



INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

*Project-Team Virtual Plants*

*Modeling plant morphogenesis at different  
scales, from genes to phenotypes*

*Sophia Antipolis - Méditerranée*

Theme : Observation, Modeling, and Control for Life Sciences

*Activity*  
*R* *eport*

2009



## Table of contents

<b>1. Team</b>	<b>1</b>
<b>2. Overall Objectives</b>	<b>1</b>
<b>3. Scientific Foundations</b>	<b>2</b>
3.1. Analysis of structures resulting from meristem activity	2
3.2. Meristem functioning and development	3
3.3. OpenAlea: An open-software platform for plant modeling	3
<b>4. Software</b>	<b>4</b>
4.1. V-Plants	4
4.2. OpenAlea	5
4.3. Alinea	6
<b>5. New Results</b>	<b>7</b>
5.1. Analysis of structures resulting from meristem activity	7
5.1.1. Acquisition and design of plant geometry	7
5.1.2. Modeling the plant ontogenic programme	9
5.1.3. Analyzing the influence of the environment on the plant ontogenic programme	11
5.2. Meristem functioning and development	12
5.2.1. Data acquisition and design of meristem models	12
5.2.2. Transport models	14
5.2.3. Mechanical model	15
5.2.4. Cell cycle model	15
5.2.5. Gene regulatory networks	16
5.2.6. Model integration	16
<b>6. Other Grants and Activities</b>	<b>17</b>
6.1. National Grants	17
6.1.1. Agropolis computational plant seminar	17
6.1.2. Advanced Markovian techniques in population dynamics	17
6.1.3. OpenAlea	17
6.1.4. vTissue	17
6.1.5. Alinea	18
6.1.6. M2A3PC	18
6.1.7. Fruit3D	18
6.1.8. PlantScan3D	18
6.1.9. GeneShape	19
6.2. International Bilateral Relations	19
6.2.1. ANR-BBSRC Grant	19
6.2.2. Other bilateral relations	20
<b>7. Dissemination</b>	<b>20</b>
7.1. Services to the scientific community	20
7.2. Academic teaching	21
7.2.1. Master Biostatistics	21
7.2.2. Master Computer Science	21
7.2.3. Master Biotraçabilité, Biodétection, Biodiversité	21
7.2.4. Master Classes	21
7.2.5. Undergraduate Classes	21
7.2.6. High School class	21
7.3. Participation in workshops, seminars and miscellaneous invitations	21
7.4. Theses and Internships	22
7.4.1. Theses defenses	22
7.4.2. Ongoing Theses	22

7.4.3. Internships	22
<b>8. Bibliography</b> .....	<b>23</b>

# 1. Team

## Research Scientist

Christophe Godin [ DR, Team Leader, HdR ]  
Yann Guédon [ DR, CIRAD, vice-Head, HdR ]  
Christophe Pradal [ IR, CIRAD ]  
Frédéric Boudon [ CR, CIRAD ]  
Etienne Farcot [ CR ]

## Faculty Member

Jean-Baptiste Durand [ MC, on leave from ENSIMAG and LJK/Mistis ]  
Florence Chaubert-Pereira [ ATER, University Montpellier 2 ]

## External Collaborator

Christian Cilas [ DR, CIRAD ]  
Evelyne Costes [ DR, INRA, HdR ]  
Pascal Ferraro [ MC, Bordeaux I University ]  
Christian Fournier [ CR, INRA ]  
Christian Jay-Allemand [ PR, University Montpellier 2 ]  
Laurent Laplaze [ CR, IRD ]  
Grégoire Malandain [ DR, INRIA Sophia-Antipolis, HdR ]  
Jan Traas [ DR, ENS Lyon, HdR ]  
Catherine Trottier [ MC, Montpellier 3 University ]  
Jean-Luc Verdeil [ DR, CIRAD, HdR ]

## Technical Staff

Daniel Barbeau [ Expert Engineer, RTRA INRIA ]  
Thomas Cokelear [ Expert Engineer, RTRA ]  
Eric Moscardi [ Junior Engineer, ADT INRIA ]

## PhD Student

Damien Fumey [ CIFRE Grant, Agronomy, 2010 ]  
Romain Fernandez [ CIRAD/Région Grant, Computer Science, 2009 ]  
Chakkrit Preuksakarn [ Grant from University of Kasetsart, Bangkok, Thailand, Computer Science, 2011 ]  
Yassin Refahi [ INRA/INRIA Grant, Computer Science, 2011 ]  
Szymon Stoma [ European Grant, Computer Science, 2008 ]  
Anaëlle Dambreville [ CIRAD Grant, Biology, 2012 ]

## Post-Doctoral Fellow

Jérôme Chopard [ ANR Flower Model Grant ]  
Mikaël Lucas [ CPIB ]  
Michael Walker [ ANR Geneshape Grant ]

## Administrative Assistant

Annie Aliaga [ INRIA, partial time ]  
Valérie Caruana [ CIRAD, partial time ]

# 2. Overall Objectives

## 2.1. Overall Objectives

The **Virtual Plants** team is a joint team between **INRIA**, **CIRAD** and **INRA** located in Montpellier. The long-term focus of the project is to study plant development 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 believe that a detailed analysis of apical meristem processes, based on advanced mathematical and computational methods and tools, will lead us 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 organisation of these complex biological objects,
- and models for morphogenesis.

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

## 3. Scientific Foundations

### 3.1. Analysis of structures resulting from meristem activity

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

- *Combinatorial approaches*: plant structures exhibit complex branching organizations of their organs like internodes, leaves, shoots, axes, branches, etc. These structures can be analysed with combinatorial methods in order to compare them or to reveal particular types of organisation. 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 (hidden) variable-order Markov chains and lumped processes constructed from Markov chains. Variable-order Markov chains are in particular applied to identify complex branching patterns resulting from local inhibition phenomena.

- 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 Markovian and hidden Markovian models (in this latter case to explore the hidden state sequence or tree 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 analyse their dynamic and complex spatial interaction. To carry out this integration, we need to develop a complete methodological approach containing:

- image processing on stacks of images coming from confocal microscopy,
- algorithms to reconstruct the meristem surface or volume (partially based on classical image processing techniques),
- lineage algorithms that automatically track cell division throughout time,
- tools for structural and statistical analysis of 3D meristem structure (spatial statistics, multiscale geometric and topological analysis),
- physical models of cell interaction based on spring-mass systems or on tensorial mechanics at the level of cells,
- models of fluxes and physiological interactions between cells based on differential equations and partial differential equations,
- and models of cell development taking into account cell division and gene control (using either differential equations, finite state automata or Petri nets).

## 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** 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 10 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 main data structures such as multiscale tree graph 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 modellers for various purposes (research, teaching, rapid model prototyping, communication, etc.).

## 4. Software

### 4.1. V-Plants

**Participants:** Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal [coordinator], Daniel Barbeau, Florence Chaubert-Pereira, Jérôme Chopard, Thomas Cokelaer, David Da Silva, Jean-Baptiste Durand, Pascal Ferraro, Eric Moscardi, Szymon Stoma.

*Other participant:* Aida Ouangraoua (LaBRI, Bordeaux).

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.

In 2009, the *V-Plants* packages have been integrated as components of the *OpenAlea* platform (see Section 4.2). Several components are distributed and usable through the visual programming environment (see figure 2):

- Multi-scale geometric modelling and visualisation. VPlants.PlantGL is a geometric library which provides a set of graphical tools and algorithms for 3D plant modelling at different scales [15]. 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 datastructure and provides efficient algorithms and original geometrical shapes (parametric surfaces, dedicated envelops) useful for plant modeling.
- Statistical sequence and tree analysis. Different statistical packages (i.e. VPlants.StatTool, VPlants.SequenceAnalysis, VPlants.TreeMatching and VPlants.TreeAnalysis) are available into *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 plant and tissue. *OpenAlea.Container* and *OpenAlea.MTG* are two packages which implement generic graph data structure to represent the topological structure of the meristem and of the plant architecture, as well as the dataflow graph in *OpenAlea*. These components make it possible to share plant representations between users and fosters the interoperability of new models.
- Simulation system. The L-Py package couples the well known L-system formalism for simulating fractal structures and plant development with the Python modeling language (basis of *OpenAlea*). Extensions to integrate multiscale models are currently being developed in collaboration with P. Prusinkiewicz and his team from the University of Calgary.



