Activity Report 2014

Project-Team VIRTUAL PLANTS

Modeling plant morphogenesis at different scales, from genes to phenotype

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

Table of contents

Project-Team VIRTUAL PLANTS

Keywords: Plant Development, Computational Biology, Multiscale Models, Data Analysis, Simulation

Creation of the Project-Team: 2007 July 01.

1. Members

Research Scientists
> Christophe Godin [Team leader, Inria, Senior Researcher, HdR]
> Frédéric Boudon [CIRAD, Researcher]
> Yann Guédon [CIRAD, Senior Researcher, HdR]
> Christophe Pradal [CIRAD, Researcher]
> Christian Fournier [INRA, Researcher, part time]
> Sarah Cohen-Boulakia [Inria, on leave from Univ. Paris Sud, Associate Professor]

Engineers
> Guillaume Baty [Inria, ADT]
> Julien Coste [Inria, ADT, until Oct 2014]
> Julien Diener [UM2, Labex Numev Grants until June 2014]

PhD Students
> Pierre Fernique [CIRAD/Univ. Montpellier 2 Grant]
> Mathilde Balduzzi [INRA/Inria, ANR Phenome Grant]
> Jean-Philippe Bernard [Inria Grant]
> Léo Guignard [Univ. Montpellier 2 Grant]
> Jonathan Legrand [ENS Lyon Grant]
> Maryline Lièvre [INRA, CIFRE INRA/Bayer Grant]
> Beatriz Moreno Ortega [INRA and European EUROOT Grants]
> Sixtine Passot [Univ. Montpellier 2, ENS Paris Grant]
> Guillaume Garin [INRA, CIFRE ITK Grant]

Post-Doctoral Fellows
> Romain Azaïs [Inria, Inria Grant, from Oct 2013]
> Yassin Refahi [INRA/Inria Grant, Computer Science, Cambridge and ERC Morphodynamics (J. Traas) grants]
> Olivier Ali [INRA, ERC Morphodynamics (J. Traas) Grant, Montpellier]
> Maryam Aliee [Inria, ANR Morpholeaf, until Aug 2014]
> Eugenio Azpeitia Espinosa [Inria]
> Guillaume Cerutti [Inria, from Feb 2014]
> Emmanuel Faure [Univ. Montpellier II, IBC, from Oct 2014]
> Sophie Ribes [Univ. Montpellier II, IBC, from Sep 2014]
> Ibrahim Cheddadi [INRA Avignon, unité PSH, from july 2014]
> Katarina Smolenova [Post doctorate from University of Göttingen, Mar 2014]

Visiting Scientist
> Farah Djelloul [Assistant Professor at the University Djillali Liabés Sidi Bel-Abbès, Aug 2014]

Administrative Assistant
> Laurence Fontana

Other
> Anne-Sarah Briand [CIRAD, internship, from Apr 2014 until Sep 2014]

2. Overall Objectives

2.1. Overall Objectives

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

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

This study is performed from two complementary perspectives.

- First, at a macroscopic level, we develop an extensive methodology to analyze *the structures produced by meristems*. This can be seen as a methodology that aims to solve an inverse problem in which one tries to infer meristem functioning from the complex structures they produce. This analysis is carried out at different spatial and temporal scales.

- Second, at a more microscopic level, we intend to exploit the recent spectacular scientific and technological progresses in developmental biology in order to understand how physiological and genetic processes control meristem growth at cell scale.

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

- multiscale models for the spatial (topological and geometrical) representation of structured biological objects (which range from meristem tissues to branching structures),

- methods and models for deciphering the organization of these complex biological objects,

- and models for morphogenesis.

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

3. Research Program

3.1. Analysis of structures resulting from meristem activity

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

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

- *Statistical modeling*: We investigate different categories of statistical models corresponding to different types of structures.

- – Longitudinal data corresponding to plant growth follow up: the statistical models of interest are equilibrium renewal processes and generalized linear mixed models for longitudinal count data.

- – Repeated patterns within sequences or trees: the statistical models of interest are mainly (hidden) variable-order Markov chains. Hidden variable-order Markov chains were in particular applied to characterize permutation patterns in phyllotaxis and the alternation between flowering and vegetative growth units along sympodial tree axes.

- – Homogeneous zones (or change points) within sequences or trees: most of the statistical models of interest are hidden Markovian models (hidden semi-Markov chains, semi-Markov switching linear mixed models and semi-Markov switching generalized linear models for sequences and different families of hidden Markov tree models). A complementary approach consists in applying multiple change-point models. The branching structure of a parent shoot is often organized as a succession of branching zones while the succession of shoot at the more macroscopic scale exhibit roughly stationary phases separated by marked change points.

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

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

3.2. Meristem functioning and development

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

- algorithms for the automatized segmentation in 3D, and cell lineage tracking throughout time, for images coming from confocal microscopy,

- design of high-level routines and user interfaces to distribute these image analysis tools to the scientific community,

- tools for structural and statistical analysis of 3D meristem structure (spatial statistics, multiscale geometric and topological analysis),

- physical models of cells interactions based on spring-mass systems or on tensorial mechanics at the level of cells,

- models of biochemical networks of hormonal and gene driven regulation, at the cellular and tissue level, using continuous and discrete formalisms,

- and models of cell development taking into account the effects of growth and cell divisions on the two previous classes of models.

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

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

OpenAlea is the result of a collaborative effort associating 20 french research teams in plant modeling from Inria, CIRAD, INRA and ENS Lyon. The Virtual Plants team coordinates both development and modeling 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. New Software and Platforms

4.1. OpenAlea

4.1.1. *OpenAlea 2.0*

Participants: Julien Coste, Guillaume Baty, Christophe Pradal, Christophe Godin, Frédéric Boudon, Christian Fournier.

Plant models are usually developed at different scales using various modeling paradigms: (i) imperative using a script or a compiled language, (ii) declarative to define a set of rewriting rules like in L-systems, (iii) interactive using a sketch-based interface for creating 3D models of plants, or (iv) visual programming to combine existing components.

However, all these computational paradigms have been developed in different software platforms in the plant modeling community, and, as of today, none of them provides all the modeling paradigms in an integrated software environment. However, the need to develop more complex and integrated models, often assembling many sub-models, led us to consider a modeling framework capable of supporting multiple design paradigms and models, and make them interoperable.

To address this problem we developed the OpenAlea platform. The Version 1.0 of the platform consisted of a middleware implementing a modular and component-based software architecture for assembling models written in different computer languages. *OpenAlea 2.0* adds to OpenAlea 1.0 a high-level formalism dedicated to the modeling of morphogenesis that makes it possible to use several modeling paradigms (Blackboard, L-systems, Agents, Branching processes, Cellular Automata) expressed with different languages (Python, L-Py, R, Visual Porgramming, ...) to analyse and simulate shapes and their development.

It offers an integrated modeling software environment *OpenAleaLab* that provides users with flexible and interactive tools to combine different modeling paradigms to support the computational investigation.

4.1.2. *OpenAleaLab*

Participants: Julien Coste, Guillaume Baty, Christophe Pradal, Christophe Godin, Frédéric Boudon, Christian Fournier.

This research theme is supported by the Inria ADT OpenAlea.

OpenAleaLab is a new integrated modeling environment (IME) for OpenAlea. This IME provides an IPython shell, a text editor, a project manager, a toolbox installer, a world data structure containing the objects and state variables shared by the different models and a 3D viewer window that makes it possible to observe the objects of the world. Different modelling paradigms, languages and tools for plant modelling are available as plug-ins, such as a visual programming environment, a L-system language, or a R editor and interpreter. OpenAleaLab is based on IPython architecture and is built using PyQt.

The core of the system is made up of a central data structure (the blackboard) called the world. This data structure may contain various computational objects that altogether define the state of the modeling system, and can be accessed (in read and write) by all the models. The investigation process can be seen as executing the system's models in turn to explore or change dynamically the world objects.

Models are knowledge sources that can modify the world when executed. A model can call for the execution of another model as a function. In this case the model passes an input value to the called model, that inturn returns an output value. In addition it may be possible that the called model changed the world as a side effect. The user launches the execution of a first model (then referred to as the master model), which then entails recursively the hierarchical execution of all the other models downstream of it. One can see that in this framework, the execution controller is then itself considered as a model (the master model).

4.1.3. *Similarity and Provenance in OpenAlea workflows*

Participants: Sarah Cohen-Boulakia, Christophe Pradal, Moussa Yattara [IBC], Patrick Valduriez [Inria].

This research theme is supported by IBC and Inria.

The number of available scientific workflows, designed in OpenAlea or in other worflow systems such as Galaxy or Taverna, is increasing over time. Methods to compare the scientific workflows become a necessity, to allow duplicate detection or similarity search. Scientific workflows are complex objects, and their comparison entails a number of distinct steps from comparing atomic elements to comparison of the workflows as a whole. Various studies have implemented methods for scientific workflow comparison and came up with often contradicting conclusions upon which algorithms work best. Comparing these results is cumbersome, as the original studies mixed different approaches for different steps and used different evaluation data and metrics.

We first contribute to the field [27] by (i) comparing in isolation different approaches taken at each step of scientific workflow comparison, reporting on an number of unexpected findings, (ii) investigating how these can best be combined into aggregated measures, and (iii) making available a gold standard of over 2000 similarity ratings contributed by 15 workflow experts on a corpus of 1500 workflows and re-implementations of all methods we evaluated.

