



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*

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# 1. Team

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# 2. Overall Objectives

## 2.1. Overall Objectives

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

Plants are branching living organisms that develop throughout their lifetimes. Organs are created by small embryogenetic regions at the tip of each axis, called *apical meristems*. In the project Virtual Plants, we are interested in studying plant apical meristem functioning and development. We 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 organization of these complex biological objects,
- and models for morphogenesis.

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

## 3. Scientific Foundations

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

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

- *Combinatorial approaches*: plant structures exhibit complex branching organizations of their organs like internodes, leaves, shoots, axes, branches, etc. These structures can be analyzed with combinatorial methods in order to compare them or to reveal particular types of organization. We investigate a family of techniques to quantify distances between branching systems based on non-linear structural alignment (similar to edit-operation methods used for sequence comparison). Based on these techniques, we study the notion of (topology-based) self-similarity of branching structures in order to define a notion of degree of redundancy for any tree structure and to quantify in this way botanical notions, such as the physiological states of a meristem, fundamental to the description of plant morphogenesis.
- *Statistical modeling*: We investigate different categories of statistical models corresponding to different types of structures.
  - Longitudinal data corresponding to plant growth follow up: the statistical models of interest are equilibrium renewal processes and generalized linear mixed models for longitudinal count data.
  - Repeated patterns within sequences or trees: the statistical models of interest are mainly (hidden) variable-order Markov chains. Hidden variable-order Markov chains were in particular applied to characterize permutation patterns in phyllotaxis and the alternation between flowering and vegetative growth units along sympodial tree axes.

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

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

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

## 3.2. Meristem functioning and development

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

- algorithms for the automatized segmentation in 3D, and cell lineage tracking throughout time, for images coming from confocal microscopy,
- design of high-level routines and user interfaces to distribute these image analysis tools to the scientific community,
- tools for structural and statistical analysis of 3D meristem structure (spatial statistics, multiscale geometric and topological analysis),
- physical models of cells interactions based on spring-mass systems or on tensorial mechanics at the level of cells,
- models of biochemical networks of hormonal and gene driven regulation, at the cellular and tissue level, using continuous and discrete formalisms,
- and models of cell development taking into account the effects of growth and cell divisions on the two previous classes of models.

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

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

*OpenAlea* is the result of a collaborative effort associating 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 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

### 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.

*Other participant:* Aida Ouangraoua (INRIA, Lille).

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 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 [8]. 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 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 plant and tissue. *OpenAlea.Container* and *OpenAlea.MTG* are two packages which implement a generic graph data structure to represent the topological structure of the meristem and of the plant architecture, as well as the data-flow 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 [19] 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.



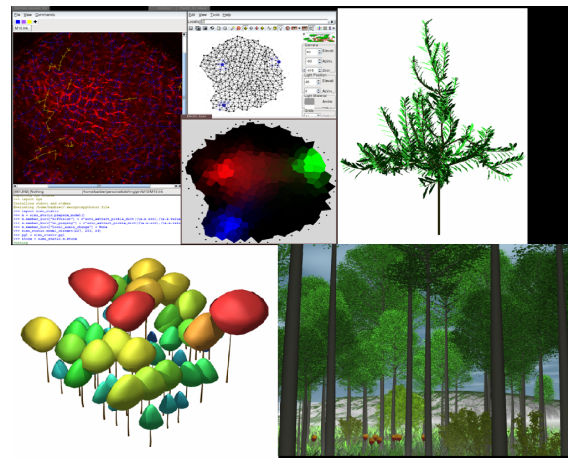


Figure 1. V-Plants components of the OpenAlea platform: simulating plant processes at different scales. Top Left: Reconstruction of a virtual meristem, analysis and simulation of the auxin fluxes inside the meristem. Top Right: Reconstruction of a virtual apple tree from digitized data. Bottom: Simulation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

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

OpenAlea[38], [34], [33] 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 2010, two major releases were done : Openalea 0.8 and Openalea 0.9. 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.
  - OpenAlea.GraphEditor is a new python library designed to ease the implementation of viewers and editors of graph structures (in the sense of a set of vertices connected by