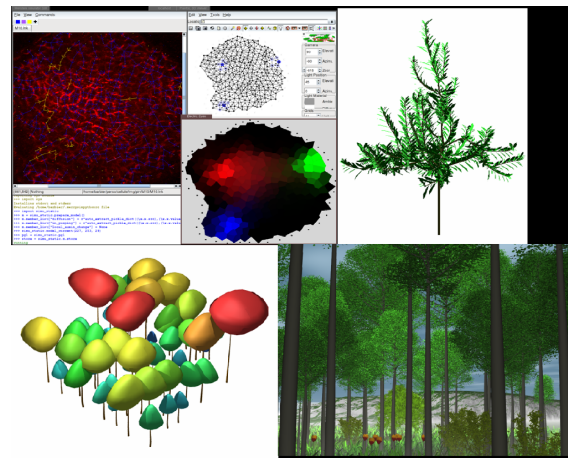


Figure 1. V-Plants components of the OpenAlea platform: simulating plant processes at different scales. Top Left: Reconstruction of a virtual meristem, analysis and simulation of the auxin fluxes inside the meristem. Top Right: Reconstruction of a virtual apple tree from digitized data. Bottom: Simulation 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.

## 4.2. OpenAlea

**Participants:** Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal [coordinator], Daniel Barbeau, Florence Chaubert-Pereira, Jérôme Chopard, Thomas Cokelaer, Christian Fournier, Eric Moscardi.

*This research theme is supported by an INRIA ADT Grant and by a RTRA Grant.*

*Other participant: Nicolas Donès (INRA - UMR PIAF, Clermont Ferrand).*

*OpenAlea* [19] is an open source and collaborative software project primarily dedicated to the plant research community 3.3.

*OpenAlea* is designed as a component framework to dynamically glue together models from different plant research labs, and to enhance reusability of existing models in the plant research community.

In 2009, the following steps have been performed:

1. Develop and extend the component platform architecture
  - OpenAlea.Core is the kernel of OpenAlea. It provides a component architecture, a package manager and a dataflow to build models by interconnecting components in a directed graph.
  - OpenAlea.Visualea is a visual programming application allowing us to build intuitively new models by connecting available components together. For each component, a graphical user interface is automatically generated based on the type of its interfaces (see figure 2).
  - OpenAlea.Deploy : Deploy extends the python setuptools package to simplify the deployment and the installation of the different OpenAlea packages. It is able to research available OpenAlea packages on different web repositories (like GForge), and provides an uniform way to the user to install and update components on different platforms.
2. Animation and diffusion

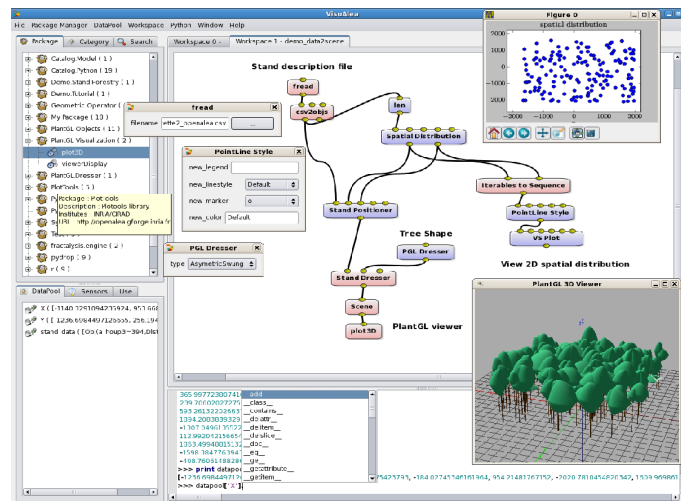


Figure 2. OpenAlea.Visualea: Visual programming interface. The package manager shows the available components. The components can be interconnected on a workspace to form a dataflow. The python interpreter allows low level interaction with the system.

- Developers and modelers of different teams start collaboration and work together in pairs on a common objective during coding and modeling sprint sessions. Since 2006, 13 coding sprint and modeling sprints have been organised. These sessions enhance collaboration between developers and modellers and facilitate co-development.
- The project has been presented in various conferences (FSPM, EuroPython06, EuroPython07, EuroSciPy09). Software demonstrations have been held in the FSPM conference and in the INRIA 40 ans, presenting a set of plant modeling scenarii provided by different modelers of the OpenAlea community.
- The OpenAlea project is hosted at the Inria's gforge. The web site is visited by more than 300 unique visitor each month; 339000 web pages have been visited and the different available components of OpenAlea have been downloaded more than 190000 during the last two years.

### 4.3. Alinea

**Participants:** Christophe Pradal [coordinator], Christian Fournier.

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.

In 2009, several research group from INRA and CIRAD have worked together on reconstruction and simulation of plant development for different species of gramineous such as rice, wheat, or maize. Different components have been integrated into the OpenAlea platforms:

- Alinea.Adel is a module to simulate the 3D architectural development of gramineous crops.
- Alinea.Caribu is a modelling 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.TopVine is a component to reconstruct grapevine canopy structure.

## 5. New Results

### 5.1. Analysis of structures resulting from meristem activity

#### 5.1.1. Acquisition and design of plant geometry

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

*This research theme is supported by RTRA project PlantScan3D.*

Virtual 3D model of plants are required in many areas of plant modelling. 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 architecture in 3D [40], [28]. 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 topic, we explore the use of laser scanner and direct sketching. Resulting models should be parsimonious. We also consider the definition of methods to post-process these complex representations into compact ones and apply them on streaming.

- *Reconstruction of plant architecture from 3D laser scanner data.* (Chakkrit Preuksakarn, Frédéric Boudon, Christophe Godin, Jean-Christophe Chambellan [UMR PIAF, Clermont-Ferrand], Bernard Mourrain [INRIA, Galaad], Hervé Sinoquet [UMR PIAF, Clermont-Ferrand], Wenping Wang [University of Hong Kong], Dong-Ming Yan [University of Hong Kong])

In this topic, we investigate the possibility to use 3D laser scanners to automate plant digitizing. We are currently designing algorithms to reconstruct branching systems without leaves 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 Evasion from Grenoble, different INRA team : PIAF-Clermont Ferrand, LEPSE- and AFEF-Montpellier and Lusignan, the University of Helsinki, Finland and the CFCC in England. The project PlantScan3D has been funded in 2009 by the Agropolis Foundation and started in septembre. A new proposal to the 2009 ARC INRIA call has been made to obtain grants for postdoctoral positions.

With the GALAAD team, we already proposed a first reconstruction pipeline made up of three main steps: segmentation, reconstruction and modeling. Based on a variational k-means clustering algorithm, cylindrical components and branching regions of data points are identified and located. An adjacency graph is then built from neighborhood information of components. Simple heuristics allow us to extract a tree structure and identified branches from the graph. Finally, a B-spline model is computed to give a compact and accurate reconstruction of the branching system. This work has been accepted for publication as short paper at the IEEE International conference on Computer-Aided Design and Computer Graphics [18].

We continue this work by investigating new methods based on Space Colonization Algorithm [39] in the context of the PhD of Chakkrit Preuksakarn. An evaluation procedure to assess accuracy of the reconstruction is also currently being investigated. It is based on topological edit distance [25] to compare two tree graphs weighted with geometrical information.

- *Sketching of plants.* (Frédéric Boudon, Christophe Godin, Jamie Wither [INRIA, Evasion], Marie-Paule Cani [INRIA, Evasion])

Modeling natural elements such as trees in a plausible way, while offering simple and rapid user control, is a challenge. In collaboration with the EPI Evasion we developed a method based on the design of plants from silhouettes. This sketching paradigm allows quick and intuitive specification of foliage at multiple scales. This choice allows us to incorporate botanical knowledge to infer branches that connect in a plausible way to their parent branch and have a correct 3D distribution. We illustrated these ideas by building a seamless sketch-based interface, used for sketching foliage silhouettes from the scale of an entire tree to the scale of a leaf. Each sketch serves for inferring both the branches at that level and construction lines to support sub-silhouette refinement. When the user finally zooms out, the style inferred for the branching systems he has refined (in terms of branch density, angle, length distribution and shape) is duplicated to the unspecified branching systems at the same level. Meanwhile, knowledge from botany is again used for extending the branch distribution to 3D, resulting in a full, plausible 3D tree that fits the user-sketched contours. As our results show, this system can be of interest to both experts and novice users: while experts can fully specify all parts of a tree and over-sketch specific branches if required, any user can design a basic 3D tree in one or two minutes, as easily as sketching it with paper and pen, as illustrated on Figure 3. This work has been accepted at the Eurographics 2009 conference and has been published in Computer Graphics Forum [17]. The next step will consist of sketching growing plants. In this case, the user refinement will correspond to addition of elements through time.



Figure 3. Output of an eucalyptus, as produced from the sketch pictured on the upper-right.