Then, we introduced a novel and intuitive workflow similarity measure that is based on layer decomposition [39]. Layer decomposition accounts for the directed dataflow underlying scientific workflows, a property which has not been adequately considered in previous methods. We comparatively evaluate our algorithm using our gold standard and show that it a) delivers the best results for similarity search, b) has a much lower runtime than other, often highly complex competitors in structure-aware workflow comparison, and c) can be stacked easily with even faster, structure-agnostic approaches to further reduce runtime while retaining result quality.

Ongoing work includes considering *provenance* traces of executions in the similarity metrics and augmenting the number of workflows to be shared between scientists by working on the *provenance-equivalence* aspects between workflows and (Python) scripts. This work will be done in the context of the IBC Young researcher grant we obtained (co-leaded by S. Cohen-Boulakia and Ch. Pradal) in collaboration with members of Zenith and the INRA phenome platform.

5. New Results
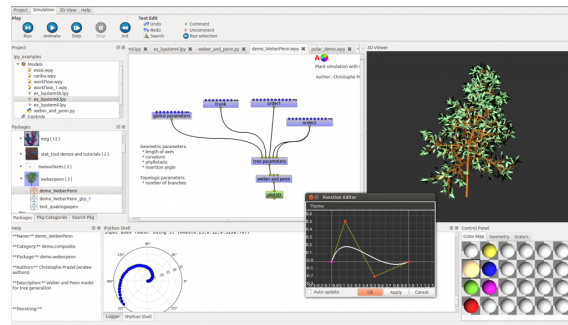
5.1. Highlights of the Year

Figure 1. OpenAleaLab - A highly modular environment for modeling morphogenesis.

- 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 [2]. This paper obtained the 2014 prize "la Recherche" in the biology category http://www.leprixlarecherche.com. 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.

- To study and model morphogenesis, the team has been working in the last 8 years on modeling mechanical forces and deformations in tissues in collaboration with the UMR RDP at ENS-Lyon. This work has given rise to the development of a 3D computational framework to model the mechanics of 3D plant tissues during growth at cellular resolution and has been finalized this year with a publication in PLoS Comp. Biology (to appear in 2015). This framework makes it possible to construct models of meristem development, showing how the regulation of regional identities can lead to realistic shape development by dynamically modulating the mechanical properties of cells. It has been used also to study the influence of a specific signalling cascade (the ABP1-Kat1 signalling pathway) and its putative mechanical consequences on primordium initiation [25]. The expertize gained by our groups on physical models of plant tissue development has been wrapped up in a review paper [12].

5.2. Analysis of structures resulting from meristem activity

5.2.1. *Acquisition and design of plant geometry*

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

Virtual 3D model of plants are required in many areas of plant modeling. They can be used for instance to simulate physical interaction of real plant structures with their environment (ligth, 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 [61], [52]. 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 and video.

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

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

For branching systems, 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 reconstruction accuracy. A laser scan database on which experts built reference reconstructions is used as a basis of the evaluation. A graphical editor has been developed to help experts to reconstruct semi automatically reference structures. The evaluation pipeline is given two plant structures and compares 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 is 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 published in the special issue of Annals of Botany on FSPMs [16]. A procedure to automatically determine phyllotactic angles from scans of small plants has been added recently to the reconstruction pipeline.

Xu *et al.*, 07   Livny *et al.*, 10   Preuksakarn *et al.*, 10
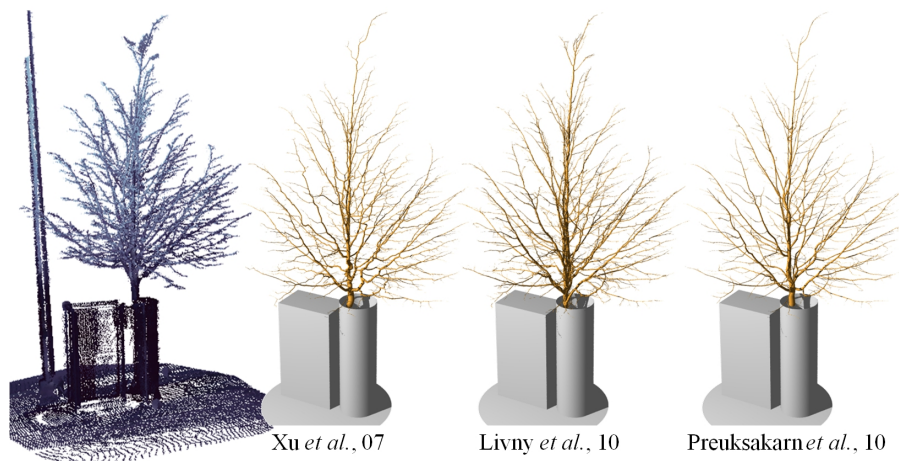
Figure 2. Comparison of different methods of the litterature to reconstruct plant architecture from laser scanner data. On the left, the original scan and on the rigth, the resulting reconstructions using three different methods. These reconstructions are quantitivelly assessed using our evaluation pipeline presented in [16]

In the context of the PhD of M. Balduzzi, we also investigated the reconstruction of tree foliage from 3D scans. Such elements are crucial to study the interaction of the plant with its environment. However, laser scans contain outliers in the silhouette of the scans that make the meshing of the pointset extremely difficult. New generation of laser scanners provide intensity of the laser reflected on the surface of scanned objects. This intensity depends on the distance to the object, its optical property and the incidence angle. A first work on this topic showed that after correcting the distance effect, the incidence angle can be deduced from the intensity. From this result, we developed a reconstruction pipeline using the scan intensities and based on Shape-From-Shading. Outliers being along the edge of the surface point cloud, we chose to develop a propagation SFS method initialized with points of the scans with high quality. We proved that surface with constant intensity are necessarily surfaces of constant slope or sand-pile surfaces. Using this result, a propagation method

along iso-intensity regions was developed. These surfaces can then be sampled to provide a smooth point set without outliers. This work has been presented by M. Balduzzi for her thesis defense in november.

- *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, dedicated methods for generating 3D plant models must be devised due to the high complexity of plant topology. In collaboration with our colleagues from IRIT, Toulouse, we developed an analysis-by-synthesis method which generates 3D models of plants 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. 2D projections 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 2D projection criterion. Realistic results are obtained on different species of plants, in particular vineyards. This work has been presented at the Mathematical Methods for Curves and Surfaces conference and published in LNCS [42].

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

  This research theme is supported by the Agropolis project MecaFruit3D.

  The aim of this work is to provide methods for generating fruit structure that can be integrated with models of fruit function. To this end, we used a modeling pipeline previously developped by Mik Cieslak in the OpenAlea platform. This methods 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. Previous studies demonstrated the possibility to create species-specific models of fruit structure with relatively low effort [49]. We focus now on validating the vasculature networks by quantitatively comparing them to experimental data from the litterature.

  These physiological data will be combined with a mechanical model of fruit growth, to investigate the effects of fruit structure on quality (see section 5.4.2).

- *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])

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

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

  1. We integrated a validation step in the workflow based on the comparison method presented in [16].
  2. We participated in an international collaboration with the Université Catholique de Louvain (Belgium), the CPIB of the University of Notthingham (UK), the University of Vienna

(Austria), the Jülich research center (Germany) and INRA, to develop a standard file format for root architecture. The resulting format (RSML) is described in a publication to appear in *Plant Physiology* in 2015 (details can be found at rootsystemml.github.io).

3. We have initiated a collaboration to integrate visual data mining methods developed by the Zenith team in order to improve the automation of the image analysis pipeline.

4. In general, the robustness of the pipeline has been improved. In particular, an optimization method has been designed to select the root axes hierarchy that respect specific botanical constraints.

5.2.2. *Modeling the plant ontogenic programme*

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

This research theme is supported by two PhD programmes.

The remarkable organization of plants at macroscopic scales may be used to infer particular aspects of meristem functioning. The fact that plants are made up of the repetition of many similar components at different scales, and the presence of morphological gradients, e.g. [46], [54], [55], [51], 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" [59], "age state" [50] or "physiological age" [48]. 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 [50], [48]. Here we develop computational methods to decipher these rules.

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

  Shoot branching structures often take the form of a succession of homogeneous branching zones and have been analyzed using segmentation models such as hidden semi-Markov chains. Axillary meristem fates are influenced by local properties of the parent shoot such as for instance its growth rate or local curvature. The objective of this work, which 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 partitioned conditional GLMs [38] that enable to tackle hierarchically-structured 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 partitioned conditional GLMs and have been applied to apple and pear tree branching structures.

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

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

Indices were proposed for early detection of alternation during the juvenile phase. They were based on a trend model and a quantification of the deviation amplitudes and dependency, with respect to the trend. This allows to quantify alternation from the yearly numbers of inflorescences at tree scale.

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

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

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

  In multitype branching processes, the plant development is viewed as a demographic process, a parent entity of a given type generating child entities of different types (e.g. vegetative and flowering entities). Formally, the botanical entity properties are summarized as a categorical state variable. The number of child entities in each state is modeled through discrete multivariate distributions. Model selection procedures are necessary to specify parsimonious generation distributions. We developed an approach based on probabilistic graphical models to identify and exploit properties of conditional independence between numbers of children in different states, so as to simplify the specification of their joint distribution. The graph building stage was based on exploring the space of possible chain graph models, which required defining a notion of neighbourhood of these graphs [33]. To relax the strong constraints regarding dependencies induced by parametric distributions, mixture of graphical models were also considered [41]. Multitype branching processes were applied to the analysis of the patchiness pattern (consisting of canopies made of clumps of either vegetative or flowering growth units) in mango trees.

