

Activity Report 2012

Project-Team virtual plants

Modeling plant morphogenesis at different scales, from genes to phenotype

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

RESEARCH CENTER
Sophia Antipolis - Méditerranée

THEME Computational Biology

Table of contents

1.	Members	<u>1</u>			
2.	Overall Objectives				
	2.1. Introduction				
	2.2. Highlights of the Year				
3.	Research Program	<mark>3</mark>			
	3.1. Analysis of structures resulting from meristem activity	3			
	3.2. Meristem functioning and development	4			
	3.3. OpenAlea: An open-software platform for plant modeling				
4.	Software and Platforms	5			
	4.1. V-Plants	5			
	4.2. OpenAlea	5			
	4.3. Alinea	7			
5.	New Results	<mark>8</mark>			
	5.1. Analysis of structures resulting from meristem activity	8			
	5.1.1. Acquisition and design of plant geometry	8			
	5.1.2. Modeling the plant ontogenic program	11			
	5.1.3. Analyzing the influence of the environment on the plant ontogenic program	14			
	5.2. Meristem functioning and development	15			
	5.2.1. Data acquisition and design of meristem models	15			
	5.2.2. Shape analysis of meristems	17			
	5.2.3. Transport models	17			
	5.2.4. Mechanical model	18			
	5.2.5. Gene regulatory networks	18			
	5.2.6. Model integration	20			
	5.3. Multi-scale models and analysis: from cells to plant architecture (and back)	20			
	5.3.1. Transport model in roots	20			
	5.3.2. Transport in fruits	21			
	5.3.3. Analazing shoot and leaf elongation	22			
	5.3.4. Analyzing perturbations in Arabidopsis thaliana phyllotaxis	22			
6.	Partnerships and Cooperations	<u>23</u>			
	6.1. Regional Initiatives	23			
	6.1.1. OpenAlea	23			
	6.1.2. Fruit3D	23			
	6.1.3. PlantScan3D	23			
	6.1.4. Agropolis computational plant seminar	24			
	6.1.5. Rhizopolis	24			
	6.2. National Initiatives	24			
	6.2.1. ANR	24			
	6.2.1.1. Morpholeaf	24			
	6.2.1.2. HydroRoot	25			
	6.2.2. Other national grants	25			
	6.2.2.1. OpenAlea 2.0	25			
	6.2.2.2. Echap	25			
	6.2.2.3. Morphogenetics	26			
	6.2.2.4. Rose	26			
	6.3. International Bilateral Relations	26			
	6.3.1. ERASysBio+ iSAM	26			
	6.3.2. Other bilateral relations	27			
	6.4. International Initiatives	27			

	6.5. Inte	ernational Research Visitors	27
	6.5.1.	Visits of International Scientists	27
	6.5.2.	Visits to International Teams	28
7.	Dissemina	ation	28
	7.1. Sci	entific Animation	28
	7.2. Teaching - Supervision - Juries		29
	7.2.1.	Teaching	29
	7.2.2.	Supervision	29
	7.2.3.	Juries	30
	7.3. Pop	pularization	30
8.	Bibliogra	phy	30

Project-Team virtual plants

Keywords: Modeling, Plant Development, Systems Biology, Markovian Model, Data Analysis, 3d Modeling, Biological Images, Domain-specific Languages

Creation of the Project-Team: 2007 July 01.

1. Members

Research Scientists

Christophe Godin [DR, Team Leader, HdR]

Yann Guédon [DR, CIRAD, vice-Head, HdR]

Christophe Pradal [IR, CIRAD]

Frédéric Boudon [CR, CIRAD]

Etienne Farcot [CR]

Christian Fournier [IR, INRA, part time]

External Collaborators

Jean-Baptiste Durand [MC, on leave from ENSIMAG and LJK/Mistis]

Marc Béziz [Professeur de lycée, mathématiques]

Christian Cilas [DR, CIRAD, HdR]

Evelyne Costes [DR, INRA, HdR]

Laurent Laplaze [DR, IRD, HdR]

Patrick Lemaire [DR, CNRS, HdR]

Grégoire Malandain [DR, Inria Sophia-Antipolis, HdR]

François Parcy [DR, CNRS, HdR]

Jan Traas [DR, INRA, HdR]

Teva Vernoux [CR, CNRS, HdR]

Christine Granier [DR, INRA, HdR]

Farah Ben Naoum [MC, Université Djillali Liabès]

Frédéric Normand [DR, CIRAD, HdR]

Engineer

Julien Coste [Junior Engineer, ADT Inria]

PhD Students

Mathilde Balduzzi [Labex Numev Grant, Montpellier 2 University, Computer Science, 2012]

Anaëlle Dambreville [CIRAD Grant, Biology, 2012]

Chakkrit Preuksakarn [Grant from University of Kasetsar, Bangkok, Thailand, Computer Science, 2012]

Jonathan Legrand [ENS Lyon Grant, Biology, 2013]

Jean Peyhardi [Montpellier 2 University Grant, Statistics, 2013]

Pierre Fernique [CIRAD/Montpellier 2 University Grant, Statistics, 2014]

Léo Guignard [Montpellier 2 University Grant, Computer Science, 2014]

Maryline Lièvre [CIFRE INRA/Bayer Grant, biology, 2014]

Jean-Philippe Bernard [Inria Action d'envergure Grant (Morphogenetics), Computer Science, 2015]

Guillaume Garin [CIFRE INRA/ITK Grant, biology, 2015]

Post-Doctoral Fellows

Mik Cieslak [Agropolis fundation Grant (Fruit3D), Montpellier]

Julien Diener [Agropolis fundation Grant (Rhizopolis), Montpellier]

Michael Walker [Geneshape/iSam Grant, Inria, Montpellier]

Olivier Ali [ERC Grant (Morphodynamics), Montpellier]

Yassin Refahi [INRA/Inria Grant, Computer Science, Cambridge and Montpellier]

Administrative Assistants

Geneviève Carrière [Inria, part time] Valérie Caruana [CIRAD, part time]

2. Overall Objectives

2.1. Introduction

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

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

This study is performed from two complementary perspectives.

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

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

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

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

2.2. Highlights of the Year

- Move of the team to a new campus to join other Inria teams. Until this year, the team was located at the Cirad Lavalette campus in Montpellier. In May 2012, it moved to the Maison de la Modélisation pour le vivant et l'environnement in Montpellier close to the campus of Computer Science research (LIRMM). This move is intended to strengthen the presence of Inria in Montpellier by gathering several Inria teams at the same place, fostering interactions between them and consequently augment the visibility of Inria in the region. It is also meant to support the creation of the Computational Biology Institute of Montpellier, IBC, that succeeded to the national call on investissements d'avenir of ANR, and in which both Zenith and Virtual Plants Inria teams are strongly involved.
- Acceptation of the Inria Large Scale Initiative Morphogenetics. The Inria action d'envergure Morphognetics was evaluated by Inria and accepted. The project gathers 3 Inria teams (Imagine, Morpheme and Virtual Plants) from 2 Inria centers (Rhône-Alpes and Sophia-Antipolis-Méditerranée) and 2 Inra teams (RDP and RFD) from Lyon an Grenoble respectively to address the problem of flower development at early stages. The kick-off meeting of the project was held in November in Montpellier. The project will last 4 years and will focus in particular on the modelling of meristem mechanics during the early phases of organogenesis and how it is related to genes.

- **First paper on L-Py published.** The first paper describing our simulation system language *L-Py* has been published in Frontiers in Plant Science. The maturity and the diffusion of this software module increases and is now the basis of the work of several groups worldwide. Several training sessions have been organized by the team in the last two years and will be at the core of the future training program proposed by the Virtual Plants team on plant modeling.
- Completion of a series of papers on tree development analysis using various types of stochastic processes. Understanding tree development over several years has been the object of active research since about 10 years. This has generated the development of integrative models for analyzing tree growth components (ontogeny, climate and local environment influence) and patterns, in particular models combining latent state variables, tree response variables and environmental explanatory variables but also individual and population parameters [39] [2]. This approach has been applied to forest and fruit trees, to tropical and temperate species growing in various conditions (orchard, managed forest stand and unmanaged forest understory) [7] [49], [16].

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

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

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

4. Software and Platforms

4.1. V-Plants

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

Computer algorithms and tools developed by the Virtual Plants team are integrated in a common software suite *V-Plants*, dedicated to the modeling and analysis of plant development at different scales (e.g. cellular tissue, whole plant, stand). The VPlants packages are integrated in OpenAlea as Python components. Several components are distributed and usable through the visual programming environment (see figure 2):

- Multi-scale geometric modeling and visualization. VPlants.PlantGL is a geometric library which
 provides a set of graphical tools and algorithms for 3D plant modeling at different scales [9]. It is
 used by many other components to represent the geometry of biological shapes from 3D meristems,
 plant architectures to plant populations. VPlants.PlantGL is built around a scene-graph data structure
 and provides efficient algorithms and original geometrical shapes (parametric surfaces, dedicated
 envelops), that are useful for plant modeling.
- Statistical sequence and tree analysis. Different statistical packages (i.e. VPlants.StatTool, VPlants.SequenceAnalysis, VPlants.TreeMatching and VPlants.TreeAnalysis) are now available in OpenAlea. They provide different models and algorithms for plant architecture analysis and simulation.
- Meristem functioning and development. A first set of components has been created in the last 4-years
 period to model meristem development in OpenAlea. These tools are currently being integrated
 thoroughly in the platform so that modelers and biologists can use them, and reuse components
 easily (for meristem 3D reconstruction, cell tracking, statistical analysis of tissues, creating and
 manipulating atlases, creating or loading models of growth that can further be run on digitized
 structures, etc).
- Standard data structure for plants. A new implementation of the MTG formalism for representing and manipulating multiscale plant architecture has been developed. It provides a central data-structure to represent plants in a generic way in OpenAlea. This implementation is available through the packages OpenAlea.MTG. These components make it possible to share plant representations between users and fosters the interoperability of new models.
- Simulation system. The study of plant development requires increasingly powerful modeling tools to help understand and simulate the growth and functioning of plants. In the last decade, the formalism of L-systems has emerged as a major paradigm for modeling plant development. Previous implementations of this formalism were made based on static languages, i.e. languages that require explicit definition of variable types before using them. These languages are often efficient but involve quite a lot of syntactic overhead, thus restricting the flexibility of use for modelers. We developed L-Py an adaptation of L-systems to the Python language (basis of OpenAlea). Thanks to its dynamic typing property, syntax is simple, code execution is made easy and introspection property of the language makes it possible to parameterize and manipulate simply complex models. Independent L-systems can be composed to build-up more complex modular models. MTG structures (that are a common way to represent plants at several scales) can be translated back and forth into L-system data-structure and thus make it easy to reuse in L-systems tools for the analysis of plant architecture based on MTGs. Extensions to integrate multiscale dynamic models are currently being developed in collaboration with P. Prusinkiewicz and his team from the University of Calgary. A paper presenting L-Py [14] has been published to Frontiers in Technical Advances in Plant Sciences.