- *Compression and streaming of plant geometry for distributed environments.* (Frédéric Boudon, Christophe Pradal, Wei Cheng [National University of Singapour], Romulus Grigoras [IRIT, Toulouse], Jean-Christophe Hoelt [IRIT, Toulouse], Sebastien Mondet [IRIT, Toulouse], Geraldine Morin [IRIT, Toulouse], Wei Tsang Ooi [National University of Singapour])

Much effort has been made in realistic modeling of plants for instance as support of physical simulation. As the trend moves towards networked and distributed virtual environment, however, the current models are inadequate as they are not designed for progressive transmissions. In this work, we fill in this gap by proposing a progressive representation for plants based on generalized cylinders. We proposed a differential coding of plants: an average branch is computed for any chosen group of branches and then, for each branch, we only need to code some transformations for instantiation and differences for geometry refinement. To be able to stream, we identify and take advantage of two types of dependencies: topological and dependencies due to differential coding. We obtain a progressive model that makes it possible to select a lightweight representation of a plant while preserving branch density. To facilitate the transmission of the plants in the network, we

quantify the visual contribution of each branch and use this weight in packet scheduling. We show the efficiency of our representations and effectiveness of our packet scheduler through simulations. This work was presented at ACM Multimedia 2008 Conference [35] and received the Best Paper Award. An extended version of this work was published this year in ACM TOMCCAP [14]. Moreover, a technical demonstration of an implementation of this technique for Mobile, named MobiTree [16], has been made at the ACM Multimedia 2009 Conference.

### 5.1.2. Modeling the plant ontogenic programme

**Participants:** Christophe Godin, Yann Guédon, Evelyne Costes, Jean-Baptiste Durand, Pascal Ferraro, Yassin Refahi, Etienne Farcot.

*This research theme is supported by a PhD programme.*

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. [22], [30], [31], [6], 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 organisations such as "morphogenetic programme" [36], "age state" [27] or "physiological age" [23]. 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 [27], [23]. Here we develop computational methods to decipher these rules.

- *Branching and axillary flowering structures of fruit tree shoots.* (Yann Guédon, Evelyne Costes, Ted DeJong (UC Davis), Claudia Negron (UC Davis))

In the context of a collaboration with Claudia Negron, David Da Silva and Ted DeJong, stochastic models (hidden semi-Markov chains) for the branching and axillary flowering structures of different categories of peach and almond shoots were built. These stochastic models have been integrated in simulation systems which combine stochastic models with different mechanistic models of biological function, in particular carbon partitioning models. This collaboration extends the work initiated on apple trees [38], [24]; see 5.1.3.

- *Axis structure of fruit trees.* (Yann Guédon, Evelyne Costes)

During the past years, a set of methods was proposed to characterize the growth components (mainly ontogenetic and environmental components) of forest trees [29], [11] on the basis of main axes measured at the growth unit or annual shoot scale. We started to study axis structure of fruit trees. The agronomic context (grafted cultivars, irrigated orchard) renders very rapid the ontogenetic changes and reduces the environmental influence compared to forest trees. We studied in particular the structures of apple tree cultivars at the growth unit (GU) scale. Hidden variable-order Markov chains were applied to identify repeated patterns corresponding to the alternation between vegetative and flowering GUs along axes. In these models, GU categories are deduced from morphological characteristics (number of nodes and presence/absence of flowering) and their succession modeled by a non-observable variable-order Markov chain. This integrative statistical model enabled us to reveal a two-scale structuring of the successive differentiation stages during apple tree ontogeny, a coarser scale corresponding to the succession of two developmental phases and a finer scale corresponding to the alternation between flowering and vegetative GUs of a given type. This approach led us to propose a synthetic scheme of apple tree ontogeny that combines polycyclism, flowering and morphogenetic gradients.

- *Hidden Markov tree models for investigating physiological states within plants.* (Jean-Baptiste Durand, Patrick Heuret (UMR AMAP))

During plant ontogeny, different kinds of patterns emerge, among which homogeneous stages of growth, or remarkable succession or alternation of given features. To unravel such patterns that characterize plant architecture, statistical analyses have been performed, based on hidden Markov

tree (HMT) models. The global aim of these analyses is to infer several levels of differentiation of the meristems from the structures they produce [3]. Since these levels are assumed to be ordered, they are referred to as "physiological state of the meristems".

Based on HMT models, a study was conducted on *Symphonia globulifera* (Clusiaceae) (a tree species of the rain forest in French Guyana) to characterize the effect of light on the architecture, and more specifically to quantitatively assess the connection between illuminance, the number of growth cycles necessary for the plant to reach the canopy, and the rate of synchronism among the plant entities.

- *Self-nested structure of plants.* (Christophe Godin, Pascal Ferraro)

To study the redundancy of structure embedded at various levels in tree architectures, we investigated the problem of approximating trees by trees with particular self-nested structures. Self-nested trees are such that all their subtrees of a given height are isomorphic. We show that these trees present remarkable compression properties, with high compression rates. In order to measure how far a tree is from being a self-nested tree, we introduced a quantitative measure of the degree of self-nestedness for any tree. For this, we construct a self-nested tree that minimizes the distance of the original tree to the set of self-nested trees that embed the initial tree:

$$NEST(T) = \arg \min_{S \in \mathcal{S}^+(T)} D(T, S),$$

where  $T$  is a tree,  $D(\cdot, \cdot)$  is a distance on the set of trees (chosen so as to preserve certain structural properties between the compared trees) and  $\mathcal{S}^+(T)$  is the set of self-nested trees that contain  $T$ , i.e. that can be obtained from  $T$  by inserting nodes only.

To solve this optimization problem, we designed a polynomial-time algorithm that makes it possible to quantify the degree of self-nestedness of a tree in a precise manner. The distance to this nearest embedding self-nested tree (NEST) is then used to define compression coefficients that reflect the compressibility of a tree. In the context of the structural analysis of botanical plants, it is possible to give a strong biological interpretation of the NEST of a tree based on the hypothesis that isomorphic tree structures at macroscopic levels are actually produced by meristems in identical physiological states (scaling hypothesis). This makes it possible to show that the reduction graph of the NEST of a plant may be interpreted as the maximum sequence of differentiation states that any meristem of a plant may go through. We characterized this approach on both a database of artificial plants with degraded degree of self-nestedness and on a real plant (a rice panicle) whose structure was completely measured, see Figure 4. We showed that the NEST of this plant may be interpreted in biological terms and reveals important aspects of the plant growth. This work has been accepted by IEEE Transactions on Computational Biology and Bioinformatics (IEEE/ACM TCBB).

- *Perturbed phyllotaxis of Arabidopsis thaliana AHP6 mutant.* (Etienne Farcot, Yann Guédon, Yassin Refahi, Christophe Godin, Fabrice Besnard (RDP, Lyon), Teva Vernoux (RDP, Lyon))

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 on the cytokinin signaling pathway. At the macroscopic scale, this mutation induces perturbations of the phyllotaxis, barely sensible on single plants. Based on a sample of approximately 40 wild-type and 40 mutant plants, we have developed a method to characterize these perturbations. In both wild-type and mutant plants, the theoretical spiral of organs along the main axis is in fact affected by local permutations (i.e. the interchange of adjacent organs in the sequence). Using a statistical model (hidden variable-order Markov chain) and a combinatorial model, we have shown that a regular spiral with such permutations provides an appropriate description for more than 95% of the data, the mutant plants exhibiting significantly more local permutations than the wild-type.

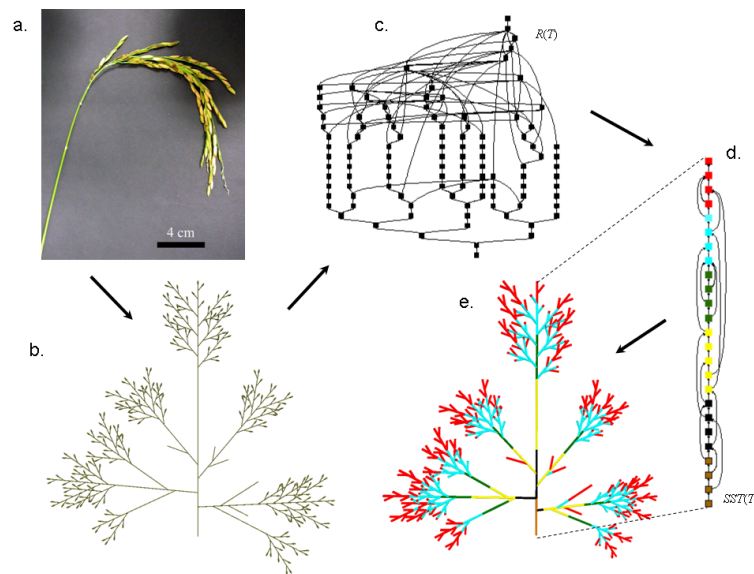


Figure 4. (a) Photo of a rice panicle (b) tree representing the topological structure of the panicle (c) Reduced graph of the panicle tree (d) Corresponding NEST that can be interpreted as the maximal sequence of differentiation states that a meristem can go through when building the panicle (e) color map of the meristem differentiation states obtained by projecting the NEST states back to the original topological tree

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

**Participants:** Florence Chaubert-Pereira, David Da Silva, Damien Fumey, Frédéric Boudon, Christophe Godin, Yann Guédon, Christian Cilas, Evelyne Costes, Pascal Ferraro, Christian Lavergne, Hervé Sinoquet, Catherine Trottier.

