Jonathan Legrand.

5.2.3. Transport models

Participants: Michael Walker, Christophe Godin, Etienne Farcot, Jan Traas, Yuan Yuan [University of Newfoundland, Canada].

This research theme is supported by the ANR GeneShape and ERASysBio+ iSAM projects and Morphogenetics.

Active transport of the plant hormone auxin has been shown to play a key role in the initiation of organs at the shoot apex, and vein formation in both leaves and the shoot apical meristem. Polar localized membrane proteins of the PIN1 and AUX/LAX family facilitate this transport and observations and models suggest that the coherent organization of these proteins in the L1 layer is responsible for the creation of auxin maxima (surrounded by a depletion zone), which in turn triggers organ initiation close to the meristem center [58] [1]. Furthermore, canalized PIN allocations are thought to play a crucial role in vein formation in the leaf and in the L2. Previous studies have typically modeled the L1 and L2 with different models to explain different patterns of PIN allocations. In the last two years, we developed a unifying model showing that a unique flux-based model could be sufficient to explain PIN patterns in both L1 and L2 [27]. Contrary to our previous study [9], here no change in the model parameters is needed for this. Our approach is based on inherent topological and geometrical differences between the L1 and L2, specifically their dimensionality and the distribution of sources and sinks.

In a different perspective, another study on auxin transport models have been submitted this year. In this work, a generic, adimensional flux-based model of auxin transport was studied using a combination of analytic and numeric approach. The steady-states with uniform auxin distribution were characterised for arbitrary tissues, and some of their bifurcations (loss of stability and Hopf) were described [18]. This work, initiated during an "Explorateur" project funded by Inria during the period October 2012-January 2013, results from the collaboration between E. Farcot and Y. Yuan (Memorial University of Newfoundland, Canada).

5.2.4. Mechanical model

Participants: Olivier Ali, Christophe Godin, Benjamin Gilles, Frédéric Boudon, Jan Traas, Olivier Hamant [ENS-Lyon], Arezki Boudaoud [ENS-Lyon], Jérôme Chopard [University of Western Australia, Perth].

This research theme is supported by the ANR VirtualFlower and Geneshape projects together with the Inria project Morphogenetics and the ERC from Jan Traas.

The rigid cell walls that surround plant cells are responsible for their shape. These structures are under constraint due to turgor pressure inside the cell. To study the changes of shape in plant tissues during organogenesis, we need a mechanical model of tissue development at cellular resolution. We developed such a model, in which walls are characterized by their mechanical properties like the Young modulus which describes the elasticity of the material. Wall deformation results from forces due to turgor pressure. Growth results from cell wall synthesis that is triggered when wall deformation exceeds a particular threshold. The final shape of the tissue integrates mechanically all the local deformations of each cell.

To model this process, we used a tensorial approach to describe both tissue deformation and stresses. Deformations were decomposed into elementary transformations that can be related to underlying biological processes. However, we showed that the observed deformations does not map directly local growth instructions given by genes and physiology in each cell. Instead, the growth is a two-stage process where genes are specifying how cell walls should yield to mechanical stresses. In this way, different regions in the tissue with different cell identities can have different growth properties. The final shape of the tissue results from the integration of all these mechanical properties and stresses at organ level under the growth force due to turgor pressure at tissue scale.

A paper describing the mechanical model and its application to model primorium formation in the shoot apical meristem has been submitted to PNAS in December. Additionally, a redesign of our mechanical model using the SOFA framework is being finalized.

5.2.5. Gene regulatory networks

Modeling gene activities within cells is of primary importance since cell identities correspond to stable combination of gene expression [25].

- *Complex dynamics and spatial interactions in gene networks* (Yassin Refahi, Etienne Farcot, Christophe Godin)

Complex computational and mathematical questions arise in the study of gene networks at two levels: (i) the single cell level, due to complex, nonlinear interactions, (ii) the tissue level, where multiple cells interact through molecular signals and growth, so that even simple local rules can challenge our intuition at higher scales.

At the single cell level, new results were obtained in the framework of piecewise-linear models, it is in general very difficult to entirely characterize the attractors of a given system. In an attempt to improve our ability on this question, a probabilistic approach has been proposed in [14], in which it is shown that a Markov chain can be built as an approximation of a given piecewise-linear system, and actually used to make predictions about its periodic attractors.