4.2. OpenAlea

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

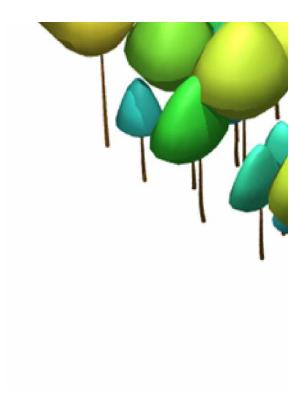


Figure 1. V-Plants components of the OpenAlea platform: simulating plant processes at different scales. Top Left: Reconstruction of a virtual meristem, analysis and simulation of the auxin fluxes inside the meristem. Top Right: Reconstruction of a virtual apple tree from digitized data. Bottom: Simulation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

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

OpenAlea[10] is an open source and collaborative software project primarily dedicated to the plant research community. It is designed as a component framework to dynamically glue together models from different plant research labs, and to enhance re-usability of existing models in the plant research community.

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

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

In 2012, one major release was done: Openalea 1.0. The following progresses were accomplished:

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

2. Animation and diffusion

- The first OpenAlea Workshop have been held in Montpellier and has been attended by more than 60 scientists. A scientific board has been defined to manage the development and diffusion of OpenAlea. It is composed by 12 scientists.
- StandAlone binary installers have been released on Windows and Mac to ease the installation of a large number of packages without relying on a web server. A Ubuntu repository has been set up on Launchpad.
- A continuous integration server has been set up To test the reliability of all the components after every commit.
- The OpenAlea project is hosted at the Inria gforge (link http://openalea.gforge.inria.fr). The web site is visited by more than 370 unique visitor each month; 650000 web pages have been visited and the different available components of OpenAlea have been downloaded more than 520,000 times during the last two years. OpenAlea is the first project at Inria Gforge in term of number of downloads and of page views.

4.3. Alinea

Participants: Christian Fournier, Christophe Pradal, Frédéric Boudon, Christophe Godin.

Other participants: Bruno Andrieu, Michael Chelle, Gaetan Louarn, Benoit de Solan, Mariem Abichou, Liqi Han, Elmer Ccopa-Rivera, Frederic Baret, Rafaele Casa, Youcef Mammeri, Didier Combes, Camille Chambon, Romain Barillot, Pierre Huynh, Jean-Christophe Soulie, Delphine Luquet.

The aim of this Action Ciblée Incitative of INRA is to constitute a consortium of modelers from INRA around the OpenAlea platform, and to integrate various ecophysiological models of simulation in OpenAlea (radiative transfer, interaction between plant and pest, circulation of hydric fluxes, and dispersion). The project includes 3 INRA teams and the Inria Virtual Plants project.

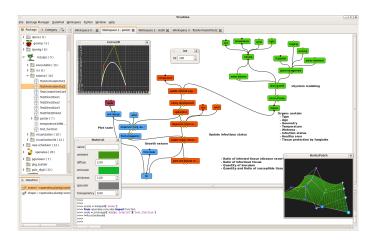


Figure 2. OpenAlea. Visualea: Visual programming interface. The package manager shows the available components. The components can be interconnected on a workspace to form a data-flow. The python interpreter allows low level interaction with the system.

Different components have been integrated into the OpenAlea platform:

- Alinea. Adel is a module to simulate the 3D architectural development of gramineous crops.
- Alinea.Caribu is a modeling suite for lighting 3D virtual scenes, especially designed for the
 illumination of virtual plant canopies such as virtual crop fields. It uses a special algorithm, the
 nested radiosity, that allows for a precise estimation of light absorption at the level of small canopy
 elements.
- Alinea. Top Vine is a component to reconstruct grapevine canopy structure.
- Ecomeristem is a crop growth, eco-physiological model that was designed for rice (model plant for cereals) to account for plant morphogenesis and its plasticity depending on genetic potential and sensitivity to the environment (water, temperature, radiation).
- Alinea.Nema is a module used for modeling of nitrogen dynamics between leaves.
- MAppleT is a FSPM model of an apple tree taking into account stochastic models for the topological development, a biomechanical model for branch bending, physiological laws as well as light interception.
- M2A3PC is a generic model to simulate spread of a pathogen on a growing plant like vine/powdery mildew and apple tree/apple scab.

In 2012, a 3D model of gramineous leave has been developped and presented at the PMA conference [28]. This dynamic leaf model is used to simulate different species of annual plants such as rice, wheat and maïze.

5. New Results

5.1. Analysis of structures resulting from meristem activity

5.1.1. Acquisition and design of plant geometry

Participants: Chakkrit Preuksakarn, Mathilde Balduzzi, Frédéric Boudon, Christophe Pradal, Christophe Godin, Christian Fournier.

This research theme is supported by RTRA project named PlantScan3D.

Virtual 3D model of plants are required in many areas of plant modeling. They can be used for instance to simulate physical interaction of real plant structures with their environment (light, rain, wind, pests, ...), to set up initial conditions of growth models or to assess their output against real data. In the past decade, methods have been developed to digitize plant architectures in 3D [48], [42]. These methods are based on direct measurements of position and shape of every plant organ in space. Although they provide accurate results, they are particularly time consuming. More rapid and automated methods are now required in order to collect plant architecture data of various types and sizes in a systematic way. In this aim, we explore the use of pictures, laser scanner, video and direct sketching.

Automated reconstruction of plant architecture (Chakkrit Preuksakarn, Mathilde Balduzzi, Julien Diener, Frédéric Boudon, Jean-Baptiste Durand, Christophe Godin, Bernard Mourrain [Inria, Galaad], Franck Hetroy [Inria, Morpheus], Marie-Paule Cani [Inria, Imagine], Pascal Ferraro [Labri, Bordeaux])

We investigate the possibility to use 3D laser scanners to automate plant digitizing. We are developping 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 this we collaborate with the EPI Galaad from Sophia-Antipolis, the EPI Imagine from Grenoble, different INRA teams, UMR PIAF in Clermont Ferrand, UMR LEPSE and AFEF team in Montpellier and Lusignan, the University of Helsinki, Finland and the CFCC in England. We developed a reconstruction pipeline composed of several procedures. A contraction procedure, first aggregates points at the center of the point cloud. The team proposed a simple adaptive scheme to contract points. In a second step, a skeleton procedure uses a Space Colonization Algorithm [47] to build the skeleton of the shape from the contracted point set. This method is adaptive to the local density of the point set. Then a pipe-model based procedure makes it possible to estimate locally diameters of the branches. Finally, an evaluation procedure has been designed to assess the accuracy of the reconstruction and a comparison with alternative methods has been carried out. Publication of this work is in progress.



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

An automated reconstruction pipeline is also developed for processing 2D images of root system architecture (RSA) in the context of the Rhizopolis project. The analysis of these data is currently a major challenge in understanding root development. Existing tools either focus on specific applications, on simple structures (for example one root segment) or require long manual work. Here, we develop a processing pipeline that takes as an input 2D high resolution images of petri plates containing root systems. The pipeline makes it possible to extract from the images the whole architecture of root systems, with minimal or no user intervention. In order to obtain this result,

the problem was decomposed in several steps: filter and label the input image, extract the image skeleton as a general graph structure and then convert it into a tree structure representing the visualised RSA, using a priori knowledge to solve inconsistencies. The pipeline has been added to the OpenAlea platform, thus allowing resulting data to be directly processed by other advanced high-level computational or statistical tools. The developed pipeline is currently being tuned and tested on several databases of 2D images with varying complexities of both arabidopsis and rice.

Additionnally, we also investigate the reconstruction of tree foliage from laser scanners in the context of Mathild Balduzzi's PhD thesis. Such elements are crucial to study the interaction of the plant with its environment. However, laser scans contain outliers on the silhouette of the scans that make the meshing of the point set difficult. New generation of laser scanners provides intensity of the laser reflected) on the surface of scanned objects. This intensity is dependant of the distance to the object, its optical property and the incidence angle. A first work on this topic shows that after correcting the distance effect, the incidence angle can be deduced from the intensity. From this result, we develop a reconstruction technique using the scan intensities and based on Shape-From-Shading approaches. The idea is to generate a new point set from the intensities and a set of seed points. This new point set has the property of being smooth but is not necessarly the exact representation of the scanned object. To consolidate the reconstruction, we are working on merging it with the orignal noisy point set coming from the scans using Kalman filtering. As a result, a final point set will be obtained without noise and with outiers naturally removed.