*This research theme is supported by a CIFRE contract and two PhD programmes.*

The ontogenetic programme of a plant is actually sensitive to environmental changes. If, in particular cases, we can make the assumption that the environment is a fixed control variable (see section 5.1.2), in general the structure produced by meristem results from a tight interaction between the plant and its environment, throughout its lifetime. Based on observations, we thus aim to trace back to the different components of the growth (ontogenetic development and its control 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 variates that represent the environment variations. The design of estimation procedures for these models make it possible to separate the plant ontogenetic programme from its modulation by the environment. On the other hand, we build reactive models that make it possible to simulate in a mechanistic way the interaction between the plant development and its environment.

- *Analyzing growth components in trees.* (Florence Chaubert-Pereira, Yann Guédon, Yves Caraglio (AMAP), Christian Lavergne, Emilie Lebarbier (AgroParisTech), Catherine Trottier, Olivier Tau-gourdeau (AMAP))

Observed growth, as given for instance by the length of successive annual shoots along a forest tree trunk, is assumed to be mainly the result of three components: (i) an endogenous component assumed to be structured as a succession of roughly stationary phases separated by marked change points that are asynchronous between individuals [29], (ii) a time-varying environmental component assumed to take the form of fluctuations that are synchronous between individuals, (iii) an individual

component corresponding to the local environment of each tree. This environmental component is thus assumed to be a "population" component as opposed to the individual component. In order to identify and characterize these three components, we proposed to use semi-Markov switching linear mixed models [11], [12]. The underlying semi-Markov chain represents the succession of growth phases (endogenous component) while the linear mixed model attached to each state of the underlying semi-Markov chain represents -in the corresponding growth phase- both the influence of time-varying climatic explanatory variables (environmental component) as fixed effects, and inter-individual heterogeneity (individual component) as random effects. We investigated the estimation of Markov and semi-Markov switching linear mixed models in a general framework using MCEM-like algorithms. Concerning the application to forest trees, the proposed statistical modeling approach relies on the availability of climatic data. In the case where climatic data are not available, we are studying Markov and semi-Markov switching linear mixed models with year random effects common to all the trees to model the synchronous part of the growth fluctuations. With semi-Markov switching linear mixed models, the response variable is constrained to be approximately normally distributed. We are now studying the statistical methodology for semi-Markov switching generalized linear mixed models to take into account non-normally distributed response variables (e.g. number of growth units, apex death/life, non-flowering/flowering character). It should be noted that the estimation algorithms proposed for Markov switching linear mixed models can be directly transposed to other families of hidden Markov models such as, for instance, hidden Markov tree models; see Section 5.1.2.

- *Coupling stochastic models with mechanistic models for plant development simulation.* (Damien Fumey, Yann Guédon, Christophe Godin, Thomas Cokelaer, Evelyne Costes, Pierre-Eric Lauri (UMR DAP))

Arboricultural practices such as pruning, artificial bending or fruit thinning are crucial interventions in orchard management and are used for controlling tree size, penetration of light into the canopy and the equilibrium between vegetative and reproductive growth. The aim of the PhD of Damien Fumey is to explore the possibility of integrating such practices in a model of apple tree development. To this end, a field experiment was designed to study the effects of pruning (thinning or heading cuts) on two apple cultivars with contrasted architecture, 'Fuji' and 'Braeburn'. The first results of this experiment [26] showed that thinning cuts of laterals tended to be compensated by an increase in lateral branching. Based on these field experiments, a model is currently being developed to account for pruning practices on fruit trees. This model relies on a formalization of the competition of meristems by combining a carbon allocation strategy and a competition mechanism in a stochastic manner. The resulting model is reactive to human interventions and should enable us to capture plant reactions to pruning practices in a robust way.

## 5.2. Meristem functioning and development

In axis 2 work focusses 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

**Keywords:** *Meristem, automatic lineaging, cell segmentation, image reconstruction, laser microscopy.*

**Participants:** Romain Fernandez, Jérôme Chopard, Frédéric Boudon, Christophe Godin, Vincent Mirabet, Jan Traas, Grégoire Malandain, Jean-Luc Verdeil.

*This research theme is supported by the ATP CIRAD Meristem and the ANR GeneShape and FlowerModel projects.*



Studies on plant development require the detailed observation of the tissue structure with cellular resolution. In this context it is important to develop methods that enable us to observe the inner parts of the organs, in order to analyse and simulate their behaviour. Here we focus on the apical meristems, that have been extensively studied using live imaging techniques and confocal microscopy. An important limitation of the confocal microscope lies in the data anisotropy. To overcome this limitation, we designed new protocols to achieve an accurate segmentation of the cells. Using these segmentations, a geometrical and topological representation of the meristem is built. Such representations may be used to analyze the meristem structure at cell level, to support the description of gene expression patterns and to initiate and assess virtual meristem simulations.

- *Microscopy image reconstruction and automatic lineage tracking of the growing meristem cells*

**Participants:** Romain Fernandez [Correspondant], Christophe Godin, Grégoire Malandain, Jean-Luc Verdeil, Jan Traas, Pradeep Das, Vincent Mirabet.

We studied the tracking of meristem cells using time-lapse confocal microscopy acquisition on early stages flowers of Arabidopsis shoot apical meristems. We designed a reconstruction method (MARS, figure 5) and a tracking algorithm (ALT) in order to map the segmentations of the same meristem at different times, based on a network flow representation in order to solve the cell assignment problem. We validated the MARS-ALT pipeline on a four-steps timecourse of an early stage floral bud. The validation by biologists showed the efficiency of the segmentation algorithm on the reconstructed images (near to 96 % of well-identified cells) and of the lineaging algorithm (100 % of well-identified lineages in the easier case and 90 % in the harder) and leads to a better understanding of the floral bud dynamics. This work was submitted to the journal Nature Methods and is currently under review.

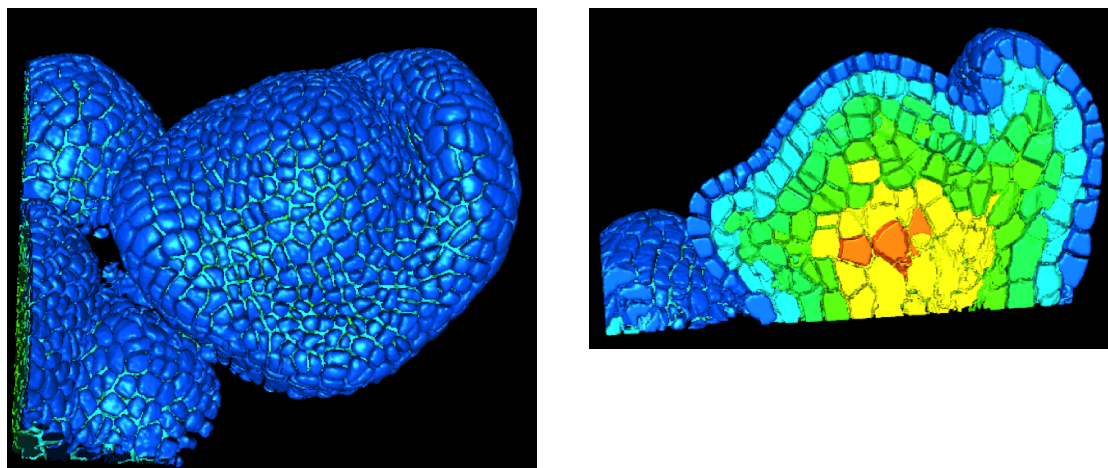


Figure 5. Surface view of a flower meristem automatically segmented using MARS at cell resolution and a transversal cut showing the inner segmented tissues

- *Design of a structural database for specifying gene expression patterns* (Jérôme Chopard, Christophe Godin, Jan Traas, Françoise Monéger (ENS Lyon))

*This research theme is supported the ANR GeneShape and FlowerModel projects.*

To organise the various genetic, physiological, physical, temporal and positional informations, we build a spatialised 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 retrieve and manipulate the information

visually, 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 polarisation (transporters, microtubules), and gene expression patterns. Such a database is mainly descriptive. However, like for classical databases, specific tools make it possible to explore the database 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 database.

A prototype version of such a database is currently being built and is integrated in *V-Plants*. Algorithms to explore such database at various levels of abstraction will have to be developed. Queries such as: get the number of cell of the L1 layer, get the volume ratio between two zones with different gene expression identities, perform the intersection of two expression zones, compute the curvature at the topmost cell, find the lineage of cells descending from this region, etc. would typically be carried out efficiently with such a database. The prototype of a 3D database presented on figure 6 shows a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity, etc.)