- *Simulating fruit tree phenology* (A.S. Briand, Frédéric Boudon, Frédéric Normand [CIRAD, HortSys, Réunion Island], Anaëlle Dambreville, Jean-Baptiste Durand, Pierre Fernique, Yann Guédon, Christophe Pradal, Pierre-Eric Lauri [AFEF team, AGAP])

  Mango is a tropical tree characterized by strong asynchronisms within and between trees. To study more precisely the interplay between the plant structural components, we built an integrative model to simulate the plant development based on the L-system formalism and GLM to model the dependencies between events. This model has been started during the internship of A. Jestin last year and has been continued during the visit of F. Boudon at the Hortsys lab in the Réunion island. The model has been extended this year to model growth and phenology of shoots and inflorescences (internship of A.S. Briand). For this, the sizes of the different organs is modelled by statistical laws estimated from measurements that depends on their positions in the architecture. The growth speed of organs is modulated by the temperature. This model will serve as a basis for further ecophysiological study in silico.

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

  Plant growth, i.e. the increase of organ dimensions over time, and development, i.e. the change in plant structure, are often studied as two separate processes. However, there is structural and functional evidence that these two processes are strongly related. Our aim was to investigate the coordination between growth and development using mango trees, which have well-defined developmental stages. Developmental stages, determined in an expert way, and organ sizes, determined from objective measurements, were collected during the vegetative growth and flowering phases of two cultivars of mango. For a given cultivar and growth unit type (either vegetative or flowering), a multistage model based on absolute growth rate sequences deduced from the measurements was first built, and then growth stages deduced from the model were compared with hand-annotated developmental stages. Strong matches were obtained between both stages, leading to a consistent definition of integrative developmental growth stages. The growth stages highlighted growth asynchronisms between

two topologically connected organs, namely the vegetative axis and its leaves. Integrative developmental growth stages emphasize that developmental stages are closely related to organ growth rates and can be interpreted in terms of the possible physiological processes (hydraulics, biomechanics and carbohydrate partitioning) underlying these stages.

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

  Our aim was to characterize the successive flowering phases of perpetual flowering strawberry genotypes, which is of particular importance for better predicting fruit production. We applied multiple change-point models for the synchronous segmentation of the individuals of a given genotype in successive flowering phases. We identified two groups of genotypes that differ by the intensity of the flowering at the end of the flowering period. Using a genetic approach, we identified a locus controlling the flowering intensity at the end of the flowering period that likely explain these two groups of genotypes.

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

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

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

  The degree of self-nestedness is defined in [6] as the edit-distance between the considered tree structure and its nearest embedded self-nested version. Indeed, finding the nearest self-nested tree of a structure without more assumptions is conjectured to be an NP-complete or NP-hard problem. We thus designed a heuristic method based on interacting simulated annealing algorithms to tackle this difficult question. This procedure is also a keystone in a new topological clustering algorithm for trees that we propose. In addition, we obtain new theoretical results on the combinatorics of self-nested structures. The redaction of an article is currently in progress.

5.2.3. *Analyzing the influence of the environment on the plant ontogenic programme*

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

This research theme is supported by three PhD programs.

The ontogenetic programme of a plant is actually sensitive to environmental changes. If, in particular cases, we can make the assumption that the environment is a fixed control variable (see section 5.2.2), 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 [24] 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])

  We identified robust indicators that summarize the respective importance of ontogeny and environmental constraints (mainly related to light environment) in forest tree development. In this context, tree growth data correspond to the retrospective measurement of annual shoot characteristics (e.g. length, number of branches) along the main stem. We applied segmentation models to identify tree growth phases. These segmentation models, which are hidden semi-Markov chains, were compared with simple hidden Markov chains that correspond to the environment-driven development assumption. This statistical modelling approach was applied to both evergreen (Corsican pine and silver fir) and deciduous (sessile oak and Persian walnut) tree species growing in contrasted conditions ranging from managed forest stands to unmanaged understoreys. Growth phase duration distributions estimated within these segmentation models characterize the respective importance of ontogeny and environmental constraints in tree development at the population scale and have very contrasted characteristics in terms of shape and relative dispersion between ontogeny-driven and environment-driven tree development. These characteristics may change over tree life, reflecting changes in tree competition. Growth phase duration distributions summarize the joint trajectory of tree ontogeny and environment without requiring tree growth follow-up data for their estimation.

- *Analyzing fruit tree phenology in various climatic conditions from the shoot to the orchard scale* Yann Guédon, Juliano Dutra Schmitz [Universidade Federal de Pelotas, Brazil], Pierre-Eric Lauri [AFEF team, AGAP], Jean-Michel Legave [AFEF team, AGAP], Gustavo Malagui [Universidade Tecnológica Federal do Paraná]

  A first study was conducted at the shoot scale on four apple cultivars characterized by various chilling requirements and grown in two contrasting winter temperature conditions [20]. Our hypothesis was that shoot architecture is strongly affected by winter temperatures determining both the position and budburst of vegetative laterals with a lower effect on their outgrowth. A two-step approach was designed to quantify at the shoot scale i) the branching pattern and ii) two phenological stages of vegetative laterals, budburst and outgrowth. The branching pattern analysis combined various methods: branching sequence alignement and clustering, hidden semi-Markov chain and multiple change point model for segmenting branching sequences into homogeneous zones. A categorical variable, the branching zone, was built to summarize the lateral position along the shoot. It was integrated into the phenological analysis, based on a zero-inflated Poisson model, as a factor together with the cultivar and the winter temperature. We showed in this way that temperature had a main effect on the distribution of vegetative laterals along the shoot. It also strongly affected budburst, which was also affected by the cultivar and the branching zone. The outgrowth of the lateral was not significantly affected by temperature but was significantly affected by the cultivar and the branching zone. Furthermore, the delayed senescence and subsequent leaf persistence during winter, characterizing the apple tree in the mild winter temperature condition, had only a weak effect on the distribution of vegetative laterals and on budburst and lateral outgrowth. The actual shoot architecture and budburst result thus from an ordered sequence of events with a pivotal role of winter temperatures on the dormancy completion of individual lateral buds.

  A second study was conducted at the orchard scale. The time-course variation of dates of flowering stages was established for seventeen chronological sequences corresponding to various apple tree

cropping areas in Europe (Belgium, France, Germany, Italy, Switzerland), north Africa (Morocco) and southern Brazil. Our aim was to characterize the relationship between flowering advances in fruit trees and global warming and to compare the northern and the southern hemisphere situations. We applied piecewise constant and linear homoscedastic models to these phenological series. The sudden advance of flowering dates detected at the end of the 1980s in the European locations can be explained by changes in rates for completion of heat requirements, essential to the development of floral primordia within buds. No effect of the global warming could be detected in the Brazilian flowering series and we only found a direct effect of the chilling temperature on the flowering date the same year (the colder the Austral winter, the earlier the flowering date).

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

  Sustainable agriculture requires the identification of new, environmentally responsible strategies of crop protection. Modelling of pathosystems can allow a better understanding of the major interactions inside these dynamic systems and may lead to innovative protection strategies. In particular, functional–structural plant models (FSPMs) have been identified as a means to optimize the use of architecture-related traits. A current limitation lies in the inherent complexity of this type of modelling, and thus the purpose of this paper is to provide a framework to both extend and simplify the modelling of pathosystems using FSPMs.

  Different entities and interactions occurring in pathosystems were formalized in a conceptual model [21]. A framework based on these concepts was then implemented within the open-source OpenAlea modelling platform, using the platform's general strategy of modelling plant–environment interactions and extending it to handle plant interactions with pathogens. New developments include a generic data structure for representing lesions and dispersal units, and a series of generic protocols to communicate with objects representing the canopy and its microenvironment in the OpenAlea platform. Another development is the addition of a library of elementary models involved in pathosystem modelling. Several plant and physical models are already available in OpenAlea and can be combined in models of pathosystems using this framework approach.

  Two contrasting pathosystems are implemented using the framework and illustrate its generic utility. Simulations demonstrate the framework's ability to simulate multiscaled interactions within pathosystems, and also show that models are modular components within the framework and can be extended. This is illustrated by testing the impact of canopy architectural traits on fungal dispersal. This study provides a framework for modelling a large number of pathosystems using FSPMs. This structure can accommodate both previously developed models for individual aspects of pathosystems and new ones. Complex models are dissassembled into separate *knowledge sources* originating from different specialist areas of expertise and these can be shared and reassembled into multidisciplinary models. The framework thus provides a beneficial tool for a potential diverse and dynamic research community.

5.3. 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.

5.3.1. *Data acquisition and design of meristem models*

- *Improvement of the MARS-ALT pipeline robustness* Meristem, laser microscopy, image reconstruction, cell segmentation, automatic lineaging
  Participants: Léo Guignard, Christophe Godin, Christophe Pradal, Grégoire Malandain [Morpheme, Inria], Gaël Michelin [Morpheme, IPL Morphogenetics, Inria], Guillaume Baty, Sophie Ribes [IBC, UM2], Jan Traas [RDP, ENS], Patrick Lemaire [CRBM, CNRS], Yassin Refahi [RDP, ENS].