At a higher scale, we have also continued the study of gene regulation in meristematic tissues. In the context of Y. Refahi's post-doc between Virtual Plants and the group of Henrik Jönsson in Cambridge (Sainsbury Laboratory), we have continued a work that was initiated in Y. Refahi's thesis. This work is motivated by recent biological results, indicating that gradient-like patterns originating from the external layers of meristems may play a decisive role in the specification of the pool of stem cells in a central position. Using the methods in [4], and their on-going improvements, we have acquired new 3D and 4D images that were then segmented. These structures will be used in the next few months to investigate generic patterning properties of gradient like morphogen patterns. This will require a thorough analysis of free diffusion in realistic geometries, as made possible by the newly acquired images. As a preliminary work, we are also currently investigating the formation of gradient patterns in idealised tissues, allowing for deeper analytic treatment than the complex structures obtained by microscopy.

5.2.6. Model integration

Participants: Frédéric Boudon, Christophe Godin, Eugenio Azpeitia, Laurent Laplaze, Jan Traas, François Parcy.

This research theme is supported by the ANR/BBSRC project iSam.

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). 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 submodel 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 [56] and the CPIB group in Nottingham, UK [49].

- *Development of a computer platform for the 'programmable tissue'.* (Frédéric Boudon, Christophe Godin)

One key aspect of our approach is the development of a computer platform dedicated to programming virtual tissue development. This platform will be used to carry out integration of the different models developed in this research axis. The platform is based on *OpenAlea*. Partner models can be integrated in the platform in a non-intrusive way (the code of their model need not be rewritten). In this context, model integration will i) consist of designing adequate data-structures at different levels that will be exchanged and reused among the different plug-in models and ii) defining control flows at adequate levels to avoid the burden of excessive interaction between components. In the past year, progress has been made in defining a generic tissue data structure that could be used in this platform, through several group meetings along the year. A redesign of the structure is in progress.

- *Design of a genetic model of inflorescence development.* (Etienne Farcot, Eugenio Azpeitia, Christophe Godin, François Parcy)

We studied the regulatory network that control flower development 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 repeatedly meristem fails in making a complete transition to the flower. This work couples models at different scales, since gene regulation is described by a minimal gene network, which 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. A first integrated picture of flower development could be reached in the context of the internship of Eugenio Azpeitia (PhD Student).

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

5.3.1. Transport model in roots

Participants: Mikaël Lucas [IRD], Christophe Pradal, Christophe Godin, 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 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 implement 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.

5.3.2. Transport in fruits

Participants: 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 Fruit3D.

Understanding the controlling factors of fruit quality development is challenging, because fruit quality results from the interplay between physical and physiological processes that are under the control of genes and the environment. Although process-based models have been used to make significant progress in understanding these factors, they ignored to a large extent the shape and internal structure of the fruit.

To help characterizing effects of fruit shape and internal structure on quality, the creation of a 3D virtual fruit model that integrates fruit structure and function with growth governed by environmental inputs has been investigated. For this, a modeling pipeline has been developed that includes the following steps: creation of a 3D volumetric mesh of the internal fruit structure, including vasculature (see section 3). Based on previous compartment models of fruit physiology developed at Avignon, we have then developed models of water and carbon transport that have been coupled with the 3D model of fruit. In the 3D model, different equations are describing the transport between adjacent regions of the fruit represented as a 3D mesh. The integration through space and time is carried out using a standard integration scheme (Runge-Kutta of order 4).

This approach has been applied to study tomato fruit (*Solanum lycopersicum*) by constructing 3D volumetric meshes from different sources (images of perpendicular fruit slices and MRI data), and integrating water and carbon transport processes into these meshes. To illustrate the tomato model, a simulation of one season of the fruit's growth has been performed and its results compared with an already published process-based tomato fruit model. We first showed that our spatialized model is compliant with classical results of the abstract process-based models but also provides additional information on the internal heterogeneity of the fruit, such

as a gradient in sugar concentration. Once the model is calibrated and evaluated, our approach will be suitable for studying the effects of internal fruit heterogeneity and overall shape on fruit quality development.