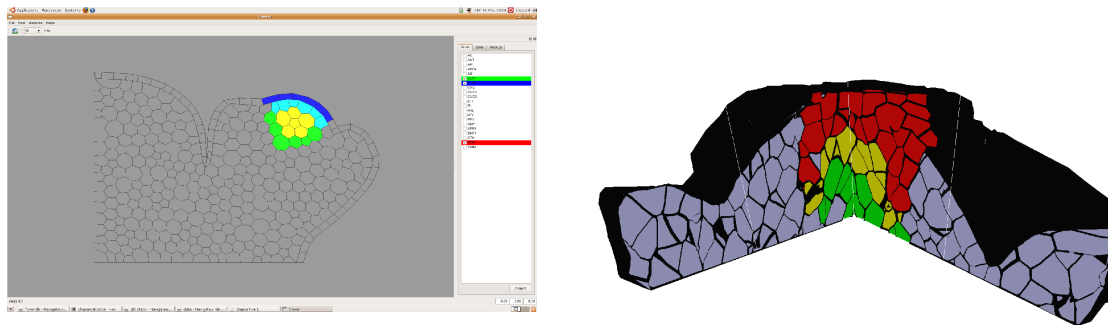


Figure 6. Prototype of a 3D database represented as a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity, ...)

### 5.2.2. Transport models

**Participants:** Mikaël Lucas, Jérôme Chopard, Christophe Godin, Yann Guédon, Laurent Laplaze, Jan Traas, Michael Walker.

*This research theme is supported by the ANR GeneShape project and a Post-doc Grant from CPIB.*

The transport of plant hormones, proteins, water and sugars is critical to plant development. In particular, the active transport of the plant hormone auxin has been shown to play a key role in the initiation of organs at the shoot apex. Polar localized membrane proteins of the PIN1 and AUX/LAX family facilitate this transport and recent observations and models suggest that the coherent organization of these proteins in the L1 layer is responsible for the creation of auxin maxima, which in turn triggers organ initiation close to the meristem centre [37] [1].

In the previous years, we built models of auxin transport in the L1 layer and inner tissues to understand the observed distribution of PIN transporters and study possible hypotheses related to their regulation. Now, we try to get farther in the understanding of auxin transport on two different systems.

- *Simulating auxin transport in 3D digital meristem cellular structures.*

Our first goal is to embed the auxin models developed previously in 3D meristem digital mock-ups obtained from confocal microscopy. This is a crucial step as main problems with auxin transport

seem to be related with the 2D approximation which has been made until now. Realistic models of auxin transport in 3D cells will make it possible to compare different hypotheses based on solid ground and to look for realistic transport parameters throughout the meristem dome.

- *Modeling axillary root initiation* (Mikael Lucas, Christophe Godin, Laurent Laplaze, Malcolm Bennet (CPIB, University of Nottingham, UK))

Root architecture is a crucial part of plant adaptation to soil heterogeneity and is mainly controlled by root branching. The process of root system development can be divided into two successive steps: lateral root initiation and lateral root development/emergence which are controlled by different fluxes of the plant hormone auxin. In previous studies we showed that a transport model based on competition for auxin between lateral organs was able to account for the branching patterns observed on lateral roots, including in mutant phenotypes [33], [34]. We now intend to study the distribution of PIN transporters (and other influx transporters) during the emergence of lateral roots. For this we are currently digitizing in 3D lateral roots during initiation and emergence. The dynamics of different transporters and key proteins is being described during this process so that we can depict a clear scenario of auxin homeostasis during lateral meristem development. A Languedoc-Roussillon Region project has just been obtained by our collaborator L. Laplaze at the end of 2009 to support further this research.

### 5.2.3. Mechanical model

**Participants:** Jérôme Chopard, Christophe Godin, Jan Traas, Olivier Hamant [ENS-Lyon].

*This research theme is supported by the ANR project Virtual Flower and Geneshape projects.*

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 overall shape of a plant tissue and morphogenesis, its evolution throughout time, we therefore need a mechanical model of cells. 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 an increase in cell wall synthesis when this deformation is too high. The final shape of the tissue integrate mechanically all the local deformation 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 by their activity a targeted shape for each cell (or small homogeneous region) and the final cell shape results from the confrontation between this specified shape and the physical constraints imposed by the cell neighbors. Hence the final shape of the tissue results from the integration of all these local rules and constraints at organ level. This work is being described in a paper which will be submitted for publication at the beginning of 2010.

### 5.2.4. Cell cycle model

**Participants:** Romain Fernandez, Christophe Godin, Pradeep Das, Jan Traas.

*This research theme is supported by the ANR project Virtual Flower and Geneshape projects.*

A very simple model of cell cycle is necessary to determine cell division events. Here cell division occurs when the cell volume gets above a certain threshold.

A model of cell division consistent with the observations coming from the confocal data is being investigated. The availability of 3-D geometric structures at cell resolution of real meristem and the possibility to follow their cell lineages will make it a unique opportunity to test in silico the validity of these cell division models.

### 5.2.5. Gene regulatory networks

Modelling gene activities within cells is of primary importance since cell identities correspond to stable combination of gene level activity.

- *Gene networks.* (Yassin Refahi, Etienne Farcot, Christophe Godin, Jan Traas, Teva Vernoux)

Both methodological and applied works have been carried on during the last year on the topic of gene networks (in a broad sense, including other metabolites than the sole gene products, whenever they play a significant role in the regulation of gene activity).

On the methodological side, in the context of Y. Refahi's thesis, some first necessary numerical experiments have been performed, as a benchmark for future implementations. These experiments have consisted in implementing already published spatial models of gene networks [32], using 3D reconstructed shoot apical meristems obtained from R. Fernandez. The main conclusion is that simulations based on nonlinear differential equations (smooth or piecewise-linear) may be performed in a manageable time on a standard computer using Python/Scipy code, only for very simple systems. Hence it seems reasonable to use these formalisms, although some innovative approaches will have to be developed next year in terms of simulation algorithms and/or model simplification.

Another methodological work was to continue the analysis of piecewise-linear formalism. Some new results have been obtained, namely existence and uniqueness of limit cycles for systems having a discrete abstraction displaying periodic trajectories. These results, published as a research report [20] have been accepted for publication in International Journal of Systems Science. Previously obtained results have also appeared during the year [13]. Finally, some new results have also been obtained concerning the control of periodic behaviour in piecewise-linear networks [21]. The main novelty is the use of dynamic control technique, i.e. the control of a gene network obtained by linking it to another network, designed to ensure (or preclude) stable periodic solutions in the first network. These technique may be used in the future to investigate specific properties of spatially interacting gene networks.

Finally, on a more applied side, an ordinary differential model of the auxin signaling pathway have been developed in collaboration with T. Vernoux. The parameters of this model can be put in correspondence with different locations in the shoot apical meristem (SAM), hence representing spatial effects without the need to implement projections of this model on a full 3D meristem. Various experimental data have been obtained by T. Vernoux and his collaborators about the main proteins involved in this pathway, in particular their spatial expression patterns and all their possible interactions. Together with the model, this data provides a very consistent improvement of our understanding of the SAM functioning. A paper on this work is in preparation.

### 5.2.6. Model integration

**Participants:** Mikael Lucas, Michael Walker, Jérôme Chopard, Frédéric Boudon, Christophe Godin, Laurent Laplaze, Jan Traas.

*This research theme is supported by the ATP CIRAD Meristem, the ANR project Carpel and the Sy-Stem European RTN Project.*

Our approach consists of building a programmable tissue able to accept different modelling components. This includes a central data structure representing the tissue in either 2- or 3-D and 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 modelling component, one or several approaches is 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. As an outcome of each modelling subtask, 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.

- *development of a computer platform for the 'programmable tissue'*. (Jérôme Chopard, 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.

## 6. Other Grants and Activities

### 6.1. National Grants

#### 6.1.1. Agropolis computational plant seminar

**Participants:** Yann Guédon, Christine Granier [INRA, LEPSE], Laurent Laplaze [IRD, DIAPC].

Funding: Agropolis fundation (Contractor for Virtual Plants: CIRAD. From 2008 to 2011)

In the context of the creation of a world-level pole on plant science in the region Languedoc-Roussillon, we organize a monthly seminar and a yearly workshop at Agropolis (see <http://www.plantnum.agropolis.fr>). The 2009 one-day workshop was devoted to models at the cellular and tissular scales and the invited speakers were J. Haseloff (U. Cambridge), N. Bertin (PSH, INRA), E. Mjolsness (UC. Irvine), N. Monk (U. Nottingham), E. Bayer (Institute of Plant Sciences, Berne) and T. Vernoux (RDP, CNRS). The seminar is organized by Yann Guédon, Christine Granier (INRA, LESPE) and Laurent Laplaze (IRD, DIAPC) with the support of Agropolis International and Agropolis Foundation.