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

The MARS-ALT (Multi-Angles Registration and Segmentation - Automatic Lineage Tracking) software pipeline automatically performs a segmentation at cell resolution from 3D or 2D voxel images where the membranes/walls are marked (by a die for example) and makes it possible to follow the lineage of these cells through time [5]. This year, a new version of this pipeline has been developed that uses informations redundancy across the movies and biological knowledge on the segmented organism to constrain and therefore improve the segmentation and the tracking. To test the new pipeline, we used 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 single angle 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 single angle with a confocal microscope (Collaboration RDP Lyon and Sainsbury lab)

– *Phallusia mammillata* embryos with from 32 cells to around 1000 cells. The organism is captured from four different angles every minute during 10 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.

To our knowledgeIt is the first time that such high-resolution 4D digital tissues have been generated taking into account the cell shapes, opening the way to quantitative analysis of morphogenesis and tissue deformation at cell resolution.
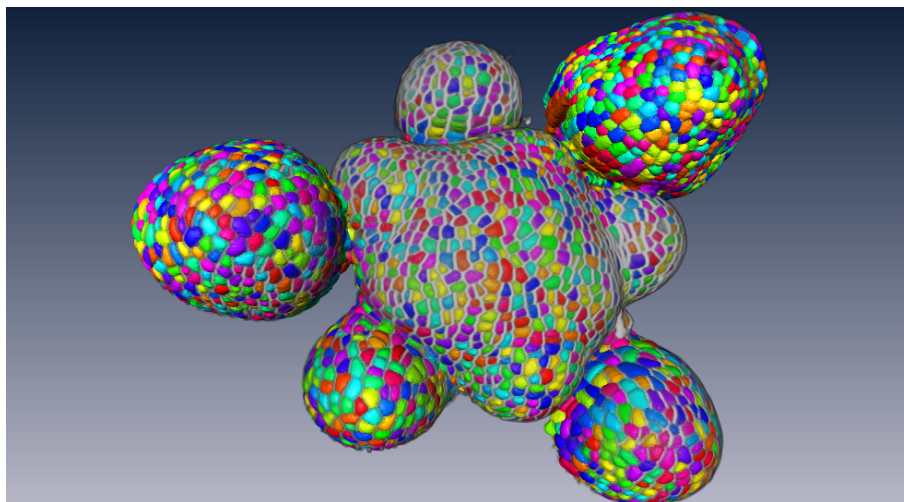
Figure 3. Superimposition of an automatic cell segmentation of an arabidopsis flower meristem using the new MARS pipeline with the original confocal image stack where the membranes are marked.

● *Creating mesh representation of cellular structures* (Guillaume Cerutti, Sohie Ribes, Christophe Godin)

Participants: Guillaume Cerutti, Sophie Ribes, Christophe Godin, Géraldine Brunoud [RDP, ENS], Carlos Galvan-Ampudia [RDP, ENS], Teva Vernoux [RDP, ENS], Yassin Refahi [RDP, ENS, Sainsbury Lab].

This research theme is supported the HFSP project Biosensors.

To produce a more efficient data structure accounting for the geometry of cellular tissues, we studied the problem of reconstructing a mesh representation of cells in a complex, multi-layered tissue structure, based either on membrane/wall images segmented using MARS or on nuclei images of shoot apical meristems. The construction of such mesh structures for plant tissues is currently a missing step in the existing image analysis pipelines. We developed a set of tools to build a triangular mesh surface representing the tissue in 3D, to evaluate the quality of the tissue reconstruction over objective aspects, to optimize a low-quality mesh simultaneously along several criteria, and to go towards a higher-scale representation pulling away from the cell resolution [31]. These methods are used in particular on nuclei images of shoot apical meristems of *Arabidopsis thaliana* to project hormonal information at cell-level on a continuous 3D tissue geometry. This work is carried out in the context of the post-doc of Guillaume Cerutti within the HFSP project BioSensors (Collaboration RDP Lyon).

These tools can produce light discrete representations of the cell interfaces that enables fast visualization, information projection, and quantitative analysis of the tissue, and give way to *in silico* physical and mechanical simulations on real-world data.
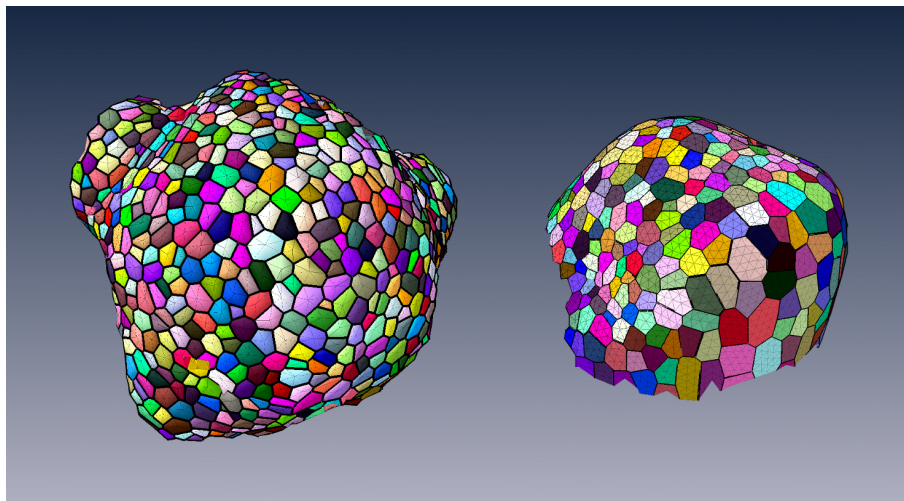
Figure 4. Triangular mesh representations of shoot apical meristem and flower meristem tissues obtained from MARS segmentations

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

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

  To organize the various genetic, physiological, physical, temporal and positional informations, we build a spatialized and dynamic database [56]. This database makes it possible to store all

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

5.3.2. *Shape analysis of meristems*

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

At cellular resolution, we studied the organization of cells in the meristems. The MARS-ALT pipeline provides rich spatio-temporal data sets for analyzing the development of meristems. A first step consisted of designing a dedicated graph for efficiently representing the spatial (adjacency between cells) and temporal (cell division) relationships between cells. Various variables can be attached either to the vertices (e.g. cell volume, inertia axes) or the edges (e.g. wall surface, distance between cell centroids). This graph may be augmented by new variables resulting from various spatial or temporal filtering (e.g. cell volumetric growth). Looking at homogeneous regions in the variable value space, cellular patterns can be identified. This work was developed in the context of the PhD of Jonathan Legrand with contributions of Pierre Fernique, another PhD student, that has been defended this year.

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

- A first one that favours the spatial structuring: In this approach, the cell neighbourhood and the cell descriptors are jointly taken into account in a clustering approach whose objective is to identify a small number of clusters corresponding to well-defined cell identities. Once the cells have been labelled using the clustering algorithm, cell generation distributions are estimated on the basis of the labelled lineage trees.

- A second one that favours the temporal structuring: In this approach, the data of interest are lineage forest and the only spatial structuring taken into account corresponds to siblings with respect to a given parent cell. In a first step, cell identities are inferred on the basis of the cell descriptors taking into account lineage relationships using hidden Markov tree models and the spatial regions that emerge from the cell identity labelling are then characterized. This second approach is supported by the fact that cell topology is only affected by division which makes highly relevant the local spatial information taken into account in this approach.

5.3.3. *Mechanical model*

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

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

The rigid cell walls that surround plant cells are responsible for the acquisition of organ shapes. These walls are submitted to stresses due to cell turgor pressure. Wall deformation is caused by the turgor forces in the cell walls. Wall synthesis is triggered by these wall deformations when some specific threshold is exceeded. The final shape of the tissue integrates mechanically all the local deformations of each cell.

To quantify this growth process at the level of a multicellular tissue, we developed a model of growth that integrates mechanical forces development at cellular resolution. In this model, walls are characterized by their mechanical properties, e.g. elasticity, extensibility and anisotropy. For this, 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 will appear in PLoS Computational Biology in 2015. We used this framework to investigate the influence of a specific signalling cascade (the ABP1- Kat1 signalling pathway) and its putative mechanical consequences on primordium initiation [25]. A review of the different mechanical concepts underlying plant morphogenesis has been carried out in [12].

In our first approach, the mechanical model rely on a finite element method (FEM) to describe the deformation of the tissue. In FEM, the tissue is represented by a mesh. The positions of the vertices at each time step are estimated from a linear system. If the tissue is big or if the mesh is fine, the linear system can be large and thus leads to computational overheads. An alternative way to classical FEM is to use a meshless method where the deformation of the tissue can be characterized by a linear combination of deformations of a finite and small set of frames. Because shape functions are no longer defined on each element but on the whole tissue, they have to be updated at each growth step by estimating a new rest configuration. With meshless method, the discretization of the system can be dynamically updated parsimoniously according to the precision required to model the emergence of shapes (PhD work of Jean-Philippe Bernard).

5.3.4. *Gene regulatory networks: Design of a genetic model of inflorescence development.*

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

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

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

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

5.3.5. *Model integration*

Participants: Frédéric Boudon, Christophe Godin, Guillaume Baty, Jan Traas.