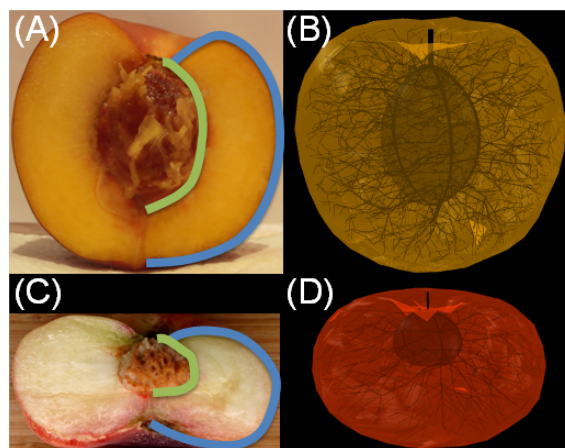


Figure 4. Virtual models of peaches reconstructed from images with simulated vasculature to simulate carbon and water transport in the fruit

5.3.3. 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. SmartRoot). The analysis of complex root phenotyping data is thus a new challenge in developmental biology.

We aim at developing a pipeline of methods for analyzing root systems at three scales:

1. tissular scale to identify and characterize the meristem, elongation and mature zones along a root using piecewise heteroscedastic linear models.
2. individual root scale to analyze the dynamics of root elongation
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).

5.3.4. Analyzing shoot and leaf elongation

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

This research theme is supported by one PhD programme.

The analysis of phenotyping data coming from automated platforms such as PHENOPSIS often focuses on the growth of a leaf at a given rank along the stem. We aim at developing a pipeline of methods for analyzing the growth of *arabidopsis* shoot at three scales:

1. tissular scale using a probabilistic model of endoreduplication for modeling the distribution of the leaf epidermis cell surfaces. Endoreduplication, which is a replication of the nuclear genome in the absence of cell division that leads to elevated nuclear gene content, strongly affects the leaf epidermis cells of *arabidopsis*.

2. organ scale using nonlinear regression model for analyzing the growth of each successive leaf.
3. shoot scale: The outputs of the analyses at the tissular and organ scales will be summarized as multivariate sequences along the shoots characterizing each successive leaf. These sequences will be augmented by supplementary morphological variables characterizing leaf shape and properties (e.g. presence/absence of trichomes). These sequences will be globally analyzed in order to take into account plant ontogeny and in particular the successive developmental stages before the floral transition for the wild type and selected mutants of *arabidopsis*.

5.3.5. Analyzing perturbations in *Arabidopsis thaliana* phyllotaxis

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

This research theme is supported by iSAM.

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.

The cytokinin hormones are known to play a significant role in the regulation of phyllotaxis. Fabrice Besnard and Teva Vernoux realized that *Arabidopsis thaliana* *ahp6* mutants, which are perturbed in the cytokinin signaling pathway, showed unusual chaotic perturbations of the phyllotaxis at macroscopic level.

In order to characterize these perturbations, we designed a pipeline of models and methods which relies on combinatorial and statistical techniques. Using this pipeline of methods, we have shown that the perturbation patterns in both wild-type and mutant plants can be explained by permutations in the order of insertion along the stem of 2 or 3 consecutive organs. The number of successive synchronized organs between two permutations reveals unexpected patterns that depend on the nature of the preceding permutation (2- or 3-permutation). We identified significant individual deviations of the level of baseline segments with reference to 137.5° , which confirms theoretical model predictions. Finally, we highlighted a marked relationship between permutation of organs and defects in the elongation of the internodes in between these organs.

We then looked at the origin of these permutations using confocal microscopy and realized that organs were in fact frequently co-initiated in the mutant, leading after development randomly in half of the cases to permutations. We concluded that the mutant is actually perturbed in the time between consecutive organ initiation (i.e. the plastochrone), while relative angular positions are not affected. 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 plastochrone. We could demonstrate that in the mutant, the absence of this field led to co-initiations and subsequently to the observed permutations.

Altogether, this study sheds a new light on our interpretation of phyllotaxis, revisiting the standard model and suggesting that several fields based on auxin and cytokinin with different properties are required to provide robustness to phyllotaxis. An overview of this work has been published in the journal *Nature* in December online [13]. Methodological developments were published more extensively in [20].

6. Partnerships and Cooperations

6.1. Regional Initiatives

6.1.1. OpenAlea

Participants: Christophe Pradal, Christophe Godin, Christian Fournier [INRA, LEPSE].