#### 6.1.2. Advanced Markovian techniques in population dynamics

**Participant:** Yann Guédon.

Funding: University Montpellier 2 (Contractor for Virtual Plants: CIRAD. From 2008 to 2009)

The objective of this joined project with Centre d'Écologie Fonctionnelle et Evolutive, (BIOSTIC project, University Montpellier 2) is to adapt hidden semi-Markov models to population dynamic problems.

#### 6.1.3. OpenAlea

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

Funding: Agropolis fundation (Contractors for Virtual Plants: CIRAD and INRIA from 2009 to 2011)

The aim of this project is to foster the development and the national and international diffusion of the platform OpenAlea. This opensource plateform provides an easy-to-use environment for plant modellers through a visual programming interface to efficiently use and combine models or computational methods from different scientific fields in order to represent, analyse 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, ...

#### 6.1.4. vTissue

**Participants:** Eric Moscardi, Christophe Pradal, Christophe Godin, Grégoire Malandain [INRIA, Asclepios].

Funding: INRIA (Contractors for Virtual Plants: INRIA from 2009 to 2011)

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

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

#### 6.1.5. *Alinea*

**Participants:** Christophe Pradal, Christophe Godin, Michael Chelle [INRA, EGC Grignon], Christian Fournier [INRA, LEPSE].

Funding: INRA (Contractor for Virtual Plants: INRA, from June 2008 until December 2009)

*Alinea: Building a modeling consortium around the OpenAlea platform to integrate various ecophysiological models to study interaction between the plant and its environment.* The aim of this Action Ciblée Incitative of INRA is twofold. We first intend to constitute a consortium of modelers from INRA around the OpenAlea platform. Second, we aim to integrate various ecophysiological models of simulation in OpenAlea (radiative transfert, interaction between plant and pest, circulation of hydric fluxes, and dispersion). Data are provided by different teams of biologists and the integrated models will be distributed through the OpenAlea website. The project includes 3 INRA teams and the INRIA Virtual Plants team.

#### 6.1.6. *M2A3PC*

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

Funding INRIA (Contractor for Virtual Plants: INRIA. From 2009 to 2010)

*M2A3PC: Modélisation de la Propagation Aérienne d'Agents Pathogènes sur une Culture Pérenne, fortement structurée et anthropisée,* the aim of this project is to model the airborne dispersal of a pathogen over a highly structured and anthropized perennial vegetal cover. This project gathers teams with different competences in biology and ecophysiology of vine and apple tree crops at different scales, 3D computer simulation of plant functioning and growth, and mathematical modeling of pest propagation in heterogenous media.

Partners: EPI Anubis (Inria Bordeaux), UMR Santé Végétale (Inra Bordeaux), EPI ALEA (Inria Bordeaux), UMR SYSTEM (INRA Montpellier), AFEF Team, UMR DAP, UMR PIAF (INRA Clermont-Ferrand), UERI de Gothon (INRA Avignon).

#### 6.1.7. *Fruit3D*

**Participants:** Ibru Mebatsion, Frédéric Boudon, Christophe Godin, Nadia Bertin [PSH, Avignon].

Funding: Agropolis foundation (Contractor for Virtual Plants: INRIA, from 2009 to 2011)

The aim of this project is to develop a virtual tomato that contains geometrical description of a growing fruit, physiological models (for sugar and hormone transfers) and mechanical model. The project gathers the competence of plant modellers, physicists and ecophysiologicalists. Physical and biological laws involved in tissue differentiation and cell growth, in relation to fruit growth and compartmentation, and a number of related traits of quality (e.g. size, composition and texture) are modelled and integrated within the virtual tomato. Nuclear Magnetic Resonance (NMR) and 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.

#### 6.1.8. *PlantScan3D*

**Participants:** Frédéric Boudon, Chakkrit Preuksakarn, Christophe Godin, Christian Fournier [INRA, LEPSE].

Funding: Agropolis foundation (Contractor for Virtual Plants: CIRAD, From 2009 to 2011)

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 (SL3D) 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 will develop methodologies for the automation of numerical 3D acquisition of vegetal structures of different sizes, and develop new methods for the reconstruction of parsimonious geometrical and structural models usable in agronomical and biological contexts.

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

### 6.1.9. *GeneShape*

**Participants:** Michael Walker, Etienne Farcot Godin, Christophe Godin.

Funding: ANR (Contractor for Virtual Plants: INRIA, From 2009 to 2011)

In this project, we propose to develop a complex systems approach to study the development of multi-cellular organisms. We have chosen two distant biological systems. One is the embryo of an ascidian organism, *Ciona intestinalis* and the other is the female reproductive organ of a flowering plant, *Arabidopsis thaliana*. These two systems are very different a priori. However, there have also striking morphological similarities. Development of both systems involves the spatial control of cell growth and proliferation, while at a higher scale morphogenetic processes such as organ outgrowth or tissue invagination and folding occur. From a fundamental point of view it will, therefore, be very interesting to study how these distant organisms have solved different problems (different mechanical constraints, different number of cells, different timing) to create morphologically similar shapes.

Partners: ENS-Lyon; P. Lemaire, Luminy, Marseille.

## 6.2. International Bilateral Relations

### 6.2.1. *ANR-BBSRC Grant*

**Participants:** Christophe Godin, Jan Traas, Etienne Farcot, Yassin Refahi, Andrew Bangham [Univ. East Anglia], Enrico Coen [John Innes Center, UK], Robert Sablowski [John Innes Center, UK], François Parcy [CNRS].

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

*Flower Model: Modeling growth and gene regulation in floral organs* is a project funded by the ANR-BBSRC programme System Biology (SysBio). Systems biology aims to explain and predict the behaviour of complex biological systems by quantitative analysis and modeling of the interactions between all the relevant components. An important challenge for the years to come is how to integrate the approaches used for growth analysis at different stages with the role of regulatory genes to produce predictive models of floral organ growth and patterning. To address this question, this project brings together leading UK and French teams with complementary expertise on imaging, floral development and quantitative modeling, to focus on a comparative analysis of sepal and petal growth in *Arabidopsis*. We will initially use live imaging and sector analysis to produce quantitative models of growth for these organs. We will integrate information on regulatory genes with spatial information to produce in silico models of the regulatory network controlling sepal and petal development. We expect that the following objectives can be reached at the end of this project:

- Capture quantitative data on sepal and petal morphogenesis
- Analyze and model the regulatory networks underlying sepal and petal development
- Link morphogenesis to regulatory networks
- Create an integrated database of complex datasets

### 6.2.2. Other bilateral relations

There is currently an active connection with the group of Malcolm Bennett, at the Center for Plant Integrative Biology (CPIB) in Nottingham. In June 2009 M. Bennett visited us in Montpellier, in July C. Godin and J. Chopard went to CPIB, several researchers and students from CPIB have visited our team, and Mikael Lucas is a post-doc sharing his time between the two groups.

The team of Pr. Prusinkiewicz at the University of Calgary (Canada) is an *associated team* of *Virtual Plants*. In this context, C. Godin and F. Boudon both spent several weeks in Calgary, and Wojtek Palubiki and Adam Runions, two PhD students, have come for a 2 months, and 2 weeks visits respectively.

Yann Guédon is working with Claudia Negron, David Da Silva and Ted DeJong (University of California, Davis) on stochastic models for the branching and axillary flowering structures of peach and almond shoots.

## 7. Dissemination

### 7.1. Services to the scientific community

- Christophe Godin has rendered the following services in 2009:
  - he is a member of the Steering Committee of UMR DAP,
  - he is a member of the board of the Fédération de Recherche (IFR) DAPHNE, coordinating joint actions of UMRs working in Plant Sciences in the region Languedoc Roussillon,
  - he is the representant of the IFR at the doctoral school of the University of Montpellier II, SIBAGH, in Plant Biology,
  - he is a member since 2003 of the INRA expert scientific commissions (CSS Ecophysiologie, génétique et biologie intégrative des plantes) that assesses INRA individual researcher activities.
  - he was a referee for 3 PhD theses (J. Diener, INRIA-INPG; A. Verdenal, INRA, Poitou-Charentes University and 'Opponent' of J. Perttunen, U. Helsinki, Finland)
  - he was a reviewer for a project submitted to the Swiss National Science Foundation.
  - he was member of commissions for CR1/CR2 researcher positions at INRIA Sophia-Antipolis and Professor position at ENS-Lyon.
  - he is member of the international advisory board of the Functional-Structural Plant Models conference since 2001 (he was chair of the conference in 2004) and member of the scientific board of FSPM'10.
  - he was a reviewer for international conferences (SMI and EuroGraphics), and journals (Transactions on Graphics, Journal of theoretical Biology, Fractals, Technique et Science Informatiques, Computer and Graphics, PNAS, Journal of Experimental Botany, Plant Journal, Computer Graphics Forum, Bioessays).
- Yann Guédon has rendered the following services in 2009:
  - he is a member of the editorial board of Annals of Botany and a member of the ERCIM working group "Computing & Statistics".
  - he was a member of the TIARE committee for the evaluation of CIRAD researchers.
  - he reviewed for Biometrics (2009, 65(4), p. 1312) the book Semi-Markov Chains and Hidden Semi-Markov Models toward Applications: Their Use in Reliability and DNA Analysis by Barbu, V. S. and Limnios, N.
  - he was a referee for papers submitted to Acta Biotheoretica, Computational Statistics & Data Analysis, Statistics and Computing, Water Resources Research and GRETSI'09 conference.