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

Our approach consists of building a programmable tissue which is able to accept different modeling components. This includes a central data structure representing the tissue in either 2-D or 3-D, which is able to grow in time, models of gene activity and regulation, models of signal exchange (physical and chemical) between cells and models of cell cycle (which includes cell division). 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 [58] and the CPIB group in Nottingham, UK [47].

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*. In the past year, progress has been made in defining a generic tissue data structure that could be used in this platform. Currently, robust geometric operations such as division are implemented and tested. Moreover, a redesign of the structure based on more elaborated formalisms such as combinatorial maps is investigated.

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

5.4.1. *Modeling water transport 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 conductivites, root architecture). One major finding is that the root hydraulic conductivity (Lpr) computed from the model is highly dependent on root architecture. This is due to the limiting role of axial (xylem) conductance, one feature that had been neglected in previous representations of root water transport. The radial hydraulic conductivity may primarily be limiting in conditions of Lpr inhibition, since its increase from values in control roots has marginal effects on Lpr. A new set of experimental data including root diameter repartitions in wild-type plants, and xylem vessel diameters in mutants with altered xylem morphology (irx3, esk1) will be used to 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.

5.4.2. *Mechanical modeling of fruit growth*
Participants: Ibrahim Cheddadi [Inra, Avignon], Mik Cieslak [U. Calgary], Frédéric Boudon, Valentina Baldazzi [Inra, Avignon], Nadia Bertin [Inra, Avignon], Michel Genard [Inra, Avignon], Christophe Godin.

This research theme is supported by the Agropolis project MecaFruit3D.

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, as well as mechanical interactions between tissue parts that are essential to properly model growth.

To help characterizing the 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 is being investigated, combining two tools previously developed in the team: on the one hand, a modeling pipeline that creates a 3D volumetric mesh of the internal fruit structure, including vasculature (see section 3), and couples it with water and carbon transport; on the other hand, a mechanical description of the growth of plant tissues (see section 5.3.3): growth is related to the extension of the cell walls, which is triggered when the so-called turgor pressure inside the cells exceeds a given threshold. The global shape of the tissue integrates mechanically all the local deformations of each cell.

In order to couple these two aspects of plant growth, we describe how volume variations are constrained by fluxes of matter, and how these fluxes depend on mechanical and physiological parameters. The corresponding set of equations are resolved thanks to the SOFA finite elements software.

This approach will be applied to study tomato fruit. 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.
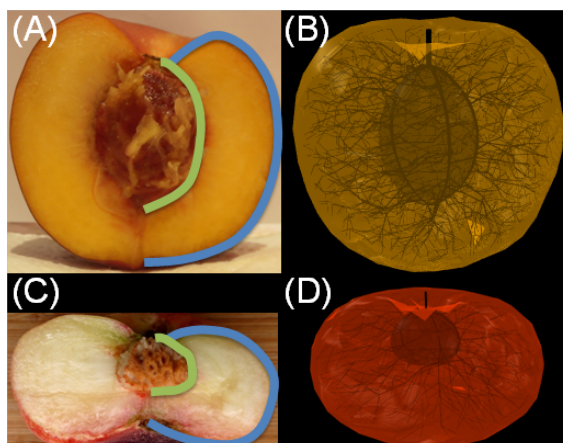
Figure 5. Virtual models of peaches reconstructed from images with simulated vasculatur to simulate carbon and water transport in the fruit

5.4.3. *Analyzing root growth and branching*

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

This research theme is supported by two PhD programmes.

New 2D and 3D root phenotyping plateforms are emerging with associated image analysis toolbox (e.g. SmartRoot). 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).

5.4.4. *Analyzing shoot and leaf elongation*

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

This research theme is supported by one PhD programme.

This study is based on the observation of a lack of methods enabling the integrated analysis of the processes controlling the vegetative development in *Arabidopsis thaliana*. We developed a pipeline of analysis methods combining image analysis techniques and statistical models to integrate the measurements made at the leaf and shoot scales. Semi-Markov switching models were built for different genotypes, allowing a more thorough characterization of the studied mutants. These models validated the hypothesis that the rosette can be structured into successive developmental phases that could change depending on the genotype. They also highlighted the structuring role of the abaxial trichome trait, although the developmental phases cannot be explained entirely by this trait. We developed a second pipeline of analysis methods combining a semi-automatic method for segmenting leaf epidermis images based on the ilastik software, and the analysis of the obtained cell areas using a gamma mixture model whose parameters of gamma components are tied by a scaling rule. This model allowed us to estimate the distribution of the number of endocycles. We highlighted in this way that the mean number of endocycles changes drastically with leaf rank. Finally, we built a multi-scale model that integrates tissular, morphological, dynamical and dimension traits for each successive leaf along the shoot. This model gave us for the first time an integrative view of the development of the *Arabidopsis* rosette.

5.4.5. *Analyzing perturbations in Arabidopsis thaliana phyllotaxis*

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

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

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

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 [60], [53] which relies of 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 leads 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 [15].

5.4.6. *A stochastic model of phyllotaxis*

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

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

To proceed further and find a mechanistic interpretation of these results, we are currently developing a stochastic extension of the standard model of phyllotaxis. We first analyzed the properties of the inhibitory fields created by the existing primordia on the initiation of new promordia, and concluded that the angular positions of organs are very robust to perturbations while plastochrons may be dramatically affected. This suggested that there exists a strong decoupling between space and time in the patterning process. To account for this observation, we modeled the perception of the initiation signal by cells using stochastic processes coupled with the intensity of inhibitory fields and showed that the observed permutation patterns emerge spontaneously from this purely local processes. A paper describing this model will be submitted for publication in 2015.

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

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

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

6. Bilateral Contracts and Grants with Industry

6.1. Bilateral Grants with Industry

Maryline Lievre has been funded by Bayer grant. Guillaume Garin has been funded by ITK. The Hydroroot project is funded by Syngenta.

7. Partnerships and Cooperations

7.1. Regional Initiatives

7.1.1. *Agropolis computational plant seminar*

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

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

In the context of the creation of a world-level pole on plant science in the region Languedoc-Roussillon, we created a monthly seminar on plant modeling and its applications. The seminar is organized by Yann Guédon, Thierry Fourcaud (CIRAD, AMAP), Christine Granier (INRA, LESPE), Soazig Guyomarc'h (Montpellier 2 University, DIADE) and Laurent Laplaze (IRD, DIADE) with the support of Agropolis International and Agropolis Foundation. In 2014, we organized a two-day workshop devoted to the modeling of plant development from the cellular to the organ scale.

7.1.2. *MecaFruit3D*

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

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

The fruit cuticle plays a major role in fruit development and shelf-life. It is involved in water losses, cracking, and protection against stress, and thus it may have major economic impacts. Objectives of the project are to better understand the multiple roles of the fruit cuticle in the control of fleshy fruit growth and quality. The project relies on a previously developed computational functional-structural tomato fruit model (Cieslak et al. 2011; 2012), that predicts the transport and accumulation of water and dry matter to various fruit tissues through a complex 3D vasculature network. This architecture-based model will serve as the backbone of a new approach for studying fruit development where interactions and feedback loops between turgor driven processes and cuticle mechanical constraints will be analysed and modelled. A collection of cuticle tomato mutants available at INRA Bordeaux will be used to validate the hypotheses.

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

7.1.3. *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 for 2D root system reconstruction from images developed in the RhizoPolis project (Agropolis foundation) to deal with large scale and high-thoughput analysis. For this we develop the project in the following directions:

1. make the analysis software more robust to various acquisition conditions using visual data mining technologies developped at Zenith.
2. Improve interoperability with other software and within the OpenAlea ecosystem.
3. Improve the reconstruction quality and its evaluation.

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

7.2. National Initiatives

7.2.1. *ANR*

7.2.1.1. *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.

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

Funding: ANR (Contractor for Virtual Plants: Cirad, From 2012 to 2015)

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.

7.2.2. *Other national grants*

7.2.2.1. *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 environnement 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

7.2.2.2. *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

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

Funding: Inria ADT (Contractors for Virtual Plants: Inria from 2014 to 2016)

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

7.2.2.4. 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 plateform 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 Nederlands) , ADAS Intitute (UK), CNRS, and IRSTEA .

7.2.2.5. Morphogenetics

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

Funding: Inria Project Lab (From 2013 to 2016)

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

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

7.2.2.6. 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

7.3. International Initiatives

7.3.1. Inria International Partners

7.3.1.1. 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. [57].

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

We have for several years a strong partnership with Ted de Jong group at UC Davis concerning the influence of various agronomic practices (water stress, pruning) on fruit tree branching and production [24]. This is a tripartite collaboration that also involves Evelyne Costes of the AGAP/AFEF team.

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

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

7.3.2. *Participation In other International Programs*

7.3.2.1. *BioSensors*

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

7.4. International Research Visitors

7.4.1. *Visits of International Scientists*

The team received several visitors from foreign research groups in 2014:

- 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.
- Pierre Barbier, post-doc researcher at the University of Bern visited the team for a few days in February.
- Yoan Coudert, from University of Cambridge, UK, visited the team for a few days days in April.
- Xavier Sirault, from High Resolution Plant Phenomics Centre at CSIRO, visited the team for one week.
- David Ford, Professor at the University of Washington, USA, visited the team for a few days days in December.