Funding: Agropolis foundation (Contractors for Virtual Plants: CIRAD and Inria from 2009 to 2013)

The aim of this project is to foster the development and the national and international diffusion of the platform OpenAlea. This opensource platform provides an easy-to-use environment for plant modelers through a visual programming interface to efficiently use and combine models or computational methods from different scientific fields in order to represent, analyze and simulate complex plant systems at different scales, from meristems to plant canopy. Work comprises the development of standard data structures, deployment tools, documentation, training, software engineering, user interface, interfaces with other platform, ...

6.1.2. *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.

6.1.3. *Fruit3D*

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

Funding: Agropolis foundation (Contractor for Virtual Plants: INRA, from 2009 to 2012)

The project gathers the competences of plant modelers, physicists and ecophysiologists for developing a virtual tomato model. The model contains the geometrical description of a growing fruit, physical and biological laws involved in tissue differentiation and cell growth, physiological models (for sugar and hormone transfers) and mechanical model. Magnetic Resonance Imaging (MRI) techniques are used to provide an in vivo validation of the model by non invasive measurements.

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

6.1.4. *Rhizopolis*

Participants: Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal.

Funding: Agropolis foundation (Contractor for Virtual Plants: INRA, from 2011 to 2013)

Rhizopolis is a multidisciplinary project on the biology and ecology of the plant root that addresses the broad roles of this organ in mineral nutrient and water acquisition. The consortium addresses central issues such as the coupling of membrane transport activity and structure-function relationships in roots and root symbioses, the integration of root-soil interactions in the rhizosphere at the whole root system level, and the development of key tools for imaging root development. Virtual Plants is mainly involved in the development of a software for automatically reconstructing root systems from 2D images.

Partners: DAR Team, UMR AGAP, UMR BPMC and UMR LEPSE (Montpellier).

6.1.5. *RhizoScanHT*

Participants: Julien Diener, Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal.

Funding: Labex Numev (Contractor for Virtual Plants: UM2, from 2013 to 2014)

In this project, we extend the pipeline of 2D root system reconstruction developed in the project RhizoPolis to deal with high-throughput data. For this we develop the project in two directions: i) make the pipeline software components more robust to various acquisition conditions and root system complexities ii) use techniques coming from the big data community to upscale the indexing and reconstruction methods.

Partners: Zenith Inria Project Team, UMR AGAP, UMR BPMC and UMR LEPSE (Montpellier).

6.2. National Initiatives

6.2.1. ANR

6.2.1.1. *Morpholeaf*

Participants: Christophe Godin, Maryam Aliee.

Funding: ANR (Contractor for Virtual Plants: Inria, From 2011 to 2014)

The goal of this project is to apply a systems biology approach combining biological investigation and modeling on leaf margin development to elucidate how gene networks and hormone signalling are translated into specific growth patterns and generate complex shapes. This project brings together three groups that have complementary expertises in biology, image analysis and modeling to provide new insights into the mechanisms of leaf margin development. We will specifically determine the dynamics of CUC/miR164A/auxin activities during leaf development and their interrelations, establish the contributions of cell proliferation and cell expansion to leaf serration and leaf shape and address the contribution of auxin and CUC2 to differential growth and hence to leaf serration and leaf shape.

Partners: RDP ENS-Lyon; INRA Versailles.

6.2.1.2. *HydroRoot*

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

Funding: ANR (Contractor for Virtual Plants: Cirad, From 2012 to 2014)

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.

6.2.2. Other national grants

6.2.2.1. *OpenAlea 2.0*

Participants: Julien Coste, Christophe Pradal, Christophe Godin, Didier Parigot [Inria, Zenith].

Funding: Inria ADT (Contractors for Virtual Plants: Inria from 2012 to 2014)

The goal of this project is to develop an integrated multi-paradigm software environment for plant modeling. This environment will allow the user to draw, model, program or combine models interactively. In a first step, the component architecture of OpenAlea1.0 will be extended to dynamically add plugin application. In a second step, we move to a decentralized architecture, capable of distributing simulations in the cloud and share virtual experiments on the web. Finally, the modeling environment to be adapted to run in a web browser using HTML5 and WebGL technology

Partners: EPI Zenith

6.2.2.2. *MARS-ALT*

Participants: Guillaume Baty, Christophe Pradal, Christophe Godin.

Funding: Inria ADT (Contractors for Virtual Plants: Inria from 2012 to 2014)

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.

Partners: EPI Asclepios, RDP ENS-Lyon/INRA, PHIV CIRAD

6.2.2.3. *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 .