• Sketching of plants. (Frédéric Boudon, Christophe Godin, Steven Longuay [University of Calgary, Canada], Przemyslaw Prusinkiewicz [University of Calgary, Canada])

Modeling natural elements such as trees in a plausible way, while offering simple and rapid user control, is a challenge. In a first collaboration with the EPI Imagine (ex-Evasion) we developed a method based on the design of plants from silhouettes [50]. This sketching paradigm allows quick and intuitive specification of foliage at multiple scales. On this topic, we started a collaboration with S. Longuay and P. Prusinkiewicz who develop iPad tools to design plants based on SCA. Combination of multitouch interface, sketching paradigm and powerfull adaptive procedural model that generate realistic trees offer intuitive and flexible design tools. This work is part of the Inria associated team with the University of Calgary. It has been published Eurographics Symposium on Sketch-Based Interfaces and Modeling [32].

• Reconstruction from video. (Frédéric Boudon, Jérôme Guenard [IRIT, Toulouse], Géraldine Morin [IRIT, Toulouse], Pierre Gurdjos [IRIT, Toulouse], Vincent Charvillat [IRIT, Toulouse])

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

Our method is based on a skeletonisation algorithm that 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 organisation of natural branching structure. 3D models are then generated. A reprojection of the models can be compared with the original image to assess the visual accuracy of the reconstruction. We optimise the parameter values of the generative model based on the reprojection criterion. Realistic results are obtained on different species of plants, in particular vineyards. Publication of this work is in progress.

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

This research theme is supported by the Agropolis project Fruit3D.

The aim of this work is to provide methods for generating fruit structure that can be integrated with models of fruit function and used to investigate such effects. To this end, we have developed a

modeling pipeline in the OpenAlea platform that involves two steps: (1) generating a 3D volumetric mesh representation of the entire fruit, and (2) generating a complex network of vasculature that is embedded within this mesh. To create the 3D volumetric mesh, we use reconstruction algorithms from the 3D mesh generation package of the Computational Geometry Algorithms Library (CGAL). To generate the pattern of vasculature within this volumetric mesh, we use a Space Colonisation Algorithm that populates the volume of the fruit by simulating competition for space of the vasculature. We have applied our modeling pipeline to generate the internal and external geometry of a cherry tomato fruit using Magnetic Resonance Imaging data as input. These studies demonstrate the possibility to create species-specific models of fruit structure with relatively low effort [26]. These volumetric meshes are then combined with models of function to form integrative computational fruit models, which will help to investigate the effects of fruit structure on quality (see section 5.3.2).

• Reconstruction of gramineous leaves. (Christian Fournier, Christophe Pradal)

This research theme is supported by the Agropolis project OpenAlea.

Unlike trees, the 3D architecture of gramineous plants is much more related to the shapes of its leaves than the arrangement of its branches. Many modeling efforts have thus concentrated on correctly capturing its complex shape at different stages and use them as scalable geometric primitives. Still, additional control of such objects is needed in the context of Functional Structural Modeling. The objective of this work is to propose a plastic and dynamic 3D leaf model that is well suited for such uses, still able to capture a variety of observed static shapes. Leaf shape is modeled by a parametric surface describing leaf midrib curvature, leaf width variation, undulation of leaf margins and twist along the midrib. Meshes can be generated form these surfaces, and reduced using a decimation algorithm. The model can be fed with data or with curves drawn by user interaction. Morphological operators are defined and allows for plastic deformation of the control curves. The dynamics of shape acquisition can also be specified, and combined with morphological operators to simulate various scenarii of evolution and responses to stresses. The capabilities of the model are demonstrated through several cases of use. Future directions of research are thought to be a better integration of mechanical or physiological constraints that would reduce the model plasticity but avoid user-induced unrealistic simulation. [28].

5.1.2. Modeling the plant ontogenic program

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

This research theme is supported by two PhD programs.

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. [37], [43], [44], [41], provides macroscopic evidence for the existence of regularities and identities in processes that drive meristem activity at microscopic scales. Different concepts have been proposed to explain these specific organizations such as "morphogenetic program" [45], "age state" [40] or "physiological age" [38]. 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 [40], [38]. Here we develop computational methods to decipher these rules.

• Relating branching structure to the shoot properties (Jean Peyhardi, Yann Guédon, Evelyne Coste, Catherine Trottier, Yves Caraglio [AMAP], Pierre-Eric Lauri [AGAP, AFEF team]) Shoot branching structures often take the form of a succession of homogeneous branching zones and have been analyzed using segmentation models such as hidden semi-Markov chains. Axillary meristem fates are influenced by local properties of the parent shoot such as for instance its growth rate or local curvature. The objective of this work, which is part of the PhD subject of Jean Peyhardi, is to develop statistical models that generalize hidden semi-Markov chains with the capability to incorporate explanatory variables that vary along the parent shoot (e.g. maximum growth rate of the leaf, surface

of the leaf, length of the internode, local curvature of the parent shoot). More precisely, the simple multinomial distributions that represent the axillary productions observed in the different branching zones are replaced by multinomial generalized linear models (GLMs). Since the two classical categories of multinomial GLMs that correspond either to nominal or ordinal categorical response variables were not appropriate in our setting, we chose to develop a new family of multinomial GLMs called multi-step multinomial GLMs that enable to tackle partially ordered categorical response variables. Typically, we need to distinguish different timing of branching (e.g. immediate shoot, one-year-delayed shoot and latent bud), different categories of offspring shoots (e.g. among one-year-delayed shoots, vegetative short shoot, vegetative long shoot and flowering shoot) and to specialize the explanatory variables for certain categories of offspring shoots (e.g. the growth of the parent shoot influence the immediate offspring shoots but not the one-year-delayed offspring shoots). The resulting integrative models are called semi-Markov switching multi-step multinomial GLMs and are applied to different data sets corresponding mainly to fruit tree branching structures.

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

The aim of this work was 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 or AS, which is the portions of stem that were grown during the same year). Two replications of each genotype were available.

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

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

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

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

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

To test the effect of some properties of a given parent shoot on the properties of its children shoots, statistical models based on multitype branching processes were developed. This kind of dependence between parent and children shoots is frequently at stake in fruit trees, for which the number of flowering or vegetative children of a parent shoot depends on its nature, with potential interactions with other factors. Thus, controlling demographic patterns of the shoots (through varietal selection or crop management strategies) is expected to bring substantial improvements in the quantity and quality of yields.

Formally, the shoot properties are summed up using the notion of shoot state. The number of children shoots in each state is modeled through discrete multivariate distributions. Model selection procedures are necessary to specify parsimonious distributions. We developed an approach based on probabilistic graphical models to identify and exploit properties of conditional independence between numbers of children in different states, so as to simplify the specification of their joint distribution. The graph building stage was based on exploring the space of possible chain graph models, which required defining a notion of neighbourhood of these graphs. A parametric distribution was associated with each graph. It was obtained by combining families of univariate and multivariate distributions or regression models. These were chosen by selection model procedures among different parametric families.

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

- Analyzing fruit tree phenology (Anaëlle Dambreville, Jean-Baptiste Durand, Pierre Fernique, Yann Guédon, Christophe Pradal, Pierre-Eric Lauri [AFEF team, AGAP], Frédéric Normand, Catherine Trottier) Mango is a tropical tree characterized by strong asynchronisms within and between trees. Causation networks explaining the vegetative and reproductive growths within and between growing cycles were studied on the basis of generalized linear models. We highlighted in this way marked interplays between structural and temporal components of tree structure development at three scales. At growth unit scale, a growth unit appeared early in the growing cycle had higher rate of burst compared to late appeared growth units. At growing cycle scale, a growth unit which flowered delayed its future vegetative growth compared to a vegetative growth unit. At tree scale, a fruiting tree delayed further vegetative growth and flowering compared to a non-fruiting tree. These results evidenced that tree phenology is strongly affected by structural components and not only by the environment. We are now investigating jointly structure development and phenology of mango using statistical models for trees in particular hidden Markov tree models and multitype branching processes.
- Integrative developmental growth stages of shoots (Anaëlle Dambreville, Yann Guédon, Pierre-Eric Lauri [AFEF team, AGAP], Frédéric Normand) Growth and development are often studied as two separated processes. Our aim is to investigate the coordination between growth and development in mango shoots. We considered three types of organ, namely the shoot axis, its attached leaves and the inflorescence. Two types of data were collected during the shoot and inflorescence follow-up: developmental stages determined in an expert way and organs sizes determined from measurements. To give an integrative view of the shoot and inflorescence growth and development, we adopted the following strategy. For a given cultivar, we first built a multi-state model on the basis of absolute growth rate sequences deduced from the measurements. Using these models, we computed growth stages. These growth stages highlighted growth asynchronisms between two topologically-connected organs: the axis and its leaves. Then, we compared these growth stages with the developmental ones and we obtained strong matches between them. The integrated developmental growth stages emphasized that the developmental stages are markedly related to growth rates an can be interpreted in terms of physiological (hydraulics, carbohydrates partitioning) and developmental (organs preformation versus neoformation) processes.
- Self-nested structure of plants. (Christophe Godin, Farah Ben Naoum) 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, equivalent to the original tree, where a given subtree class is represented only once

(compression is based on the suppression of structural redundancies in the original tree). In the compressed graph, every node representing a particular subtree in the original tree has exactly the same height as its corresponding node in the original tree. This method thus compresses a tree in width, but not in height. In this new work, we designed an extension of this compression method in which a tree is compressed in both width and height. The method is based on the detection of so-called *quasi-isomorphic paths* in a tree and on the compression of these paths in height. A paper describing the corresponding algorithms is being written.

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

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

This research theme is supported by three PhD programs.