7.4.2. Visits to International Teams

7.4.2.1. Research stays abroad

- During the year, Frédéric Boudon visited Frédéric Normand of the UR Hortsys at the CIRAD La Réunion five weeks in April.
- Sarah Cohen-Boulakia has spent one month at the University of Pennsylvania (Philadelphia, April 2014) and one week at the Humboldt University of Berlin (December 2014).

8. Dissemination

8.1. Promoting Scientific Activities

8.1.1. Scientific events organisation

8.1.1.1. general chair, scientific chair

- Yann Guédon was the chair of the Agropolis workshop: Modeling plant development from the cellular to the organ scale (Montpellier, March 27-28th).

8.1.1.2. member of the organizing committee

- Christophe Godin is a member of the scientific board of the FSPM series of conferences.
- Christophe Godin is co-organizing with Patrick Lemaire the "interdisciplinary spring school on plant and animal morphogenesis", gathering students and professors during one week of lectures, debates and practicals.

8.1.2. Scientific events selection

8.1.2.1. member of the conference program committee

- Sarah Cohen-Boulakia is member of the following PC Conferences : SIGMOD 2015, ICDE 2015, DILS 2014 (Data integration in the life sciences), BPM 2015 (Business Process Management) and PC Workshops : TAPP (Theory and Practice of Provenance) 2014 and 2015, Sweet 2014 (Int. sigmod Workshop on scalable workflow enactment engines and technologies), BeyondMR 2015 (ICDT workshop on Algorithms and Systems for MapReduce and Beyond).

8.1.2.2. reviewer

- Frédéric Boudon was referee for papers submitted to the Eurographics conference.
- Christophe Godin was referee for papers submitted to the SIGGRAPH conference.

8.1.3. Journal

8.1.3.1. member of the editorial board

- Sarah Cohen-Boulakia is member of the Editorial board of the Journal of Data Semantics (Springer)
- Christophe Godin is an associate editor of the journal Frontiers in Plant Sciences
- Christophe Godin was a guest editor of the special issue of Annals of Botany on Functional-Structural Models of Plants (FSPMs).

8.1.3.2. reviewer

- Frédéric Boudon was referee for papers submitted to Computers and Electronics in Agriculture, Agronomy and JZUS-C (Computers and Electronics).
- Yann Guédon reviewed a paper for the Journal de la Société Française de Statistique.
- Christophe Pradal reviewed a paper for the Journal Annals of Botany.
- Christophe Godin reviewed papers for PNAS, PLoS Computational Biology, Annals of Botany and reviewed a book on mathematical models of plant growth.

8.2. Teaching - Supervision - Juries

8.2.1. Teaching

- Master Computer Science: Frédéric Boudon, Christophe Godin, Christophe Pradal, Benjamin Gilles [ICAR, LIRMM] and Loïc Barthe [IRIT, Toulouse], Geometric modelling, 30h, M2, University Montpellier 2, France.

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

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

- Christophe Godin participated to an "Ecole Jeunes Chercheurs" organized by the Doctoral School SEVAB in Toulouse on "multiscale modeling of biological systems", 2h.

- Christophe Godin gave a series of 4 lectures on modeling in plant biology (10 hours) during 1 week at the Ecole of Physics des Houches on integrated structural cell biology.

8.2.2. Supervision

- PhD : Mathilde Balduzzi, *"Geometric modeling of plant canopy from 3D scanner images: Combined use of 3D information and reflected intensity for meshing"*, Montpellier 2 University, 24 Nov. 2014, C. Godin.

- PhD : Jonathan Legrand, *"Vers une compréhension multi-échelle du développement floral: des réseaux auxiniques aux patrons de la dynamique cellulaire"*, ENS Lyon, 7 Nov. 2014, A. Boudaoud, Y. Guédon.

- PhD : Pierre Fernique, *"A statistical modeling framework for analyzing tree-index data"*, Montpellier 2 University. 10 Dec. 2014, Y. Guédon, J.-B. Durand.

- PhD : Maryline Lièvre, *"Analyse et modélisation multi-échelle de la croissance foliaire chez Arabidopsis thaliana: mise au point et test d'un pipeline d'analyses permettant une analyse intégrée du développement de la cellule à la pousse entière"*, Montpellier SupAgro, 15 Dec. 2014, C. Granier, Y. Guédon.

- 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 : 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"*, ANRT Ciffre ITK, C. Robert, B. Andrieu, C. Pradal, C. Fournier.

- PhD in progress : Jean-Philippe Bernard, *"Adaptive mechanical model of early flower development based on 4D imaging"*, Montpellier 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. Laplaze, Y. Guédon.

8.2.3. Juries

- Yann Guédon was a member of the Jurys of his PhD students Pierre Fernique, Maryline Lièvre and Jonathan Legrand

- Frédéric Boudon was a member of the jury of the PhD defense of Jonathan Legrand, ENS Lyon.

- Christophe Godin was a member of the Jury of his PhD student Mathilde Balduzzi
- Christophe godin was a member of the Jury of the Habilitation (HDR) of Géraldine Morin ()

8.3. Popularization

- Christophe Godin and Frédéric Boudon presented the Secret Code of Flowers in the context of an Inria initiative at the Science Festival in October.
- Christophe Godin gave two classes on Fractals in science at Lycée Pompidou (Castelnau-Le-Lez).
- Yann Guédon gave a class about the analysis of plant architecture for high-school students "Math C2+" organized by Montpellier 2 University.

9. Bibliography

Major publications by the team in recent years

[1] P. BARBIER DE REUILLE, I. BOHN-COURSEAU, K. LJUNG, H. MORIN, N. CARRARO, C. GODIN, J. TRAAS. *Computer simulations reveal novel properties of the cell-cell signaling network at the shoot apex in Arabidopsis*, in "PNAS", 2006, vol. 103, pp. 1627-1632, http://www-sop.inria.fr/virtualplants/Publications/2006/BBLMCGT06

[2] F. BESNARD, Y. REFAHI, V. MORIN, B. MARTEAUX, G. BRUNOUD, P. CHAMBRIER, F. ROZIER, V. MIRABET, J. LEGRAND, S. LAINÉ, E. THÉVENON, E. FARCOT, C. CELLIER, P. DAS, A. BISHOPP, R. DUMAS, F. PARCY, Y. HELARIUTTA, A. BOUDAOUD, C. GODIN, J. TRAAS, Y. GUÉDON, T. VERNOUX. *Cytokinin signalling inhibitory fields provide robustness to phyllotaxis*, in "Nature", 2013, vol. 505, n° 7483, pp. 417-421 [*DOI : 10.1038/NATURE12791*], https://hal.inria.fr/hal-00926908

[3] F. BOUDON, C. PRADAL, T. COKELAER, P. PRUSINKIEWICZ, C. GODIN. *L-Py: an L-system simulation framework for modeling plant architecture development based on a dynamic language*, in "Frontiers in plant science", May 2012, vol. 3, n° 76 [*DOI : 10.3389/FPLS.2012.00076*], http://hal.inria.fr/cirad-00703085

[4] F. CHAUBERT-PEREIRA, Y. GUÉDON, C. LAVERGNE, C. TROTTIER. *Markov and semi-Markov switching linear mixed models used to identify forest tree growth components*, in "Biometrics", sept 2010, vol. 66, n° 3, pp. 753–762, http://www-sop.inria.fr/virtualplants/Publications/2010/CGLT10

[5] R. FERNANDEZ, P. DAS, V. MIRABET, E. MOSCARDI, J. TRAAS, J.-L. VERDEIL, G. MALANDAIN, C. GODIN. *Imaging plant growth in 4D: robust tissue reconstruction and lineaging at cell resolution*, in "Nature Methods", jul 2010, vol. 7, pp. 547–553, http://www-sop.inria.fr/virtualplants/Publications/2010/FDMMTVMG10

[6] C. GODIN, P. FERRARO. *Quantifying the degree of self-nestedness of trees: application to the structural analysis of plants*, in "IEEE/ACM Transactions in Computational Biology and Bioinformatics", 2010, vol. 7, pp. 688–703, http://www-sop.inria.fr/virtualplants/Publications/2010/GF10

[7] C. PRADAL, F. BOUDON, C. NOUGUIER, J. CHOPARD, C. GODIN. *PlantGL : a Python-based geometric library for 3D plant modelling at different scales*, in "Graphical Models", jan 2009, vol. 71, n° 1, pp. 1–21, http://www-sop.inria.fr/virtualplants/Publications/2009/PBNCG09

[8] C. PRADAL, S. DUFOUR-KOWALSKI, F. BOUDON, C. FOURNIER, C. GODIN. *OpenAlea: A visual programming and component-based software platform for plant modeling*, in "Functional Plant Biology", 2008, vol. 35, no 9 & 10, pp. 751–760, http://www-sop.inria.fr/virtualplants/Publications/2008/PDBFG08a

[9] S. STOMA, M. LUCAS, J. CHOPARD, M. SCHEADEL, J. TRAAS, C. GODIN. *Flux-based Transport Enhancement as a Plausible Unifying Mechanism for Auxin Transport in Meristem Development*, in "PLOS Computational Biology", 2008, vol. 4, no 10, http://www-sop.inria.fr/virtualplants/Publications/2008/SLCSTG08