6.2.2.4. *Morphogenetics*

Participants: Christophe Godin, Frédéric Boudon, Christophe Pradal, Etienne Farcot, Yann Guédon.

Funding: Inria Project Lab (From 2011 to 2015)

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: ENS-Lyon; Imagine Inria Team (Grenoble); Morpheme Inria Team (Sophia-Antipolis).

6.2.2.5. *Rose*

Participants: Christophe Godin, Frédéric Boudon, Christophe Pradal.

Funding: INRA - Projet de Pari Scientifique (From 2012 to 2014)

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

6.3. European Initiatives

6.3.1. Collaborations in European Programs, except FP7

- **iSAM** (Funding: European EraSybio+ Programme). This project aims at improving our knowledge of shoot apical meristem, and more specifically the combined action of auxin and cytokinin, using a systems biology approach. It is part of a wider program, the ERASysBio initiative, a consortium of European funding bodies, ministries and project management agencies. Four partners are involved in iSAM: the group of J. Murray will focus on mutants of cell cycle regulation, the group of Y. Helariutta is specialized in several aspects of cytokinin regulation, while the group of J. Traas in Lyon provides input regarding auxin regulation and transport, and Virtual Plants is in charge of the modeling aspects, in synergy with the three other groups.

6.4. International Initiatives

6.4.1. Inria International Partners

6.4.1.1. Informal International Partners

There is currently a very active connection with the group of Malcolm Bennett, at the Centre for Plant Integrative Biology (CPIB) in Nottingham, UK. The CPIB invests in the development of OpenAlea at the tissue level. This collaboration is expressed recently through several publication, e.g. [22].

An important collaboration with the Unit Hortsys of CIRAD et the Reunion island and in particular Frédéric Normand has been established for a number of year. 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 years.

6.5. International Research Visitors

6.5.1. Visits of International Scientists

The team received several visitors from foreign research groups in 2013:

- Farah Ben Naoum, from Sidi Bel Abbes University, Algeria, visited the team last summer for 1 month.
- Katarina Smolenova, from University of Göttingen, Germany, visited the team last fall for 2 weeks.
- Jianming Guo, from Canberra, Australia, visited the team for 5 weeks.
- Xavier Sirault, from Canberra, Australia, visited the team last spring for 2 days.
- John Fozard, from University of Nottingham, visited the team for 2 days.

6.5.1.1. Internships

- Eugenio Espinosa, from Universidad de México (UNAM), visited the team last spring for 6 month.

6.5.2. Visits to International Teams

During the year, Frédéric Boudon, Pierre Fernique and Jean Baptiste Durand visited Fred Normand of the UR Hortsys at the CIRAD La Réunion in April and November respectively.

7. Dissemination

7.1. Scientific Animation

- Christophe Godin has rendered the following services in 2013:
 - he is a member of the College de Direction of UMR AGAP
 - he is a member of the management board of IBC (Institut de Biologie Computationnelle de Montpellier)
 - he is a member of the scientific committee of the Environnement-Agromomy department at INRA
 - he is a member of the editorial board of the journal *Frontiers in Plant Sciences*
 - he is the scientific coordinator of the Inria Project Lab (former Action d'Envergure) Morphogenetics
 - he is the scientific coordinator of axis 4 of IBC on imaging and modeling (together with Patrick Lemaire)
 - he was co-chair of the 7th international conference on functional-structural models of plants (FSPM 2013) that was held in Finland in June 2013.
 - he is guest editor for the special issue on FSPMs of the journal *Annals of Botany*.