The ontogenetic program of a plant is actually sensitive to environmental changes. If, in particular cases, we can make the assumption that the environment is a fixed control variable (see section 5.1.2), in general the structure produced by meristem results from a tight interaction between the plant and its environment, throughout its lifetime. Based on observations, we thus aim to trace back to the different components of the growth (ontogenetic development and its modulation by the environment). This is made using two types of approaches. On the one hand, we develop a statistical approach in which stochastic models are augmented with additional time-varying explanatory variables that represent the environment variations. The design of estimation procedures for these models make it possible to separate the plant ontogenetic program from its modulation by the environment. On the other hand, we build reactive models that make it possible to simulate in a mechanistic way the interaction between the plant development and its environment.

- Influence of environment conditions and horticultural practices on the branching and axillary flowering structures of fruit tree shoots. (Yann Guédon, Evelyne Costes [AFEF Team, AGAP], Ted DeJong [UC Davis], Claudia Negron [UC Davis]).
 - In the context of a collaboration with Claudia Negron and Ted DeJong, we studied the influence of water availability and pruning practices on the branching and axillary flowering structures of different categories of almond shoots Stochastic models (hidden semi-Markov chains) were built for the branching and axillary flowering structures of different categories of almond shoots corresponding to different genetic backgrounds, levels of irrigation and pruning practices.
- Analyzing growth components in trees. (Yann Guédon, Yves Caraglio [AMAP], Olivier Taugourdeau [AMAP])
 - In a forest ecology context, we identified robust indicators that summarize the balance between tree ontogeny and environmental constraints (mainly related to light environment). In this context, tree growth data typically correspond to the retrospective measurement of annual shoot characteristics (e.g. length, number of branches) along the main stem. We applied segmentation models (hidden Markov and semi-Markov chains) that enable to identify tree growth phases. This statistical modeling approach was applied to both deciduous (sessile oak and Persian walnut) and evergreen (Corsican pine and silver fir) tree species growing in contrasted conditions ranging from managed forest stands to unmanaged understoreys. The growth phase duration distributions estimated within these segmentation models characterize the balance between tree ontogeny and the environmental constraints in tree development at the population scale. These distributions had very contrasted characteristics in terms of shape and relative dispersion between ontogeny-driven and environment-driven tree development. The characteristics of growth phase duration distributions may change over tree life reflecting changes in tree competition.
- Investigating the influence of geometrical traits on light interception efficiency of trees and grass (Liqi Han [AFEF Team, AGAP], Christophe Pradal, Frédéric Boudon, Christophe Godin, David Da Silva [UC Davis], Evelyne Costes, Philippe Balandier [PIAF], André Marquier [PIAF], Gaëtan Louarn [URP3F], Didier Combes [URP3F], Christian Fournier)

Light availability in forest understory is essential for many processes. It controls for instance the growth potential of species and individuals in plant communities. It is, therefore, a valuable information regarding forest and crop management. However, the effects of competition for light on short term vegetation dynamics are still poorly understood. This is in part due to a lack of tractacle and precise methods to estimate light resource within a canopy. To alleviate this difficulty, models can be used to compute light interception. At a detailed scale, they often require a lot of field data to accurately predict light distribution, particularly in the case of heterogeneous canopies.

To investigate this issue, we first analyzed the deterioration of the prediction quality of light distribution to the reduction of inputs by comparing simulations to transmitted light measurements in forests of increasing complexity in three different locations [17]. With a full set of parameters to describe the tree crown (i.e., crown extension in at least eight directions, crown height and length), the model accurately simulated the light distribution. Simplifying crown description by a geometric shape with a mean radius of crown extension led to deteriorated but acceptable light distributions. Allometric relationships used to calculate crown extension from trunk diameter at breast height seriously reduced light distribution accuracy.

We also studied the light interception of herbaceous plants with contrasting architectures (monocultures and binary mixtures) grown at high or low density and sought to determine the important architectural features necessary to account for light partitioning among individual plants [21]. It was shown that the studied plant populations were typical of a wide range of competition intensities, ranging from sparse plants to dense size-structured populations. Plant representations using whole plant envelopes with homogeneous leaf area density (LAD) were not reliable to estimate light partitioning, irrespective of the accuracy of envelope definition. Accounting for heterogeneous LAD within plants helped to solve this problem in both sparse and dense canopies. The relative importance of traits however changed with competition intensity and was different from reports made on isolated plants. Simple envelope-based reconstructions were finally shown robust enough to support parameterisation from a tractable set of traits measured in the field provided that height and vertical LAD gradient were characterised.

Using virtual growth simulation tools, a detailled analysis was also carried out to study more precisely the influence of architectural variability of apple trees on their light interception efficiency [30]. For this we used MAppleT, an in silico functional-structural plant model that has been built for simulating architectural development of apple trees. The STAR, namely the silhouette to total area ratio, of leaves, was chosen to evaluate the level of such efficiency. The strategy was to integrate MAppleT with the light interception model provided by the fractalysis module of the VPlants software library. Target values of four major traits (internode length, leaf area, branching angle and top shoot diameter), are varied in range previously observed in a segregating population of apple hybrids. A sensitivity analysis based on polynomial and generalised additive models was performed for highlighting the most influential trait on light interception and suggesting the optimal combination(s) of traits leading to the highest STAR. The contribution of stochastic processes that pilot tree topology in MAppleT is also investigated in the sensitivity analysis. This study not only provides a time- and resource-saving alternative for data collection, but also sets a methodology for ideotype definition and further genetic improvement of apple trees.

5.2. Meristem functioning and development

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

5.2.1. Data acquisition and design of meristem models

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

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

• Improvement of the MARS-ALT pipeline robustness Meristem, laser microscopy, image reconstruction, cell segmentation, automatic lineaging

Participants: Léo Guignard, Christophe Godin, Grégoire Malandain, Jan Traas, Pradeep Das [RDP, ENS], Vincent Mirabet [RDP, ENS].

The MARS-ALT (Multi-Angles Registration and Segmentation - Automatic Lineage Tracking) software pipeline automatically performs a segmentation at cell resolution from 3D or 2D voxel images where the membranes/walls are marked (by a die for example) and makes it possible to follow the lineage of these cells through time [5]. A new version of this pipeline is currently being developed. MARS-ALT Version 2 is based on the same algorithms and methods and is intended to improve the overall robustness of the pipeline (protocol, noise in the input image) and automate completely the process. To test the new pipeline, we use different acquisition protocols and different organisms (floral and apical meristems and the early stages of development of a marine animal *Phallusia mammillata*). The segmentation is corrected a posteriori to deal with imaging artifacts due to uncertainties of acquisition. The image data set on which we develop the methods consists of:

- Arabidopsis thaliana shoot apical meristem and primordia with around 6000 cells. The
 organ is captured from three different angles every 20 hours 3 or 4 times with a confocal
 microscope (Collaboration Sainsbury lab, Cambridge)
- Arabidopsis thaliana flower meristems with around 2000 cells. The organ is also captured from three different angles every 20 hours 3 to 5 times with a confocal microscope (Collaboration RDP Lyon)
- Phallusia mammillata and Ciona intestinalis embryos with from 32 cells to around 1000 cells. The organism is captured from four different angles every 2 minutes during 2 to 3 hours with a SPIM (Single Plane Illumination Microscope) (Collaboration CRBM Montpellier / EMBL Heidelberg)

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

 Design of 3D virtual atlases for specifying gene expression patterns (Jérôme Chopard, Christophe Godin, Jan Traas, Françoise Monéger [RDP, ENS])

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

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

A prototype version of the 3D virtual atlas was built last year [8]. Further developments of this tool will rely on the segmented images produced from microscopy, as presented in the previous section. In particular, a common underlying data structure has to be developed transversally to these two scientific developments. The definition of this data structure has been initiated last year through several team meetings, and should lead to a revised implementation next year.

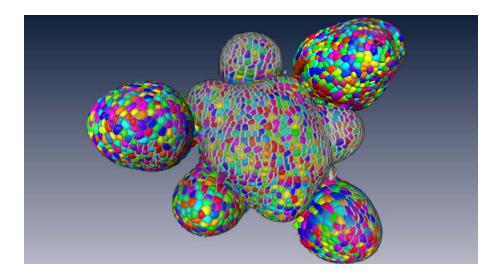


Figure 4. Superimposition of an automatic cell segmentation of an arabidopsis flower meristem using the new MARS pipeline with the original confocal image stack where the membranes are marked.

5.2.2. Shape analysis of meristems

(Jonathan Legrand, Clémence Hatt [BURST, AGAP], Jean-Baptiste Durand, Frédéric Boudon, Christophe Godin, Yann Guédon, François Mankessi [BURST, AGAP], Olivier Monteuuis [BURST, AGAP], Jean-Luc Verdeil [PHIV, AGAP])

Plants that grow several forms or type of leaves along a shoot, depending on age or shoot length, are called heteroblastic. The influence of heteroblasty on morphological and histocytological characteristics of Acacia mangium shoot apical meristems (SAMs) was assessed comparing materials with mature and juvenile leaf morphology in natural and in vitro conditions. For this we introduced a workflow for characterizing dome shape with few parameters (SAM dome height (H), basal diameter (D) and shape factor (S)) and their joint statistical analysis to assess influence of conditions on SAM shape. In particular, a new statistical test is introduced here for multivariate analysis. This is a generalization of univariate ANOVA that takes into account statistical dependencies between the shape parameters. As a result, we found that SAM dome height (H) and basal diameter (D) were highly correlated. The joint analysis revealed that H, D, and shape (S) varied significantly according to the four plant origins investigated, with the higher scores for the outdoor mature source "Mat". Overall, heteroblasty induced more conspicuous differences of SAM characteristics for the outdoor than for the in vitro materials. A paper presenting these results has been published in Trees [20]

At cellular resolution, we studied the organization of cells in the meristems. The MARS-ALT pipeline provides rich spatio-temporal data sets for analyzing the development of meristems. A first step consisted of designing a dedicated graph for efficiently representing the spatial (adjacency between cells) and temporal (cell division) relationships between cells. Various variables can be attached either to the vertices (e.g. cell volume, inertia axes) or the edges (e.g. wall surface, distance between cell centroids). This graph may be augmented by new variables resulting from various spatial or temporal filtering (e.g. cell volumetric growth). We are now designing models and algorithms for finding patterns in time courses of meristems. In particular, we are investigating spectral clustering methods in order to define homogeneous regions in term of cell identities.