[10] T. VERNOUX, G. BRUNOUD, E. FARCOT, V. MORIN, H. VAN DEN DAELE, J. LEGRAND, M. OLIVA, P. DAS, A. LARRIEU, D. WELLS, Y. GUÉDON, L. ARMITAGE, F. PICARD, S. GUYOMARC'H, C. CELLIER, G. PARRY, R. KOUMPROGLOU, J. DOONAN, M. ESTELLE, C. GODIN, S. KEPINSKI, M. J. BENNETT, L. DE VEYLDER, J. TRAAS. *The auxin signalling network translates dynamic input into robust patterning at the shoot apex*, in "Molecular Systems Biology", 2011, vol. 7, no 508, http://www-sop.inria.fr/virtualplants/Publications/2011/VBFMVLODLWGAPGCPKDEG

Publications of the year

Doctoral Dissertations and Habilitation Theses

[11] P. FERNIQUE. *A statistical modeling framework for analyzing tree-indexed data*, Universite de Montpellier 2, December 2014, https://tel.archives-ouvertes.fr/tel-01095420

Articles in International Peer-Reviewed Journals

[12] O. ALI, V. MIRABET, C. GODIN, J. TRAAS. *Physical Models of Plant Development*, in "Annual Review of Cell and Developmental Biology", October 2014, vol. 30, no 1, 8 p. [*DOI :* 10.1146/ANNUREV-CELLBIO-101512-122410], https://hal.inria.fr/hal-01090778

[13] R. BARILLOT, J. ESCOBAR-GUTIERREZ, C. FOURNIER, P. HUYNH, D. COMBES. *Assessing the effects of architectural variations on light partitioning within virtual wheat – pea mixtures*, in "Annals of Botany", June 2014, vol. 114, no 4, 13 p. [*DOI :* 10.1093/AOB/MCU099], https://hal.inria.fr/hal-01095288

[14] J.-P. BERNARD, E. FRENOD, A. ROUSSEAU. *Paralic confinement computations in coastal environment with interlocked areas*, in "Discrete and Continuous Dynamical Systems - Series S", February 2015, vol. 8, no 1, pp. 45-54 [*DOI :* 10.3934/DCDSS.2015.8.45], https://hal.archives-ouvertes.fr/hal-00833340

[15] F. BESNARD, Y. REFAHI, V. MORIN, B. MARTEAUX, G. BRUNOUD, P. CHAMBRIER, F. ROZIER, V. MIRABET, J. LEGRAND, S. LAINÉ, E. THÉVENON, E. FARCOT, C. CELLIER, P. DAS, A. BISHOPP, R. DUMAS, F. PARCY, Y. HELARIUTTA, A. BOUDAOUD, C. GODIN, J. TRAAS, Y. GUÉDON, T. VERNOUX. *Cytokinin signalling inhibitory fields provide robustness to phyllotaxis*, in "Nature", 2014, vol. 505, no 7483, pp. 417-421 [*DOI :* 10.1038/NATURE12791], https://hal.inria.fr/hal-00926908

[16] F. BOUDON, C. PREUKSAKARN, P. FERRARO, J. DIENER, P. NACRY, E. NIKINMAA, C. GODIN. *Quantitative assessment of automatic reconstructions of branching systems obtained from laser scanning*, in "Annals of Botany", April 2014, epub ahead of print [*DOI :* 10.1093/AOB/MCU062], https://hal.archives-ouvertes.fr/hal-01064917

[17] R. CHOQUET, A. BÉCHET, Y. GUÉDON. *Applications of hidden hybrid Markov/semi-Markov models: from stopover duration to breeding success dynamics*, in "Ecology and Evolution", 2014, vol. 4, no 6, pp. 817 - 826 [*DOI :* 10.1002/ECE3.962], https://hal.inria.fr/hal-01084498

[18] A. Dambreville, P.-É. Lauri, F. Normand, Y. Guédon. *Analysing growth and development of plants jointly using developmental growth stages*, in "Annals of Botany", 2015, vol. 115, n° 1, 13 p. [*DOI :* 10.1093/AOB/MCU227], https://hal.inria.fr/hal-01100553

[19] J.-B. Durand, Y. Guédon. *Localizing the latent structure canonical uncertainty: entropy profiles for hidden Markov models*, in "Statistics and Computing", 2014, 19 p. , The final publication is available at Springer via http://dx.doi.org/10.1007/s11222-014-9494-9 [*DOI :* 10.1007/S11222-014-9494-9], https://hal.inria.fr/hal-01090836

[20] J. Dutra Schmitz, Y. Guédon, F. G. Herter, G. B. Leite, P.-E. Lauri. *Exploring bud dormancy completion with a combined architectural and phenological analysis: the case of the apple tree in contrasting winter temperature conditions*, in "American Journal of Botany", 2014, vol. 101, pp. 398 - 407 [*DOI :* 10.3732/AJB.1300335], https://hal.inria.fr/hal-01089580

[21] G. Garin, C. Fournier, B. Andrieu, V. Houlès, C. Robert, C. Pradal. *A modelling framework to simulate foliar fungal epidemics using functional–structural plant models*, in "Annals of Botany", 2014, mcu101 [*DOI :* 10.1093/AOB/MCU101], https://hal.inria.fr/hal-01025689

[22] S. Kenouche, M. Perrier, N. Bertin, J. Larionova, A. Ayadi, M. Zanca, J. Long, N. Bezzi, P. C. Stein, Y. Guari, M. Cieslak, C. Godin, C. Goze-Bac. *In vivo quantitative NMR imaging of fruit tissues during growth using Spoiled Gradient Echo sequence*, in "Magnetic Resonance Imaging", September 2014, n[o] 32, pp. 1418-1427 [*DOI :* 10.1016/J.MRI.2014.08.005], https://hal.archives-ouvertes.fr/hal-01065440

[23] D. Muraro, N. Mellor, M. P. Pound, H. Help, M. Lucas, J. Chopard, H. M. Byrne, C. Godin, T. C. Hodgman, J. R. King, T. P. Pridmore, Y. Helariutta, M. J. Bennett, A. Bishopp. *Integration of hormonal signaling networks and mobile microRNAs is required for vascular patterning in Arabidopsis roots*, in "Proceedings of the National Academy of Sciences U S A", 2014, vol. 111, n° 2, pp. 857-862 [*DOI :* 10.1073/PNAS.1221766111], https://hal.inria.fr/hal-00941028

[24] C. Negrón, L. Contador, B. D. Lampinen, S. G. Metcalf, Y. Guédon, E. Costes, T. M. DeJong. *Differences in proleptic and epicormic shoot structures in relation to water deficit and growth rate in almond trees (Prunus dulcis)*, in "Annals of Botany", 2014, vol. 113, n° 3, pp. 545–554 [*DOI :* 10.1093/AOB/MCT282], https://hal.inria.fr/hal-01084462

[25] M. Sassi, O. Ali, F. Boudon, G. Cloarec, U. Abad, C. Cellier, X. Chen, B. Gilles, P. Milani, J. Friml, T. Vernoux, C. Godin, O. Hamant, J. Traas. *An Auxin-Mediated Shift toward Growth Isotropy Promotes Organ Formation at the Shoot Meristem in Arabidopsis*, in "Current Biology", October 2014, vol. 24, n° 19, pp. 1 - 8 [*DOI :* 10.1016/J.CUB.2014.08.036], https://hal.inria.fr/hal-01074821

[26] R. Sievänen, C. Godin, T. De Jong, E. Nikinmaa. *Functional – structural plant models: a growing paradigm for plant studies*, in "Annals of Botany", 2014, pp. 599-603 [*DOI :* 10.1093/AOB/MCU175], https://hal.inria.fr/hal-01075790

[27] J. Starlinger, B. Brancotte, S. Cohen-Boulakia, U. Leser. *Similarity Search for Scientific Workflows*, in "Proceedings of the VLDB Endowment (PVLDB)", September 2014, 12 p. , https://hal.inria.fr/hal-01066046

[28] O. Taugourdeau, Y. Caraglio, S. Sabatier, Y. Guédon. *Characterizing the respective importance of ontogeny and environmental constraints in forest tree development using growth phase duration distributions*,

in "Ecological Modelling", 2015, vol. 300, pp. 61 - 72 [*DOI :* 10.1016/J.ECOLMODEL.2014.12.022], https://hal.inria.fr/hal-01110350

[29] J. ZHU, B. ANDRIEU, J. VOS, W. VAN DER WERF, C. FOURNIER, J. B. EVERS. *Towards modelling the flexible timing of shoot development: simulation of maize organogenesis based on coordination within and between phytomers*, in "Annals of Botany", April 2014, vol. 114, n° 4, 10 p. [*DOI :* 10.1093/AOB/MCU051], https://hal.inria.fr/hal-01096700

International Conferences with Proceedings

[30] J.-P. BERNARD, B. GILLES, C. GODIN. *Combining Finite Element Method and L-Systems Using Natural Information Flow Propagation to Simulate Growing Dynamical Systems*, in "Theory and Practice of Natural Computing", Granada, Spain, C. M.-V. ADRIAN-HORIA DEDIU (editor), Springer, December 2014, vol. 8890, pp. 218 - 230 [*DOI :* 10.1007/978-3-319-13749-0_19], https://hal.inria.fr/hal-01096602

[31] G. CERUTTI, C. GODIN. *Meshing Meristems - An Iterative Mesh Optimization Method for Modeling Plant Tissue at Cell Resolution*, in "BIOIMAGING", Lisbonne, Portugal, January 2015, https://hal.archives-ouvertes.fr/hal-01100808