- he gave 6 invited talks (4 abroad).
- he was referee for papers submitted at journals: Development, PNAS, Plos Comp Biol.
- Yann Guédon has rendered the following services in 2013:
 - he is a member of the editorial board of Annals of Botany and a member of the ERCIM working group "Computing & Statistics".
 - he was a member of the program committee of the 7th International Workshop on Functional-Structural Plant Models (FSPM 13, Saariselkä, Finlande) and evaluated 8 communications.
 - he participated to the PhD committee of Pierre Gloaguen (Ifremer, Nantes) and Gustavo Malagi (Federal University of Pelotas, Brazil and Montpellier SupAgro).
 - he was a referee for papers submitted to Signal Processing and the GretsI conference.
- Frédéric Boudon was referee for papers submitted to SIGGRAPH, SIGGRAPH Asia, Sensors, Computer Graphics Forum and International Journal of modeling and Simulation.
 - Christian Fournier give a invited talk on graphic programming at the JDEV2013 (Journée nationales du Développement Logiciel 4-5-6 septembre 2013 Ecole polytechnique Palaiseau/Ile-de-France)
- Christophe Pradal has rendered the following services in 2013:
 - he is the scientific coordinator of the Agropolis Foundation project 'OpenAlea software platform'.
 - he is the scientific coordinator of the Inria project ADT 'OpenAlea 2.0'.
 - he is the scientific coordinator of the modeling workpackage of the ANR Blanc Hydroroot.
 - he is a member of the board of the Epiarch network.
 - he is an editor of proceeding of the conference Euroscipy [26] that appeared as a special issue of the Journal of Computational Science (JoCS) (together with Gaël Varoquaux and Hans Peter Langtangen).
 - he gave 2 invited talks
 - he was referee for papers submitted at journals: Journal of Scientific Computing and Annals of Botany.

7.2. Teaching - Supervision - Juries

7.2.1. Teaching

Master Biostatistics. Jointly with Montpellier 1, Montpellier 2 Universities and Agro-Montpellier.

Yann Guédon teaches the stochastic modeling course (<http://www.agro-montpellier.fr/um2/um1/masterbiostatistique>).

This involves 21h of M2 classes.

Christophe Godin was responsible for a class of Master 2 on 'Plant modeling' with participation of Yann Guédon, Christophe Pradal, Frédéric Boudon and Christian Fournier at the University of Montpellier 2 (M2 - 25h).

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

Christophe Godin gave a class of Master 2 on 'Plant modeling' in the module plant and animal Morphogenesis of the Master in biology at ENS-Paris organized by Patrick Lemaire (M2 - 4h).

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

Christophe Pradal and Christian Fournier taught the Master class "Impact de l'architecture sur la propagation des maladies foliaires" in the module 'Démarches de modélisation' in Montpellier SupAgro (15h).

7.2.2. Supervision

PhD in progress : Mathilde Balduzzi, "*Geometric modeling of plant canopy from 3D scanner images: Combined use of 3D information and reflected intensity for meshing*", Montpellier 2 University, C. Godin, F. Tardieu.

PhD in progress : Jonathan Legrand, "*Hormon signaling and control of morphogenesis during flower development*", ENS Lyon, P. Das, Y. Guedon.

PhD : Jean Peyhardi, "*A new generalized linear model (GLM) framework for analysing categorical data; application to plant structure and development*", Montpellier 2 University. Y. Guédon, C. Trottier.

PhD in progress : Pierre Fernique, "*Hidden transition models for the phenotyping of plant architecture in relation to environmental and genetic factors*", Montpellier 2 University. Y. Guédon, J.-B. Durand.

PhD in progress : Léo Guignard, "*Segmentation, visualization and mechanical modeling of embryonic development in the ascidian*", Montpellier 2 University, C. Godin, P. Lemaire.

PhD in progress : Maryline Lièvre, "*Analysis and multiscale modeling of foliar growth in *Arabidopsis thaliana* in response to environmental stresses. Implication of the floral transition in the foliar expansion*", Montpellier 2 University, C. Granier, Y. Guédon.

PhD in progress : 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*", Montpellier 2 University, 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 2 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 2 University, L. Laplace, Y. Guédon.

7.2.3. Juries

Frédéric Boudon was a member of the jury of the PhD defense of Jerome Guenard, from University of Toulouse. Christophe Pradal participated to the PhD committee of Christophe Lecarpentier.

Christophe Godin was a Jury member of the PhD Thesis of Julien Lavenus held in October on the Analysis of the Gene Regulatory Network Controlling Lateral Root Initiation and Patterning Using Systems Biology Approach.

7.3. Popularization

Christophe Godin gave 3 conferences for high-school pupils respectively on plants and fractals and on the Secret Code of Flowers in the context of MathC2+ and fête de la science (6h).

8. Bibliography

Major publications by the team in recent years

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Publications of the year

Doctoral Dissertations and Habilitation Theses

- [11] J. PEYHARDI. , *Une nouvelle famille de modèles linéaires généralisés (GLMs) pour l'analyse de données catégorielles ; application à la structure et au développement des plantes*, Université Montpellier II - Sciences et Techniques du Languedoc, December 2013, <http://hal.inria.fr/tel-00936845>

Articles in International Peer-Reviewed Journals

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