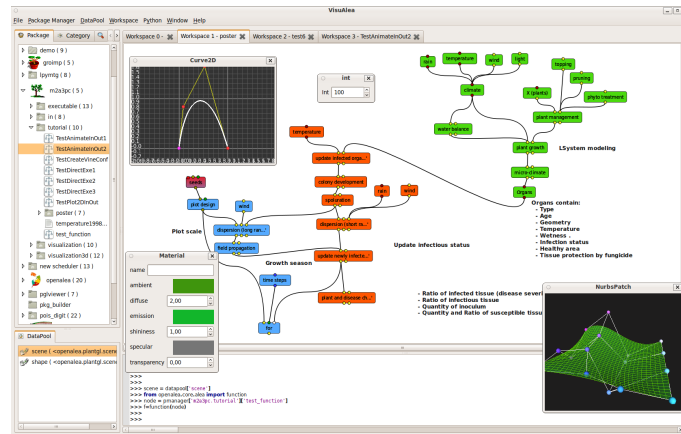


Figure 2. OpenAlea.Visualea: Visual programming interface. The package manager shows the available components. The components can be interconnected on a workspace to form a data-flow. The python interpreter allows low level interaction with the system.

edges). OpenAlea.Visualea's data-flow editing view has been reimplemented using this library. It was introduced with release 0.8.

## 2. Animation and diffusion

- 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 ( link <http://vp-continuous.cirad.fr>) to test the reliability of all the components after every commit.
- The project has been presented in various conferences (FSPM10, EuroSciPy10, IHC10). Software demonstrations have been held in the FSPM conference and in the IHC, presenting a set of plant modeling scenarii provided by different modelers of the OpenAlea community.
- The OpenAlea project is hosted at the Inria gforge. The web site is visited by more than 300 unique visitor each month; 470000 web pages have been visited and the different available components of OpenAlea have been downloaded more than 14,000,000 times during the last three years.

## 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.

In 2010, 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 [26]. 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 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.TopVine is a component to reconstruct grapevine canopy structure.
- Ecomeristem [37] 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).

## 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 and ARC projects 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 [58], [48]. 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 pictures, video, laser scanner and direct sketching.

- *Reconstruction of plant architecture from 3D laser scanner data.* (Chakkrit Preuksakarn, Frédéric Boudon, Christophe Godin, Xinghua Song [INRIA, Galaad], Bernard Mourrain [INRIA, Galaad], Dobrina Boltcheva [INRIA, Evasion], Franck Hetroy [INRIA, Evasion], Marie-Paule Cani [Inria, Evasion], Pascal Ferraro [Labri, Bordeaux] )

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 teams, 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 since September 2009 by the Agropolis Foundation and has started with an INRIA ARC project since 2010. In particular, for the Agropolis project a meeting has been organized in March in Clermont Ferrand where different types of laser scans has been tested and a first database of scans of different types of plants.

From the processing part, we propose a reconstruction pipeline composed on a contraction procedure to center points on the center of the shape and a reconnection method to build the skeleton. The team proposed a simple adaptive scheme to contract points. In parallel, Galaad team explore uses of detection of circular patterns to be contracted toward their center. The merging of these approaches is currently investigated. For the second step, the team explores the use of the Space Colonization Algorithm [57]. Some first results of this reconstruction procedure have been presented at the FSPM'10 conference [35]. Additionally, an evaluation procedure to assess accuracy of the reconstruction is currently being investigated [32]. It is based on topological edit distance [44] to compare two tree graphs weighted with geometrical information.

- *Sketching of plants.* (Jonathan Marin, 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 Evasion we developed a method based on the design of plants from silhouettes [59]. This sketching paradigm allows quick and intuitive specification of foliage at multiple scales. On this topic, we start a collaboration with S. Longuay and P. Prusinkiewicz that develop some iPad tools to design plants based on SCA. Currently, we work with them on several improvements of our previous method. We improve plants design by allowing multiple strokes for defining branches or silhouettes. Constraining SCA with strokes is currently investigated. We also explore the idea of sketching growing plants. In this case, the user refinement will correspond to the addition of elements through time.