[32] J.-B. DURAND, Y. GUÉDON. *Quantifying and localizing state uncertainty in hidden Markov models using conditional entropy profiles*, in "COMPSTAT 2014 - 21st International Conference on Computational Statistics", Genève, Switzerland, M. GILLI, G. GONZÁLEZ-RODRÍGUEZ, A. NIETO-REYES (editors), Université de Genève, August 2014, pp. 213-221, ISBN 978-2-8399-1347-8. Please check publisher, https://hal.inria.fr/hal-01058278

[33] P. FERNIQUE, J.-B. DURAND, Y. GUÉDON. *Estimation of Discrete Partially Directed Acyclic Graphical Models in Multitype Branching Processes*, in "COMPSTAT 2014, 21st International Conference on Computational Statistics", Geneva, Switzerland, The International Association for Statistical Computing (IASC), August 2014, https://hal.inria.fr/hal-01084524

[34] P. FERNIQUE, J.-B. DURAND, Y. GUÉDON. *Learning Discrete Partially Directed Acyclic Graphical Models in Multitype Branching Processes*, in "COMPSTAT 2014 - 21st International Conference on Computational Statistics", Genève, Switzerland, M. GILLI, G. GONZÁLEZ-RODRÍGUEZ, A. NIETO-REYES (editors), Université de Genève, August 2014, pp. 579-586, ISBN 978-2-8399-1347-8, https://hal.inria.fr/hal-01058284

[35] L. GUIGNARD, C. GODIN, U.-M. FIUZA, L. HUFNAGEL, P. LEMAIRE, G. MALANDAIN. *Spatio-temporal registration of embryo images*, in "ISBI - International Symposium on Biomedical Imaging", Pekin, China, IEEE, April 2014, https://hal.inria.fr/hal-00919142

[36] G. MICHELIN, L. GUIGNARD, U.-M. FIUZA, G. MALANDAIN. *Embryo Cell Membranes Reconstruction by Tensor Voting*, in "ISBI - International Symposium on Biomedical Imaging", Beijing, China, IEEE, April 2014, https://hal.inria.fr/hal-00915000

[37] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *Modèles de références de régression multinomiale. Propriétés et applications en classification supervisée*, in "46 ème journée de Statistique", Rennes, France, June 2014, https://hal.inria.fr/hal-01101058

[38] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *Partitioned conditional generalized linear models for categorical data*, in "29th International Workshop on Statistical Modelling (IWSM 2014)", Göttingen, Germany, Statistical Modelling Society, July 2014, vol. 1, https://hal.inria.fr/hal-01084505

[39] J. STARLINGER, S. COHEN-BOULAKIA, S. KHANNA, S. DAVIDSON, U. LESER. *Layer Decomposition: An Effective Structure-based Approach for Scientific Workflow Similarity*, in "IEEE e-Science conference", Guarujá, Brazil, October 2014, https://hal.inria.fr/hal-01066076

National Conferences with Proceedings

[40] J.-B. DURAND, Y. GUÉDON. *Quantification de l'incertitude sur la structure latente dans des modèles de Markov cachés*, in "46èmes Journées de Statistique", Rennes, France, June 2014, https://hal.inria.fr/hal-01058317

[41] P. FERNIQUE, J.-B. DURAND, Y. GUÉDON. *Modèles graphiques paramétriques pour la modélisation des lois de génération dans des processus de branchement multitypes*, in "46èmes Journées de Statistique", Rennes, France, June 2014, https://hal.inria.fr/hal-01058313

Scientific Books (or Scientific Book chapters)

[42] J. GUÉNARD, G. MORIN, F. BOUDON, V. CHARVILLAT. *Realistic Plant Modeling from Images Based on Analysis-by-Synthesis*, in "Mathematical Methods for Curves and Surfaces", M. FLOATER, T. LYCHE, M.-L. MAZURE, K. MØRKEN, L. SCHUMAKER (editors), Lecture Notes in Computer Science, Springer-Verlag, 2014, vol. 8177, pp. 213-229 [*DOI : 10.1007/978-3-642-54382-1_12*], https://hal.inria.fr/hal-01089744

Other Publications

[43] B. MORENO-ORTEGA, E. CHANDEZON, G. FORT, Y. GUÉDON, B. MULLER. *Why is lateral root growth so variable? A framework to analyze growth variability among lateral roots and the possible roles of auxin and carbon*, September 2014, 7th International Symposium on Root Development, https://hal.inria.fr/hal-01090030

[44] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *A new specification of generalized linear models for categorical data*, April 2014, 31 pages, 13 figures, https://hal.inria.fr/hal-00985595

[45] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *Partitioned conditional generalized linear models for categorical data*, January 2015, 25 pages, 13 figures, https://hal.inria.fr/hal-01101036

References in notes

[46] A. ARBER. *Natural philosophy of plant form*, University Press, Cambridge, 1950

[47] L. BAND, J. FOZARD, C. GODIN, O. JENSEN, T. PRIDMORE, M. BENNETT, J. KING. *Multiscale systems analysis of root growth and development: modeling beyond the network and cellular scales*, in "The Plant Cell", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/BFGJPBK12

[48] D. BARTHELEMY, Y. CARAGLIO, E. COSTES. *Architecture, gradients morphogntiques et âge physiologique chez les vgtaux*, in "Modélisation et Simulation de l'Architecture des Végétaux", J. BOUCHON, P. DE REFFYE, D. BARTHELEMY (editors), INRA, 1997, pp. 89-136

[49] M. Cieslak, M. Génard, F. Boudon, V. Baldazzi, C. Godin, N. Bertin. *Integrating architecture and physiological perspectives in fruit development*, in "7th International Conference on Functional-Structural Plant Models", Saariselkä, Finland, R. Sievänen, E. Nikinmaa, C. Godin, A. Lintunen, P. Nygren (editors), June 2013, pp. 127-130, ISBN 978-951-651-408-9, http://hal.inria.fr/hal-00850801

[50] L. E. Gatsuk, O. V. Smirnova, L. I. Vorontzova, L. B. Zaugolnova, L.A. Zhukova. *Age states of plants of various growth forms: a review*, in "Journal of Ecology", 1980, vol. 68, pp. 675-696

[51] C. Godin, Y. Caraglio. *A multiscale model of plant topological structures*, in "Journal of Theoretical Biology", 1998, vol. 191, pp. 1-46, http://www-sop.inria.fr/virtualplants/Publications/1998/GC98

[52] C. Godin, E. Costes, H. Sinoquet. *A method for describing plant architecture which integrates topology and geometry*, in "Annals of Botany", 1999, vol. 84, pp. 343-357

[53] Y. Guédon, Y. Refahi, F. Besnard, E. Farcot, C. Godin, T. Vernoux. *Pattern identification and characterization reveal permutations of organs as a key genetically controlled property of post-meristematic phyllotaxis*, in "Journal of Theoretical Biology", 2013 [*DOI :* 10.1016/J.JTBI.2013.07.026], http://hal.inria.fr/hal-00859831

[54] F. Hallé, R. A. A. Oldeman, P. B. Tomlinson. *Tropical trees and forests. An architectural analysis*, Springer-Verlag, New-York, 1978

[55] J. L. Harper, B. R. Rosen, J. White. *The growth and form of modular organisms*, The Royal Society, London, UK, 1986

[56] C. La Rota, J. Chopard, P. Das, S. Paindavoine, F. Rozier, E. Farcot, C. Godin, J. Traas, F. Monéger. *A data-driven integrative model of sepal primordium polarity in Arabidopsis.*, in "The Plant cell", December 2011, vol. 23, n° 12, pp. 4318–4333

[57] M. Lucas, K. Kenobi, D. Von Wangenheim, U. Voss, K. Swarup, I. De Smet, D. Van Damme, T. Lawrence, B. Péret, E. Moscardi, D. Barbeau, C. Godin, D. Salt, S. Guyomarc'h, E. H. K. Stelzer, A. Maizel, L. Laplaze, M. J. Bennett. *Lateral root morphogenesis is dependent on the mechanical properties of the overlaying tissues*, in "Proceedings of the National Academy of Sciences", March 2013, vol. 110, n° 13, pp. 5229-34 [*DOI :* 10.1073/PNAS.1210807110], http://hal.inria.fr/cea-00848569

[58] J. Murray, A. Jones, C. Godin, J. Traas. *Systems analysis of shoot apical meristem growth and development: integrating hormonal and mechanical signaling*, in "The Plant Cell", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/MJGT12

[59] R. Nozeran. *Integration of organismal development*, in "Positional controls in plant development", P. Barlow, D. Carr (editors), 1984, pp. 375-401

[60] Y. Refahi, E. Farcot, Y. Guédon, F. Besnard, T. Vernoux, C. Godin. *A Combinatorial Model of Phyllotaxis Perturbations in Arabidopsis thaliana*, in "22nd Annual Symposium on Combinatorial Pattern Matching, Palermo, Italy", Palermo, Italy, Lecture Notes in Computer Science - LNCS, 2011, vol. 6661, pp. 323–335, https://hal.inria.fr/hal-00828852

[61] H. Sinoquet, P. Rivet, C. Godin. *Assessment of the three-dimensional architecture of walnut trees using digitizing*, in "Silva Fennica", 1997, vol. 3, pp. 265–273