5.2.3. Transport models

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

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

Active transport of the plant hormone auxin has been shown to play a key role in the initiation of organs at the shoot apex, and vein formation in both leaves and the shoot apical meristem. Polar localized membrane proteins of the PIN1 and AUX/LAX family facilitate this transport and observations and models suggest that the coherent organization of these proteins in the L1 layer is responsible for the creation of auxin maxima (surrounded by a depletion zone), which in turn triggers organ initiation close to the meristem center [46] [1]. Furthermore, canalized PIN allocations are thought to play a crucial role in vein formation in the leaf and in the L2. Previous studies have typically modeled the L1 and L2 with different models to explain different patterns of PIN allocations. In the last two years, we developed a unifying model showing that a unique flux-based model could be sufficient to explain PIN patterns in both L1 and L2 [25]. Contrary to our previous study [11], here no change in the model parameters is needed for this. Our approach is based on inherent topological and geometrical differences between the L1 and L2, specifically their dimensionality and the distribution of sources and sinks.

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

5.2.4. Mechanical model

Participants: Jérôme Chopard, Olivier Ali, Christophe Godin, Frédéric Boudon, Jan Traas, Olivier Hamant [ENS-Lyon], Arezki Boudaoud [ENS-Lyon].

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

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

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

A paper describing the mechanical model and its application to model primorium formation in the shoot apical meristem is currently being written. Additionally, a redesign of our mechanical model using the SOFA framework is in progress.

5.2.5. Gene regulatory networks

Modeling gene activities within cells is of primary importance since cell identities correspond to stable combination of gene expression. This fact is becoming more and more acknowledged, and has led this year to the publication of several review articles including members of Virtual Plants as authors [22], [23], [24], [13].

• The auxin signaling pathway (Etienne Farcot, Yann Guédon, Christophe Godin, Yassin Refahi, Jonathan Legrand, Jan Traas, Teva Vernoux, Stéphane Robin [AgroParisTech], Jean-Benoist Leger [AgroParisTech])

The auxin signalling network involves about 50 potentially interacting factors. We applied a graph clustering method [12] that relies on 0/1 interactions between factors deduced from yeast two-hybrid (Y2H) data. The Y2H analysis involves two independent tests (X-gal and HIS3 tests). Each possible interaction was tested in the two possible configurations, where each protein was alternatively the bait and the prey protein. A binary interaction is thus a summary of the four outputs of the X-gal and HIS3 tests. In order to limit the loss of information, we designed a standardization procedure to summarize the outputs of the X-gal and HIS3 tests as a distance defined on a continuous scale. This opens the possibility to study the influence of phylogenetic distances between factors on their interactions using an extension of the mixture model for random graphs that incorporate explanatory variables. This new model evidences different behaviors between the ARF+ and the Aux/IAA factors.

Extensions of this ODE model are necessary to better understand this system in more general contexts than the shoot apical meristem development, which was the framework of our previous study. This work involves defining and studying mathematically a series of distinct network topologies for the auxin signalling pathway. This was the topic of a Master's internship for the studend Cyril Lavedrine, from September to December 2012, co-supervised by E. Farcot and T. Vernoux. This work led to qualitative predictions which remain to be tested experimentally.

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

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

At the single cell level, new results were obtained in the framework of piecewise-linear models. Since their introduction in the late 1960's, these models have been believed to present chaotic behavior in some parameter regimes. However, this was mostly observed numerically, based on intensive generation of random networks. In a long lasting collaboration between E. Farcot and R. Edwards (Univ. Victoria, Canada), with more recent input from one of his students, E. Foxall, we have introduced a method to explicitly build piecewise affine models having a return map which is conjugate to a topological horseshoe. A paper presenting these results has appeared this year [18]. For the same class of piecewise-linear models, it is in general very difficult to entirely characterize the attractors of a given system. In an attempt to improve our ability on this question, a probabilistic approach has been proposed in [15], in which it is shown that a Markov chain can built as an approximation of a given piecewise-linear system, and actually used to make predictions about its periodic attractors.

At a higher scale, we have also continued the study of gene regulation in meristematic tissues. In the context of Y. Refahi's post-doc between Virtual Plants and the group of Henrik Jönsson in Cambridge (Sainsbury Laboratory), we have continued a work that was initiated in Y. Refahi's thesis. This work is motivated by recent biological results, indicating that gradient-like patterns originating from the external layers of meristems may play a decisive role in the specification of the pool of stem cells in a central position. Using the methods in [5], and their on-going improvements, we have acquired new 3D and 4D images that were then segmented. These structures will be used in the next few months to investigate generic patterning properties of gradient like morphogen patterns. This will require a thorough analysis of free diffusion in realistic geometries, as made possible by the newly acquired images. As a preliminary work, we are also currently investigating the formation of gradient patterns in idealised tissues, allowing for deeper analytic treatment than the complex structures obtained by microscopy.

5.2.6. Model integration

Participants: Mikaël Lucas [IRD], Michael Walker, Jérôme Chopard, Frédéric Boudon, Christophe Godin, Laurent Laplaze, Jan Traas, François Parcy.

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

Our approach consists of building a programmable tissue which is able to accept different modeling components. This includes a central data structure representing the tissue in either 2-D or 3-D, which is able to grow in time, models of gene activity and regulation, models of signal exchange (physical and chemical) between cells and models of cell cycle (which includes cell division). For each modeling component, one or several approaches are investigated in depth, possibly at different temporal and spatial scales, using the data available from the partners (imaging, gene networks, and expression patterns). Approaches are compared and assessed on the same data. The objective of each submodel component will be to provide plugin components, corresponding to simplified versions of their models if necessary, that can be injected in the programmable tissue platform. This work is developed in collaboration with the RDP grou at ENS-Lyon [23] and the CPIB group in Nottingham, UK [13].

• Development of a computer platform for the 'programmable tissue'. (Michael Walker, Frédéric Boudon, Etienne Farcot, Christophe Godin)

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

• Design of a genetic model of inflorescence development. (Etienne Farcot, Christophe Godin, François Parcy)

We studied the regulatory network that control flower development during morphogenesis. To overcome the network complexity and integrate this regulation during ontogenesis, we have developed a first model of the control of floral initiation by genes, and in particular the situation of cauliflower mutants, in which the repeatedly meristem fails in making a complete transition to the flower. This work couples models at different scales, since gene regulation is described by a minimal gene network, which is used as a decision module in an L-system model of the inflorescence architecture. This mixed model has led us to make different hypotheses about gene interactions and hormonal regulation. First predictions about gene actors controling the passage to flower could be verified. However, a complete integrated picture of flower development could not be reached yet. After several unsuccessful attempts, further experiments are currently being made to verify the scenario predicted by the model.

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

5.3.1. Transport model in roots

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

This research theme is supported by the ANR project HydroRoot.

A model of Arabidopsis thaliana root hydraulics at the cellular level was developed in the OpenAlea modeling platform. The model relies on the integration throughout root architecture of elementary hydraulic components. Each component integrates local radial and axial water flows. Axial hydraulic conductivity is calculated according to Poiseuille's law, based on local size of xylem vessels. Radial hydraulic conductivity is determined in part by aquaporin activity and was set constant throughout root architecture in the first model versions. In its current state, the model is parameterized using architectural, tissular and physiological data that were experimentally determined in the Aquaporin group at BPMP. The architectural reconstruction of the root system is based on a tridimensional multi-scale tree graph (MTG). The current model is capable of predicting the water flow that is transported by a root system in the standard experimental conditions used in the Aquaporin group. This model was used to perform sensitivity analyses and determine the respective contributions to root hydraulic dynamics of various biological parameters (axial and radial hydraulic 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.

5.3.2. Transport in fruits

Participants: Mik Cieslak, Nadia Bertin [Inra, Avignon], Frédéric Boudon, Christophe Godin, Michel Genard [Inra, Avignon], Christophe Goz-Bac [Université Montpellier 2].

This research theme is supported by the Agropolis project Fruit3D.

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

Two essential functions in determining fruit quality are the transport and accumulation of water and dry matter to various fruit tissues. Since water and carbon are delivered to fruit tissues through a complex vasculature system, the internal fruit structure and pattern of vasculature may have a significant impact on their distribution within the fruit.

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

This approach has been applied to study tomato fruit (Solanum lycopersicum) by constructing 3D volumetric meshes from different sources (images of perpendicular fruit slices and MRI data), and integrating water and carbon transport processes into these meshes. To illustrate the tomato model, a simulation of one season of the fruit's growth has been performed and its results compared with an already published process-based tomato fruit model. We first showed that the classical results of the abstract process-based models could be also captured by the more detailed spatialized model. However, our model provides additional information on the internal heterogeneity of the fruit, such as a gradient in sugar concentration. Once the model is calibrated and evaluated, our approach will be suitable for studying the effects of internal fruit heterogeneity and overall shape on fruit quality development.

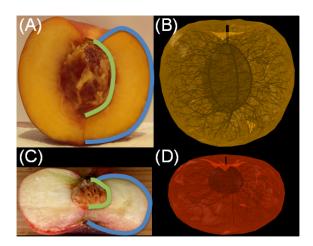


Figure 5. Virtual models of peaches reconstructed from images with simulated vasculatur to simulate carbon and water transport in the fruit

5.3.3. Analazing shoot and leaf elongation

Participants: Maryline Lièvre, Yann Guédon, Christine Granier.