- *Reconstruction of vineyards from video.* (Frédéric Boudon, Jerome Guenard [IRIT, Toulouse], Geraldine Morin [IRIT, Toulouse], Pierre Gurdjos [IRIT, Toulouse], Vincent Charvillat [IRIT, Toulouse]) In this work, we investigate the reconstruction of constrained plant geometry of a vineyard from a set of pictures coming from video. Pictures are segmented to identify the different trees of a same row in the yard. From this segmentation, a number of parameters are estimated, which makes it possible to instantiate a virtual model of a vine tree. In particular, paths of main branches and leaf volumes and densities are estimated. A preliminary version of this work has been presented to the AFIG conference [28].
- *Reconstruction of virtual fruits from pictures.* (H. K. Mebatsion, Mik Cieslak, Nadia Bertin [Inra, Avignon], Frédéric Boudon, Christophe Godin, Christophe Pradal, Michel Genard [Inra, Avignon], Christophe Goz-Bac [Université Montpellier 2])

*This research theme is supported by the Agropolis project Fruit3D.*

A novel modeling procedure for semi-symmetrical plant organs using longitudinal and transverse organ profiles was developed to simplify and improve virtual organ representation. Fruits were used as model organs. The fruits were divided into halves to capture the fruit profile. Using a regular photo camera (Nikon-Coolpix 4500), and an in-house image acquisition setup, the half fruit images were captured. In-house routine was used to determine the boundaries of the digitized images. Based on the boundary points, and using Fourier series approximation, the image boundaries were defined mathematically. Fourier series approximation defines boundary shapes using the sum of sine and cosine terms. Based on the Fourier descriptors, which are coefficients of the Fourier series approximation, fruit contours were extracted. Surface construction algorithms based on smoothed contour boundaries were developed. Because of non-axis symmetry of most fruits, and the presence of surface perturbations, for example, carpels in tomato fruits, models based on only longitudinal cross sections were not satisfactory. A complete fruit model was finally developed by combining the longitudinal cross section of half fruits and the transverse cross section of whole fruits. To our knowledge, this is the first realistic geometrical fruit model that captures the fruit shape complexities. Such a model may be useful to analyze the genetic and environmental controls of fruit morphological and biochemical properties. Our modeling approach has limitation in producing geometric models for unusual curved shape plant organs such as banana, cucumbers, cassava and Jerusalem artichoke that are not quasi-symmetrical along the longitudinal axis [16].

### 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. [39], [50], [51], [47], provides macroscopic evidence for the existence of regularities and identities in processes that drive meristem activity at microscopic scales. Different concepts have been proposed to explain these specific organizations such as "morphogenetic programme" [54], "age state" [46] or "physiological age" [40]. 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 [46], [40]. Here we develop computational methods to decipher these rules.

- *Branching and axillary flowering structures of fruit tree shoots.* (Yann Guédon, Evelyne Costes, David Da Silva [UC Davis], 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 [56], [3]; 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 [49], [42] 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 were 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 coarse scale corresponding to the succession of two developmental phases and a fine scale corresponding to the alternation between flowering and vegetative GUs. This approach led us to propose a synthetic scheme of apple tree ontogeny that combines growth phases, polycyclism and flowering [29].

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

Previous approaches for a statistical quantification of the effect of factors on tree architecture were mainly oriented toward the structure of main axes, and environmental explanatory variables (see [49], [42]). To characterize genetic determinisms of the alternation of flowering in apple tree progenies at GU scale, a first model of the transitions between GUs was built. The GUs were expertly labeled with four types: long, medium and short vegetative GUs, and flowering GUs. Our model operates on tree-structured data; it combines both Markov tree dependencies and characterization of the effect of explanatory variables (age of graft, type of connection with parent GU: succession or branching), as well as genetic effects (genotype of progenies in presence of replications), through Generalized Linear Mixed Model (GLMM)-based modeling of the transition probabilities. This work was carried

out in the context of the Master 2 internship of Jean Peyhardi (Bordeaux 2 University) and the PhD thesis of Baptiste Guitton. As a perspective, variable-order modeling of the transitions will be included in the Markovian model, to provide more accurate assessment of the dependence between the GU types and that of several ancestor GUs.