- Frédéric Boudon was referee for papers submitted to Computer and Graphics and Shape Modelling International. He was referee for 1 PhD thesis (C. LAM, XLIM, Limoge)
- Christophe Pradal coordinates the national platform for plant modeling *OpenAlea*. He was a member of a CIRAD evaluation committee.

## 7.2. Academic teaching

### 7.2.1. Master Biostatistics

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

Yann Guédon teaches the **stochastic modeling** course. He participated to the jury of this Master.

### 7.2.2. Master Computer Science

University Montpellier 2.

Christophe Godin and Frédéric Boudon teach a course with Christophe Fiorio from LIRMM on plant modeling and computational geometry, entitled **computational plant modeling**.

### 7.2.3. Master Biotraçabilité, Biodétection, Biodiversité

Montpellier 2 University.

Yann Guédon teaches a course on statistics in the context of plant biology.

### 7.2.4. Master Classes

Jérôme Chopard and Etienne Farcot taught the Master classes 'An introduction to plant modeling' and 'Models of gene network dynamics' respectively, in the module 'Systems biology and plant development' coordinated by Jan Traas in the BioScience Master of ENS-Lyon.

### 7.2.5. Undergraduate Classes

University Montpellier 2.

Yassin Refahi teaches the classes 'Initiation à la programmation et algorithmique' (42 h) and 'Les concepts de base en informatique' (20 h), as a part-time lecturer.

### 7.2.6. High School class

- C. Godin, F. Boudon and E. Farcot give classes about plant modeling in the context of a joint one-year project together with Yves Caraglio (UMR AMAP) and highschool teachers: Marc Beziz (Mathematics), Didier Lacour (Physics), Luc Comte (Biology) from the Lycée Georges Pompidou, Castelnaud (approximately 3 afternoons per month over the year).
- C. Godin and E. Farcot, helped by F. Boudon and C. Pradal, gave a one day intervention with software demonstrations and a presentation at the CIRAD day, for the "Fête de la Science", in November.
- C. Godin, with interventions from others, gave a formation on L-system for highschool teachers in June 9-10th.

## 7.3. Participation in workshops, seminars and miscellaneous invitations

- Frederic Boudon gave a talk at the seminar computational plant of Agropolis in June. He presented the work on plant sketching at the Eurographics conference. He was also attending the AFIG conference in Arles. He gave presentations at the XLIM lab and at BMV group of the University of Calagary.
- Christophe Godin an invited speaker in the following events in 2008:
  - University of Montpellier, LIRMM, *Modélisation du développement des plantes à différentes échelles*, 15 Jan 2009.

- University of Helsinki, Dept of Ecology, *Modeling meristem development : towards an integrated perspective*, 12 Feb 2009.
  - University of Calgary, Dept of Computer Science, *Structural comparison of biological forms*, 6 May 2009.
  - SEB conference, workshop on Modelling Plant Systems: *Molecules to Agro-ecosystems, Modeling meristem dynamics: towards an integrated perspective*, 28 June 2009
  - Plant Bioinformatics, Systems and Synthetic Biology Summer school, *Components of a virtual tissue*, Nottingham, UK, 27-31 July 2009
  - International conference on Plant Molecular Biology, *Virtual meristem. Modeling shape development at cellular resolution*, St Louis, MO, USA, 26 Oct. 2009
  - International conference on Integrative Post-Genomics, *The components of a virtual meristem*, Lyon, 19 Nov 2009
- Jérôme Chopard, Etienne Farcot, Christophe Godin and Michael Walker attended the second workshop of the *Flower Model* ANR-BBSRC project, in Autrans in May 2009.
  - Etienne Farcot gave talks at the "Constructing gene networks: observation, analysis and control" workshop in January in Paris, at the MERE seminar in June in Montpellier, at the Agropolis Seminar in September in Montpellier, and at the ANR project 'ANAR' workshop in La Rochelle in December.
  - Romain Fernandez gave talks at both the Asclepios and Virtual Plants seminars about his PhD results. He was an invited speaker at the CNRS Colloquium "la journée MRI" on the 13th October 2009.
  - Yassin Refahi attended the following summer school: 'Modélisation et simulation de processus biologiques dans le contexte de la génomique' from March 29th to April 3rd, 2009, near Nice. He gave a talk at the 'UMR DAP Forum' in December in Montpellier.

## 7.4. Theses and Internships

### 7.4.1. Theses defenses

- Szymon Stoma, Modelling development of shoot apical meristem of *Arabidopsis*, University Montpellier 2, February the 3rd, 2009.

### 7.4.2. Ongoing Theses

- Anaëlle Dambreville, "*3D modelling of mango phenology*", University Montpellier 2.
- Romain Fernandez, "*3D Reconstruction of meristems from bi-photon images*", University Montpellier 2.
- Chakkrit Preuksakarn, "*Acquisition et validation de modèles architecturaux virtuels de plantes en croissance.*", University Montpellier 2.
- Yassin Refahi, "*Modélisation de la croissance des organes floraux*", University Montpellier 2.

### 7.4.3. Internships

- Chloé Xavier (ENSIMAG), 'Spécification de la croissance d'arbres par sketching'.
- Hassen BenAyed (Ecole Polytechnique de Tunisie), 'Définition d'un modèle réactif pour la croissance des plantes'.
- Inès Nefzi (Ecole Polytechnique de Tunisie) Estimation de modèles linéaires mixtes et de modèles linéaire généralisés mixtes. Application à la génétique quantitative

## 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", vol. 103, 2006, p. 1627-1632, <http://www-sop.inria.fr/virtualplants/Publications/2006/BBLMCGT06>.
- [2] J.-B. DURAND, P. GONÇALVÈS, Y. GUÉDON. *Computational methods for hidden Markov tree models - An application to wavelet trees*, in "IEEE Transactions on Signal Processing", vol. 52, n<sup>o</sup> 9, 2004, p. 2551-2560.
- [3] J.-B. DURAND, Y. GUÉDON, Y. CARAGLIO, E. COSTES. *Analysis of the plant architecture via tree-structured statistical models: the hidden Markov tree models.*, in "New Phytol", vol. 166, n<sup>o</sup> 3, Jun 2005, p. 813-825, <http://dx.doi.org/10.1111/j.1469-8137.2005.01405.x>.
- [4] P. FERRARO, C. GODIN. *An edit distance between quotiented trees*, in "Algorithmica", vol. 48, 2003, p. 385-406.
- [5] P. FERRARO, C. GODIN, P. PRUSINKIEWICZ. *Toward a quantification of self-similarity in plants*, in "Fractals", vol. 13, n<sup>o</sup> 2, 2005, p. 91-109, <http://www-sop.inria.fr/virtualplants/Publications/2005/FGP05>.
- [6] C. GODIN, Y. CARAGLIO. *A multiscale model of plant topological structures*, in "Journal of Theoretical Biology", vol. 191, 1998, p. 1-46, <http://www-sop.inria.fr/virtualplants/Publications/1998/GC98>.
- [7] C. GODIN, E. COSTES, H. SINOQUET. *Plant architecture modelling - virtual plants and complex systems*, in "Plant Architecture and its Manipulation", C. TURNBULL (editor), Annual plant reviews, vol. 17, Blackwell, 2005, p. 238-287, <http://www-sop.inria.fr/virtualplants/Publications/2005/GCS05>.
- [8] Y. GUÉDON, Y. CARAGLIO, P. HEURET, E. LEBARBIER, C. MEREDIEU. *Analyzing growth components in trees*, in "Journal of Theoretical Biology", vol. 248, n<sup>o</sup> 3, 2007, p. 418-447, <http://www-sop.inria.fr/virtualplants/Publications/2007/GCHLM07>.
- [9] Y. GUÉDON, D. BARTHELEMY, Y. CARAGLIO, E. COSTES. *Pattern analysis in branching and axillary flowering sequences*, in "Journal of Theoretical Biology", vol. 212, 2001, p. 481-520.
- [10] Y. GUÉDON. *Estimating hidden semi Markov chains from discrete sequences*, in "Journal of Computational and Graphical Statistics", vol. 12, n<sup>o</sup> 3, 2003, p. 604-639.