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

- 1. tissular scale using a probabilistic model of endoreduplication for modeling the distribution of the leaf epidermis cell surfaces. Endoreduplication, which is a replication of the nuclear genome in the absence of cell division that leads to elevated nuclear gene content, strongly affects the leaf epidermis cells of *arabidopsis*.
- 2. organ scale using nonlinear regression model for analyzing the growth of each successive leaf.
- 3. shoot scale: The outputs of the analyses at the tissular and organ scales will be summarized as multivariate sequences along the shoots characterizing each successive leaf. These sequences will be augmented by supplementary morphological variables characterizing leaf shape and properties (e.g. presence/absence of trichomes). These sequences will be globally analyzed in order to take into account plant ontogeny and in particular the successive developmental stages before the floral transition for the wild type and selected mutants of *arabidopsis*.

5.3.4. Analyzing perturbations in Arabidopsis thaliana phyllotaxis

Participants: Christophe Godin, Yann Guédon, Yassin Refahi, Etienne Farcot.

This research theme is supported by iSAM.

The cytokinin hormones are known to play a significant role in the regulation of phyllotaxis. To investigate this, Fabrice Besnard and Teva Vernoux are studying *Arabidopsis thaliana ahp6* mutants, AHP6 being a protein known for its inhibitory effect in the cytokinin signaling pathway. At the macroscopic scale, this mutation induces perturbations of the phyllotaxis, barely sensible on single plants. In order to characterize these perturbations, we designed a pipeline of models and methods 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. All these results can be explained by the absence of a strict coupling between the timing of organ development and their angular and longitudinal position on the stem. Two papers (one with biological aspects and the other about methodological developments) are currently in revision.

6. Partnerships and Cooperations

6.1. Regional Initiatives

6.1.1. OpenAlea

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

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

The aim of this project is to foster the development and the national and international diffusion of the platform OpenAlea. This opensource platform provides an easy-to-use environment for plant modelers through a visual programming interface to efficiently use and combine models or computational methods from different scientific fields in order to represent, analyze and simulate complex plant systems at different scales, from meristems to plant canopy. OpenAlea makes it possible to assemble highly reusable, heterogeneous components. The central point of its architecture is to allow to integrate existing components or modules developed by different teams without rewriting them. These components are developed in multi-languages like C, C++, Fortran or Java as well as Python. Work comprises development of standard data structures, deployment tools, documentation, training, software engineering, user interface, ...

6.1.2. Fruit3D

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

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

The aim of this project is to develop a virtual tomato that contains the geometrical description of a growing fruit, physiological models (for sugar and hormone transfers) and mechanical model. The project gathers the competences of plant modelers, physicists and ecophysiologists. Physical and biological laws involved in tissue differentiation and cell growth, in relation to fruit growth and compartmentalization, and a number of related traits of quality (e.g. size, composition and texture) are modeled and integrated within the virtual tomato. Magnetic Resonance Imaging (MRI) techniques are used to provide an in vivo validation of the model by non invasive measurements.

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

6.1.3. PlantScan3D

Participants: Frédéric Boudon, Chakkrit Preuksakarn, Jean-Baptiste Durand, Christophe Godin, Christian Fournier.

Funding: Agropolis foundation (Contractor for Virtual Plants: CIRAD, From 2009 to 2012)

Automatic acquisition of plant phenotypes, and in particular of architecture phenotypes, constitutes a major bottleneck of the construction of quantitative models of plant development. Recently, 3D Laser scanners have made it possible to acquire 3D images on which each pixel has an associated depth corresponding to distance between camera and the pinpointed surface of the object. The objective of this project is to develop the use of laser scanner for plant geometry reconstruction. For this, we develop methodologies for the automation of numerical 3D acquisition of vegetal structures of different sizes, and new methods for the reconstruction of parsimonious geometrical and structural models usable in agronomic and biological contexts.

Partners: AFEF Team, UMR AGAP, UMR LEPSE (Montpellier), UMR PIAF (INRA Clermont Ferrand), UMR URP3F (Inra Lusignan), EPI Galaad (Inria Sophia Antipolis), EPI Imagine (Inria Grenoble). University of Helsinki, Finland.

6.1.4. Agropolis computational plant seminar

Participants: Yann Guédon, Christine Granier [INRA, LEPSE], Soazig Guyomarc'H [Montpellier 2 University, DIADE].

Funding: Agropolis foundation (Contractor for Virtual Plants: CIRAD. From 2008 to 2012)

In the context of the creation of a world-level pole on plant science in the région Languedoc-Roussillon, we created a monthly seminar on plant modeling and its applications. The seminar is organized by Yann Guédon, Christine Granier (INRA, LESPE) and Soazig Guyomarc'h (Montpellier 2 University, DIADE) with the support of Agropolis International and Agropolis Foundation.

6.1.5. Rhizopolis

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

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

Rhizopolis is a multidisciplinary project on the biology and ecology of the plant root that addresses the broad roles of this organ in mineral nutrient and water acquisition. The consortium addresses central issues of root development, that are operationally divided into 3 work packages.

- WP A: Integration of membrane transport activity and structure-function relationships in roots and root symbioses.
- WP B: Key tools for imaging root development: (i) a world unique platform for 4D root imaging of root cell division and root primordia formation, and (ii) an innovative image analysis software for high-throughput phenotyping of root system architecture. These tools will be used to identify mechanisms and traits associated with root system efficiency and plasticity
- WP C: Integrating root-soil interactions in the rhizosphere at the whole root system level application to water and nutrient acquisition by plants.

Virtual Plants is mainly involved in WP B and in particular in the development of a tool to automatically reconstruct root systems from 2D imaging.

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

6.2. National Initiatives

6.2.1. ANR

6.2.1.1. Morpholeaf

Participants: Christophe Godin, Etienne Farcot.

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. The leaf is the main photosynthetic organ of the plant and its margin can show diverse levels of dissections ranging from no (entire margin), mild (serration) to strong (lobes) incisions. The leaf itself can be either simple or dissected into units called leaflets. The CUC genes are part of a network involving negative regulation by a miRNA, miR164 and possible response of the signalling molecule auxin. However, the interplay between the three actors of this network (CUC, miR164 and auxin) is not understood yet. Nor are known the cellular effects of the expression of the CUC genes and their link with differential growth of the leaf margin leading to serration. 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. By combining biological observations and

manipulations, quantitative measurements and modeling, 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. We will, stepwise, build, test and validate a model of leaf margin development integrating a regulatory network, cellular behaviour and morphogenesis.

Partners: RDP ENS-Lyon; INRA Versailles.

6.2.1.2. HydroRoot

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

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

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

6.2.2. Other national grants

6.2.2.1. OpenAlea 2.0

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

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

The goal of this project is to develop an integrated multi-paradigm software environment for plant modeling. This 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

6.2.2.2. 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. This is a demonstration project focusing on the wheat septoria system, but the modeling approach is generic and intended to apply to other pathosystems. The originality of the project is based on: (i) the plant material used, consisting of innovative wheat varieties selected for their ability to produce contrasting architectures, (ii) the development of an integrative modeling tool coupling the canopy development, the fate of fungicides and the dynamics of the pathogen, and (iii) a proposed approach to multicriteria evaluation of protection strategies including estimation of yields, assessments of environmental impact of pesticides and erosion of efficacy. The project focuses on the development of a modeling tool. This tool is organized around three components: (1) the effect of the architecture of crops on epidemics, (2) the effect of fungicides on infection cycles and (3) the effect of canopy architecture on the fate of fungicides after application. The integration of the three components are performed within the OpenAlea platform that will allow the multicriteria evaluation of various scenarios (climate / varieties / architecture / fungicides) and help design new practices. Field experiments allow testing

of treatment strategies associated with a variety of architectures. Data will be used to validate the modeling tool developed. Thanks to the integrated model various scenarios combining climate architecture x fungicide treatment will be simulated to identify and propose efficient strategies for 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.

6.2.2.3. Morphogenetics

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

Funding: Inria Action d'Envergure(From 2011 to 2015)

Morphogenetics is an Inria transversal project gathering 3 Inria teams and two Inra teams. It is aimed at understanding how flower shape and architecture are controlled by genes during development. To do so, we study the spatio-temporal relationship between genetic regulation and flower shape utilizing recently developed imaging techniques together with molecular genetics and computational modeling. The project addresses flower development at different scales using the Arabidopsis flower, currently one of the best-characterised plant systems. The workplan is divided into three major parts:

- Through 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. In particular, by
 using induced gene disruption together with careful live-imaging analysis, we will obtain dynamic,
 quantitative and causal data that link gene expression and molecular interactions to morphogenesis
 at a higher scale.
- We will integrate the results generated from these experiments in a specially designed database called a 3D Atlas.
- We will use these detailed, multidimensional data as direct input to new predictive computational models for morphogenesis and gene regulation that will then be further tested through subsequent rounds of experimental perturbation and analysis. A particular emphasis will be put on the modeling of mechanics in tissues for which different approaches will be developed.

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

6.2.2.4. Rose

Participants: Christophe Godin, Frédéric Boudon, Christophe Pradal.

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

Lateral bud outgrowth of aerial stems in plants is known to regulated by hormonal signals such as auxin and cytokinin. Recently detailed modeling approaches have been successfully developed to explain such regulation. However, it is known that on many species the sugar status of the plant also plays a role in shoot branching. In this project we want to quantify this role and to understand how sugars interfere with hormonal signals to regulate bud outgrowth. For this, 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. As a result, it is expected that main branching habits can be reproduced with the model and that experiments can be designed in order to test model predictions.

Partners: UMR SAGAH, Angers

6.3. International Bilateral Relations

6.3.1. ERASysBio+ iSAM

Participants: Christophe Godin, Etienne Farcot, Jan Traas, Teva Vernoux, James A.h. Murray [Univ. Cardiff, UK], Yrjö Helariutta [Univ. Helsinki, Finland].