The PhD thesis of Baptiste Guitton also comprises the study of alternation in flowering at individual scale, with annual time step. Our approach relies on the conception of indices that characterize alternation in flowering. The difficulty is related to early detection of alternating genotypes, in a context where alternation is often concealed by a substantial increase of the number of flowers over consecutive years. To separate correctly base effect from alternation in flowering, our model relies on a parametric hypothesis on the base effect (random slopes specific to genotype and replications), which translates into mixed effect modeling. Different indices of alternation are then computed on the residuals.

- *Modeling the effect of growth conditions on the architecture of tropical trees.* (Jean-Baptiste Durand, Patrick Heuret [UMR AMAP]).

This project aims at characterizing the architectural plasticity of a tropical species, *Symphonia globulifera* (Clusiaceae), with regard to the conditions of growth, especially light environment. More generally, the goal is to assess the ability of young saplings to reach the canopy under strong competition for light, which is related to their waiting capacities in understory. The dataset is composed of architectural measures of trees grown in a semi-controlled greenhouse, and of forest individuals.

Our architecture model is based on hidden Markov trees (HMTs [43]), which allow several levels of differentiation of the meristems to be inferred from the structures they produce, at the scale of growth units (GUs). These levels correspond to the notion of "physiological state of the meristems", see introduction of section 5.1.2.

To investigate the connection between dimensional properties of the trees (height, geometric characteristics of the crown, *etc.*) and their structural properties, (number of GUs, state frequencies, *etc.*), clustering methods were carried out at individual scale using either dimensional or structural and dimensional variables. The clusters highlight ideotypes, which are related to the conditions of growth (place of growth, competition and light) using regression models.

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

To study the redundancy of structures 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 3. 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 published in IEEE Transactions on Computational Biology and Bioinformatics (IEEE/ACM TCBB) [6].

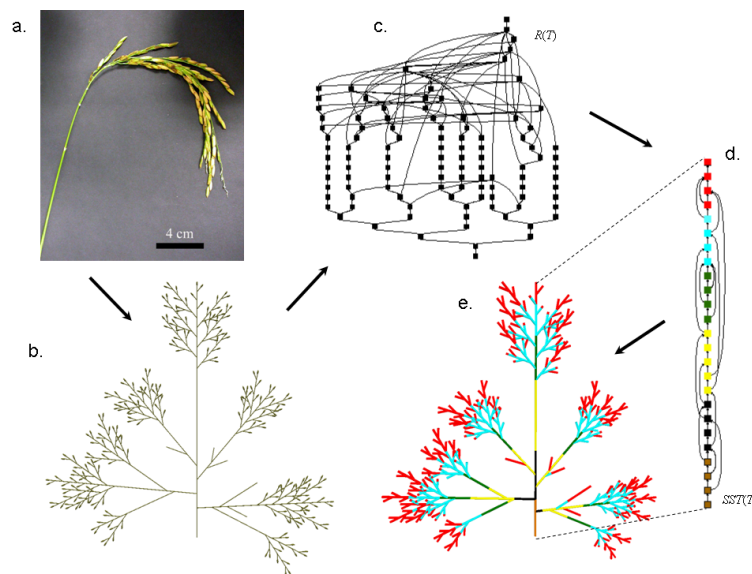


Figure 3. (a) Photo of a rice panicle (b) tree representing the topological structure of the panicle (c) Reduced graph of the panicle tree (d) Corresponding NEST that can be interpreted as the maximal sequence of differentiation states that a meristem can go through when building the panicle (e) color map of the meristem differentiation states obtained by projecting the NEST states back to the original topological tree

- *Approximate compression including geometry* (Anne-Laure Gaillard, Pascal Ferraro, Frédéric Boudon, Christophe Godin)

As a follow up to the work on compressing the topology of trees (see above), we now investigate how to include branch geometry in the compression schemes. This problem constitutes a part of the PhD thesis of Anne-Laure Gaillard co-supervised with P. Ferraro. First results show that any tree architecture can be compressed at different degrees with a varying loss in the geometric information and have been presented at FSPM'10 [27].