### Year Publications

#### Articles in International Peer-Reviewed Journal

- [11] F. CHAUBERT - PEREIRA, Y. CARAGLIO, C. LAVERGNE, Y. GUÉDON. *Identifying ontogenetic, environmental and individual components of forest tree growth.*, in "Annals of Botany", vol. 104, n<sup>o</sup> 5, 2009, p. 883-896, <http://www-sop.inria.fr/virtualplants/Publications/2009/CCLG09>.

- [12] 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", 2009, <http://www-sop.inria.fr/virtualplants/Publications/2009/CGLT09>.
- [13] E. FARCOT, J.-L. GOUZÉ. *Periodic Solutions of Piecewise Affine Gene Network Models with Non Uniform Decay Rates: The Case of a Negative Feedback Loop*, in "Acta Biotheoretica", vol. 57, n<sup>o</sup> 4, 2009, p. 429–455, <http://www-sop.inria.fr/virtualplants/Publications/2009/FG09a>.
- [14] S. MONDET, W. CHENG, G. MORIN, R. GRIGORAS, F. BOUDON, W. TSANG OOI. *Compact and Progressive Plant Models for Streaming in Networked Virtual Environments*, in "ACM Transactions on Multimedia Computing, Communications, and Applications (TOMCCAP)", vol. 5, n<sup>o</sup> 3, aug 2009, p. 1–22, <http://www-sop.inria.fr/virtualplants/Publications/2009/MCMGBT09>.
- [15] 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", vol. 71, n<sup>o</sup> 1, jan 2009, p. 1–21, <http://www-sop.inria.fr/virtualplants/Publications/2009/PBNCG09>.

### International Peer-Reviewed Conference/Proceedings

- [16] A. DORAN, S. MONDET, R. GRIGORAS, G. MORIN, W. TSANG OOI, F. BOUDON. *A Demonstration of MobiTree: Progressive 3D Tree Models Streaming on Mobile Clients*, in "ACM Multimedia 2009, Beijing", ACM, oct 2009, <http://www-sop.inria.fr/virtualplants/Publications/2009/DMGMTB09>.
- [17] J. WITHER, F. BOUDON, M.-P. CANI, C. GODIN. *Structure from silhouettes: a new paradigm for fast sketch-based design of trees*, in "Computer Graphic Forum. Special issue: Eurographics 2009", vol. 28 (2), 2009, p. 541–550, <http://www-sop.inria.fr/virtualplants/Publications/2009/WBCG09>.
- [18] D.-M. YAN, J. WINTZ, B. MOURRAIN, W. WANG, F. BOUDON, C. GODIN. *Efficient and robust reconstruction of botanical branching structure from laser scanned points*, in "11th IEEE International conference on Computer-Aided Design and Computer Graphics (CAD/Graphics 2009)", 2009, <http://www-sop.inria.fr/virtualplants/Publications/2009/YWMWBG09>.

### Workshops without Proceedings

- [19] T. COKELAER, C. PRADAL, C. FOURNIER. *Plant modelling with Python components in OpenAlea*, in "EuroSciPy 2009", 2009, <http://www-sop.inria.fr/virtualplants/Publications/2009/CPF09>.

### Research Reports

- [20] E. FARCOT, J.-L. GOUZÉ. *Limit cycles in piecewise-affine gene network models with multiple interaction loops*, n<sup>o</sup> RR-6875, INRIA, Mar 2009, <http://www-sop.inria.fr/virtualplants/Publications/2009/FG09>, INRIA Research Report.
- [21] E. FARCOT, J.-L. GOUZÉ. *Qualitative control of periodic solutions in piecewise affine systems; application to genetic networks*, n<sup>o</sup> RR-7130, INRIA, Dec 2009, <http://www-sop.inria.fr/virtualplants/Publications/2009/FG09b>, INRIA Research Report.

### References in notes

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

- [23] D. BARTHELEMY, Y. CARAGLIO, E. COSTES. *Architecture, gradients morphogénétiques et âge physiologique chez les végétaux*, in "Modélisation et Simulation de l'Architecture des Végétaux", J. BOUCHON, P. DE REFFYE, D. BARTHELEMY (editors), 1997, p. 89-136.
- [24] 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", vol. 35, n° 9 & 10, 2008, p. 936–950, <http://www-sop.inria.fr/virtualplants/Publications/2008/CSRGPG08>.
- [25] P. FERRARO, C. GODIN. *A distance measure between plant architectures*, in "Annals of Forest Science", vol. 57, n° 5/6, 2000, p. 445-461, <http://www-sop.inria.fr/virtualplants/Publications/2000/FG00>.
- [26] D. FUMEY, P. LAURI, Y. GUÉDON, C. GODIN, E. COSTES. *Effects of pruning on the apple tree: from tree architecture to modeling*, in "International Symposium on Integrating Canopy, Rootstock and Environmental Physiology in Orchard Systems", 2008, <http://www-sop.inria.fr/virtualplants/Publications/2008/FLGGC08>.
- [27] 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", vol. 68, 1980, p. 675-696.
- [28] C. GODIN, E. COSTES, H. SINOQUET. *A method for describing plant architecture which integrates topology and geometry*, in "Annals of Botany", vol. 84, 1999, p. 343-357.
- [29] Y. GUÉDON, Y. CARAGLIO, P. HEURET, E. LEBARBIER, C. MEREDIEU. *Analyzing growth components in trees*, in "Journal of Theoretical Biology", vol. 248, n° 3, 2007, p. 418–447, <http://www-sop.inria.fr/virtualplants/Publications/2007/GCHLM07>.
- [30] F. HALLÉ, R. A. A. OLDEMAN, P. B. TOMLINSON. *Tropical trees and forests. An architectural analysis*, Springer-Verlag, New-York, 1978.
- [31] J. L. HARPER, B. R. ROSEN, J. WHITE. *The growth and form of modular organisms*, The Royal Society, London, UK, 1986.
- [32] H. JÖNSSON, M. HEISLER, G. V. REDDY, V. AGRAWAL, V. GOR, B. E. SHAPIRO, E. MJOLSNESS, E. M. MEYEROWITZ. *Modeling the organization of the WUSCHEL expression domain in the shoot apical meristem*, in "Bioinformatics", vol. 21, n° 1, 2005, p. 232–240, <http://dx.doi.org/10.1093/bioinformatics/bti1036>.
- [33] M. LUCAS, Y. GUÉDON, C. JAY-ALLEMAND, C. GODIN, L. LAPLAZE. *An auxin transport-based model of root branching in Arabidopsis thaliana*, in "PLoS ONE", vol. 3, n° 11, 2008, <http://www-sop.inria.fr/virtualplants/Publications/2008/LGJGL08>.
- [34] M. LUCAS. *Etude et modélisation des déterminismes de mise en place et de développement des racines latérales chez Arabidopsis Thaliana*, Université Montpellier II, 2008, Ph. D. Thesis.
- [35] S. MONDET, W. CHENG, G. MORIN, R. GRIGORAS, F. BOUDON, W. TSANG OOI. *Streaming of Plants in Distributed Virtual Environments*, in "ACM Multimedia 2008 - Systems and Networking Track", 2008, <http://www-sop.inria.fr/virtualplants/Publications/2008/MCMGBT08>.
- [36] R. NOZERAN. *Integration of organismal development*, in "Positional controls in plant development", P. BARLOW, D. CARR (editors), 1984, p. 375-401.

- [37] 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", vol. 426, n<sup>o</sup> 6964, November 2003, p. 255–260, <http://dx.doi.org/10.1038/nature02081>.
- [38] M. RENTON, Y. GUÉDON, C. GODIN, E. COSTES. *Similarities and gradients in growth-unit branching patterns during ontogeny in Fuji apple trees: A stochastic approach.*, in "Journal of Experimental Botany", vol. 57, n<sup>o</sup> 12, 2006, p. 3131–3143, <http://www-sop.inria.fr/virtualplants/Publications/2006/RGGC06>.
- [39] A. RUNIONS, B. LANE, P. PRUSINKIEWICZ. *Modeling Trees with a Space Colonization Algorithm*, in "Eurographics Workshop on Natural Phenomena", 2007, p. 63-70, <http://www.eg.org/EG/DL/WS/NPH/NPH07/063-070.pdf>.
- [40] H. SINOQUET, P. RIVET, C. GODIN. *Assessment of the three-dimensional architecture of walnut trees using digitizing*, in "Silva Fennica", vol. 3, 1997, p. 265–273.