(Contractor for Virtual Plants: Inria. From September 2008 to September 2011)

This project essentially aims at improving our knowledge of shoot apical meristem, and more specifically the combined action of auxin and cytokinin, using a systems biology approach. It is part of a wider program, the ERASysBio initiative, a consortium of European funding bodies, ministries and project management agencies. The purpose of this consortium is to develop fundamental and strategic collaboration in the funding of systems approaches to biological research. The iSAM project is one of the 16 transnational consortia that have been selected out of 51 proposals; in total they comprise 85 working groups from 14 countries. Four partners are involved in iSAM: the group of J. Murray will focus on mutants of cell cycle regulation, the group of Y. Helariutta is specialized in several aspects of cytokinin regulation, while the group of J. Traas in Lyon provides input regarding auxin regulation and transport, and Virtual Plants is in charge of the modeling aspects, in synergy with the three other groups.

More information on the project can be found at http://www.erasysbio.net/index.php?index=277.

6.3.2. Other bilateral relations

Yann Guédon is working with Claudia Negron (PhD student) and Ted DeJong (University of California, Davis) on the influence of water stress and pruning practices on the branching and axillary flowering structures of almond shoots.

6.4. International Initiatives

6.4.1. Inria 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. In this context, both groups have regular meetings and visio conference to progress jointly on the definition of the platform. In particular, C. Godin, M. Walker and E. Farcot went to a 1-week meeting on tissue data-structure definition and several researchers from CPIB came to Montpellier to continue this work and start implementation.

The team of Pr. Prusinkiewicz at the University of Calgary (Canada) has been an *associated team* of *Virtual Plants* from 2009 to 2011. see http://www-sop.inria.fr/virtualplants/wiki/doku.php?id=projects:eqass-vp-uc. In 2012 the collaboration continued and a major paper the L-Py language for modeling plants was published in the context of this collaboration.

6.5. International Research Visitors

6.5.1. Visits of International Scientists

The team received several visitors from exterior research groups in 2012:

- Farah Ben Naoum, from Sidi Bel Abbes University, Algeria, visited the team last spring for 1 month. She worked with C. Godin on combinatorial algorithms to compress trees.
- Risto Sievanen, from University of Helsinki, visisted the team for 3 months sabbatical leave in spring. He worked in particular with C. Pradal and C. Godin to integrate the model Lignum developed in his group within OpenAlea.
- Philip Benfey, from the University of Duke, USA, visited the group for 1 day at spring. Contacts have been established to exchange students/researchers between the labs for short periods. Julien Diener, working on automated methods for 2D root reconstruction from 2D images, should pay a visit to their lab in 2013.
- Xavier Sirault, from CSIRO and the High Resolution Plant Phenomics Centre in Canberra, Australia, visited the team during one day. It was decided during this visit to launch a project for coupling the phenotyping platform developed in Australia, a similar one developed in Montpellier by the group of F. Tardieu, and OpenAlea. The objective of this project will be to develop an integrated pipeline allowing the thorough analysis of a large number of genotypes, in particular assessment of growths of individual organs, of plant geometry, and of derived variables such as light interception. There is a strong complementarity between the three teams and the combination of expertise brought in the project by the different groups can result in a reference pipeline of model-assisted image analysis for plant phenotyping.

6.5.2. Visits to International Teams

Yann Guédon was invited by Miroslava Rakocevic (IAPAR, Londrina, Parana state) in Brazil during two weeks in september. This visit was funded by an Embrapa project. He visited three research centers: (i) EPAGRI, Caçador, Santa Catarina state; IAPAR, Londrina, Parana state; Embrapa, Campinas, Sao Paulo state. He gave a 8h course about plant architecture analysis at Londrina and gave a talk at Campinas.

Christophe Godin was invited at the Sainsbury Lab in Cambridge. A first collaboration with Henrik Jonsson based on the joint supervision of a post-doc fellow coming from Virtual Plants to Sainsbury was assessed. Other collaboration projects about meristem modeling and imaging were discussed.

7. Dissemination

7.1. Scientific Animation

- Christophe Godin has rendered the following services in 2012:
 - he is a member of the College de Direction of UMR AGAP
 - he is a member of the management board of IBC (Institut de Biologie Computationnelle de Montpellier)
 - he is a member of the scientific committee of the Environnement-Agromomy department at INRA
 - he is a member of the editorial board of the journal Frontiers in Plant Sciences
 - he is the scientific coordinator of action d'envergure Morphogenetics
 - he is the scientific coordinator of axis 4 on imaging and modeling (together with Patrick Lemaire)
 - he was a member of the expert committee for the selection of an assistant professor at Labri, University of Bordeaux.
 - he was a member of a Jury for the habilitation of high-school teachers in computer science (Jan 2012) in the context of the introduction of computer science as a new discipline at high school.
 - he participated to a commission of experts that wrote a report on the organization of research on complex systems for the University of Montpellier 2.
 - he participated to the PhD committee of Jonathan Legrand.
 - he is co-chair of the 7th international conference on functional-structural models of plants (FSPM 2013) that will be held in Finland in June 2013.
 - he gave 6 invited talks (4 abroad)
 - he was referee for papers submitted at journals: Development, Journal of mathematical biology, Journal of theoretical biology and at conferences: SIGGRAPH, SIGGRAPH Asia, Eurographics.
- Yann Guédon has rendered the following services in 2012:
 - he is a member of the editorial board of Annals of Botany and a member of the ERCIM working group "Computing & Statistics".
 - he was a member of a jury for recruiting research engineers at INRA.
 - he was a referee for papers submitted to Forest Ecology and Management and Journal of Statistical Planning and Inference.
- Frédéric Boudon was referee for papers submitted to SIGGRAPH, SIGGRAPH Asia, IEEE Transaction On Visualisation and Computer Graphics and Computers and Electronics in Agriculture.

Etienne Farcot served as a referee for papers submitted to Physica D, Chaos, Plant Physiology, Mathematical Modeling of Natural Phenomena, Nonlinear Analysis Series B: Real World Applications, Journal of Mathematical Biology, PLoS One.

7.2. Teaching - Supervision - Juries

7.2.1. Teaching

Master Biostatistics. Jointly with Montpellier 1, Montpellier 2 Universities and Agro-Montpellier. Yann Guédon teaches the stochastic modeling course (http://www.agro-montpellier.fr/um2/um1/masterbiostatistique). This involves 21h of M2 classes.

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

Christophe Godin gave a class of Master 2 on 'Tree comparison algorithm' in the Master of Bioinformatique (M2 - 4h).

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

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

Yann Guédon gave a 8h lecture about plant architecture analysis at the state University of Londrina (Parana, Brazil)

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

Master Computer Science. University Montpellier 2.

Frederic Boudon, Christophe Godin and Christophe Fiorio from LIRMM teach a course of 30h on plant modeling and computational geometry.

Christophe Godin and Frédéric Boudon gave a 2 days training session on L-Py and plant modeling for a group of students in Ecole Préparatoire aux Erandes Ecoles.

7.2.2. Supervision

PhD: Preuksakarn Chakkrit, Reconstructing Plant Architecture from 3D Laser Scanner Data, Université de Montpellier 2, 19 december 2012, F. Boudon and C. Godin.

PhD in progress: Anaëlle Dambreville, "Determinants and modeling of mango phenology: interactions between structural and temporal components in a branching structure and temperature effect", Montpellier 2 University, F. Normand, P.E. Lauri, Y. Guedon.

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

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

PhD in progress: Jean Peyhardi, "Markov and semi-Markov switching generalized linear mixed models applied to the analysis of plant architecture in relation to environmental and genetic factors", Montpellier 2 University. C. Trottier, Y. Guédon.

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

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

PhD in progress: 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", Montpellier 2 University, 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.

7.2.3. Juries

Christophe Godin participated was a referee of the theses of Romain Barillot and Wojtek Palubicki and participated to the defenses of these theses. Christophe Godin and Frédéric Boudon, co-supervising Chakkrit Preuksakarn thesis, were also part of the jury of his defense.

7.3. Popularization

Christophe Godin gave 2 conferences for high-school pupils respectively on plants and fractals and on meristem modeling in the context of MathC2+ and fête de la science (6h).

8. 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. 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^o 3, pp. 753–762, http://www-sop.inria.fr/virtualplants/Publications/2010/CGLT10
- [3] E. COSTES, C. SMITH, M. RENTON, Y. GUÉDON, P. PRUSINKIEWICZ, C. GODIN. *MAppleT: simulation of apple tree development using mixed stochastic and biomechanical models*, in "Functional Plant Biology", 2008, vol. 35, n^o 9 & 10, pp. 936–950, http://www-sop.inria.fr/virtualplants/Publications/2008/CSRGPG08
- [4] D. DA SILVA, F. BOUDON, C. GODIN, H. SINOQUET. *Multiscale Framework for Modeling and Analyzing Light Interception by Trees*, in "Multiscale Modeling and Simulation", aug 2008, vol. 7, n^o 2, pp. 910-933, http://www-sop.inria.fr/virtualplants/Publications/2008/DBGS08
- [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] Y. GUÉDON, Y. CARAGLIO, P. HEURET, E. LEBARBIER, C. MEREDIEU. *Analyzing growth components in trees*, in "Journal of Theoretical Biology", 2007, vol. 248, n^o 3, pp. 418–447, http://www-sop.inria.fr/virtualplants/Publications/2007/GCHLM07
- [8] 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, no 12, pp. 4318–4333
- [9] 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^o 1, pp. 1–21, http://www-sop.inria.fr/virtualplants/Publications/2009/PBNCG09
- [10] C. PRADAL, S. DUFOUR-KOWALSKI, F. BOUDON, C. FOURNIER, C. GODIN. *OpenAlea: A visual programming and component-based software platform for plant modeling*, in "Functional Plant Biology", 2008, vol. 35, n^o 9 & 10, pp. 751–760, http://www-sop.inria.fr/virtualplants/Publications/2008/PDBFG08a
- [11] 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
- [12] 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. GUYOMARCH, C. CELLIER, G. PARRY, R. KOUMPROGLOU, J. DOONAN, M. ESTELLE, C. GODIN, S. KEPINSKI, M. 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

Articles in International Peer-Reviewed Journals

- [13] 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
- [14] 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, no 76 [DOI: 10.3389/FPLS.2012.00076], http://hal.inria.fr/cirad-00703085
- [15] M. CHAVES, E. FARCOT, J.-L. GOUZÉ. *Probabilistic approach for predicting periodic orbits in piecewise affine differential models*, in "Bulletin of Mathematical Biology", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/CFG12
- [16] E. COSTES, Y. GUÉDON. *Deciphering the ontogeny of a sympodial tree*, in "Trees Structure and Function", 2012, vol. 26, n^o 3, pp. 865–879, http://www-sop.inria.fr/virtualplants/Publications/2012/CG12
- [17] D. DA SILVA, P. BALANDIER, F. BOUDON, A. MARQUIER, C. GODIN. *Modeling of light transmission under heterogeneous forest canopy: an appraisal of the effect of the precision level of crown description*, in "Annals of Forest Science", 2012, vol. 69, n^o 2, pp. 181–193, http://www-sop.inria.fr/virtualplants/Publications/2012/DBBMG12

- [18] R. EDWARDS, E. FARCOT, E. FOXALL. *Explicit construction of chaotic attractors in Glass networks*, in "Chaos, Solitons & Fractals", 2012, vol. 45, n^o 5, pp. 666–680, http://www-sop.inria.fr/virtualplants/Publications/2012/EFF12
- [19] C. GAUCHEREL, F. BOUDON, T. HOUET, M. CASTETS, C. GODIN. *Understanding patchy land-scape dynamics: Towards a landscape language*, in "PLoS ONE", April 2012, vol. 7, n^o 9, 16 p. [DOI: 10.1371/JOURNAL.PONE.0046064], http://hal.inria.fr/halshs-00750971
- [20] C. HATT, F. MANKESSI, J.-B. DURAND, F. BOUDON, F. MONTES, M. LARTAUD, J.-L. VERDEIL, O. MONTEEUIS. Characteristics of Acacia mangium shoot apical meristems in natural and in vitro conditions in relation to heteroblasty, in "Trees Structure and Function", 2012, vol. 26, n^o 3, pp. 1031-1044, PDF version of the authors can be published in January 2013 [DOI: 10.1007/s00468-012-0680-0], http://hal.inria.fr/hal-00699815
- [21] G. LOUARN, D. DA SILVA, C. GODIN, D. COMBES. Simple envelope-based reconstruction methods can infer light partitioning among individual plants in sparse and dense herbaceous canopies, in "Agricultural and Forest Meteorology", 2012, vol. 166-167, pp. 98–112, http://www-sop.inria.fr/virtualplants/Publications/ 2012/LDGC12
- [22] A. MIDDLETON, E. FARCOT, M. OWEN, T. VERNOUX. *Modeling regulatory networks to understand plant development: small is beautiful*, in "The Plant Cell", 2012, vol. 24, n^o 10, pp. 3876–3891, http://www-sop.inria.fr/virtualplants/Publications/2012/MFOV12
- [23] 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
- [24] M. OLIVA, E. FARCOT, T. VERNOUX. Plant hormone signaling during development: insights from computational models, in "Current Opinion in Plant Biology", 2012
- [25] M. WALKER, E. FARCOT, J. TRAAS, C. GODIN. The flux-based PIN allocation mechanism can generate either canalyzed or diffuse distribution patterns depending on geometry and boundary conditions, in "PloS one", 2012

International Conferences with Proceedings

- [26] M. CIESLAK, F. BOUDON, S. KENOUCHE, M. ZANCA, C. GOZE-BAC, M. GÉNARD, C. GODIN, N. BERTIN. Generating 3D volumetric meshes of internal and external fruit structure, in "HortiModel2012 Models for Plant Growth, Environmental Control and Farm Management in Protected Cultivation. Acta Horticulturae", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/CBKZGGGB12
- [27] T. M. DEJONG, C. NEGRON, R. FAVREAU, E. COSTES, G. LOPEZ, Y. GUÉDON. *Using concepts of shoot growth and architecture to understand and predict responses of peach trees to pruning*, in "7th International Peach Symposium, Lleida. Acta Horticulturae", 2012, vol. 962, pp. 225–232, http://www-sop.inria.fr/virtualplants/Publications/2012/DNFCLG12
- [28] C. FOURNIER, C. PRADAL. A plastic, dynamic and reducible 3D geometric model for simulating gramineous leaves, in "Fourth International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications", 2012, pp. 125–132, http://www-sop.inria.fr/virtualplants/Publications/2012/FP12

- [29] Y. GUÉDON. *Incertitude sur la segmentation pour les modèles de détection de ruptures multiples*, in "44èmes Journées de Statistique, Bruxelles", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/Gue12
- [30] L. HAN, D. DA SILVA, F. BOUDON, T. COKELAER, C. PRADAL, E. COSTES. *Investigating the Influence of Geometrical Traits on Light Interception Efficiency of Apple Trees: a Modelling Study with MAppleT*, in "Fourth International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/HDBCPFC12/
- [31] S. KENOUCHE, J. LARIONOVA, N. BEZZI, Y. GUARI, N. BERTIN, M. ZANCA, L. LARTIGUE, M. CIESLAK, C. GODIN, G. MORROT, C. GOZE-BAC. *NMR investigations of functionalized magnetic nanoparticles Fe3O4 as T1 T2 contrast agents*, in "7ème colloque Science et Technologie des poudres", France, July 2012, 33 p., http://hal.inria.fr/hal-00735403
- [32] S. LONGAY, A. RUNIONS, F. BOUDON, P. PRUSINKIEWICZ. *TreeSketch: Interactive Procedural Modeling of Trees on a Tablet*, in "EUROGRAPHICS Symposium on Sketch-Based Interfaces and Modeling", L. KARA, K. SINGH (editors), Eurographics, 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/LRBP12
- [33] G. LOUARN, S. CARRÉ, F. BOUDON, D. COMBES. *Characterization of whole plant leaf area properties using laser scanner point clouds*, in "Fourth International Symposium on Plant Growth Modeling, Simulation, Visualization and Applications", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/LCBC12
- [34] J. PEYHARDI, C. TROTTIER, Y. GUÉDON. *GLM multinomial hiérarchique*, in "44èmes Journées de Statistique, Bruxelles", 2012, http://www-sop.inria.fr/virtualplants/Publications/2012/PTG12

National Conferences with Proceedings

[35] A. KISS, M. CORTIZO, E. BIOT, J. BURGUET, C. GODIN, P. LAUFS, A. BOUDAOUD. *Quantification de la morphodynamique des dents des feuilles d'Arabidopsis thaliana*, in "7eme Symposium Morphométrie et Evolution des Formes", 2012

Research Reports

[36] J.-B. DURAND, Y. GUÉDON., Localizing the latent structure canonical uncertainty: Entropy profiles for hidden Markov models., Inria, 2012, no 7003, http://www-sop.inria.fr/virtualplants/Publications/2012/DG12

References in notes

- [37] A. Arber, Natural philosophy of plant form, University Press, Cambridge, 1950
- [38] 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
- [39] F. CHAUBERT-PEREIRA, Y. CARAGLIO, C. LAVERGNE, Y. GUÉDON. *Identifying ontogenetic, environmental and individual components of forest tree growth.*, in "Annals of Botany", 2009, vol. 104, n^o 5, pp. 883–896, http://www-sop.inria.fr/virtualplants/Publications/2009/CCLG09
- [40] 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

- [41] 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
- [42] 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
- [43] F. HALLÉ, R. A. A. OLDEMAN, P. B. TOMLINSON., *Tropical trees and forests. An architectural analysis*, Springer-Verlag, New-York, 1978
- [44] J. L. HARPER, B. R. ROSEN, J. WHITE., *The growth and form of modular organisms*, The Royal Society, London, UK, 1986
- [45] R. NOZERAN. *Integration of organismal development*, in "Positional controls in plant development", P. BARLOW, D. CARR (editors), 1984, pp. 375-401
- [46] D. REINHARDT, E.R. PESCE, P. STIEGER, T. MANDEL, K. BALTENSPERGER, M. BENNETT, J. TRAAS, J. FRIML, C. KUHLEMEIER. *Regulation of phyllotaxis by polar auxin transport*, in "Nature", November 2003, vol. 426, no 6964, pp. 255–260, http://www.nature.com/nature/journal/v426/n6964/abs/nature02081.html
- [47] A. RUNIONS, B. LANE, P. PRUSINKIEWICZ. *Modeling Trees with a Space Colonization Algorithm*, in "Eurographics Workshop on Natural Phenomena", 2007, pp. 63-70 [DOI: 10.2312/NPH/NPH07/063-070], http://www.eg.org/EG/DL/WS/NPH/NPH07/063-070.pdf
- [48] 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
- [49] O. TAUGOURDEAU, F. CHAUBERT-PEREIRA, S. SABATIER, Y. GUÉDON. Deciphering the developmental plasticity of walnut saplings in relation to climatic factors and light environment, in "Journal of Experimental Botany", 2011, vol. 62, n^o 15, pp. 5283–5296, http://www-sop.inria.fr/virtualplants/Publications/2011/TCSG11
- [50] J. WITHER, F. BOUDON, M.-P. CANI, C. GODIN. Structure from silhouettes: a new paradigm for fast sketch-based design of trees, in "Eurographics", 2009