- *Toward a statistical characterization of the branching properties of trees at individual scale – application to the quantification of approximate self-nestedness.* (Jean-Baptiste Durand, Yann Guédon, Christophe Godin)

To test different hypotheses related to the role of apical control on local branching properties within tree architecture, statistical models of the fates of the apical meristem and its production at a given scale were specified. They extend the hidden Markov tree models [43] to variable number of children of a given entity, and provide a model for their dependencies. Moreover, they allow for the comparison of different hypotheses regarding the relevance of the children ordering (absence of

ordering, partial or total ordering). In the next years, these models will be used on mango and apple tree cultivars. Particularly, they will found new approaches to compare the effect of various strategies of culture.

These models are based on a notion of state that extends the concept of equivalence classes for tree isomorphism used in the above paragraph, to the notion of classes of approximate isomorphism (*i.e.* isomorphism as a stochastic process). As a consequence, the hidden Markov tree models offer new insight for lossy compression of trees, which will be investigated in future work.

- *Analyzing perturbations in Arabidopsis thaliana phyllotaxis.* (Yann Guédon, Yassin Refahi, Etienne Farcot, 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. In order to characterize these perturbations, we have designed a pipeline of models and methods [36] which decompose into three steps: (i) identification of perturbation patterns, (ii) characterization of perturbation patterns using hidden variable-order Markov chains and hidden combinatorial models both with von Mises observation distributions (Gaussian-like periodic distribution for circular variables), (iii) classification of plant phyllotaxis among wild-type and *ahp6* mutant phyllotaxies. Using this pipeline of models and methods, we have shown that in both wild-type and mutant plants, the perturbations affecting the theoretical spiral of organs along the main axis are not a direct consequence of noise. In this work, we could show that the great majority of these perturbations is actually due to local permutations between successive organs. This phenomenon is particularly important in *ahp6* mutant sequences, that exhibit far more 2-permutations and 3-permutations than wild-type plants. Along these lines, we could further show that even the most complex perturbations found in the *ahp6* mutant plants could be interpreted in terms of chained permutations.

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

**Participants:** Florence Chaubert-Pereira, Jean-Baptiste Durand, Damien Fumey, Frédéric Boudon, Christophe Godin, Yann Guédon, Jean Peyhardi, Christian Cilas, Evelyne Costes, Pascal Ferraro, 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 modulation by the environment). This is made using two types of approaches. On the one hand, we develop a statistical approach in which stochastic models are augmented with additional time-varying explanatory variables that represent the environment variations. The design of estimation procedures for these models make it possible to separate the plant ontogenetic programme from its modulation by the environment. On the other hand, we build reactive models that make it possible to simulate in a mechanistic way the interaction between the plant development and its environment.

- *Analyzing growth components in trees.* (Florence Chaubert-Pereira, Yann Guédon, Jean-Baptiste Durand, Jean Peyhardi, Yves Caraglio [AMAP], Emilie Lebarbier [AgroParisTech], Catherine Trottier, Olivier Taugourdeau [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 [49], (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 Markov and semi-Markov switching linear mixed models [42] [2]. The underlying Markov or semi-Markov chain represents the succession of growth phases (endogenous component) while the linear mixed model attached to each state of the underlying Markov or 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. These integrative statistical models were in particular applied in a forest ecology context to characterize the opportunistic development of understory samplings in relation to light environment. 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 Markov and semi-Markov switching linear mixed models, the response variable is constrained to be approximately normally distributed. We are now studying the statistical methodology for Markov and 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 [45] 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 [22].

## 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:** Romain Fernandez, Jérôme Chopard, Mahmoud Omidvar, 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 analyze and simulate their behavior. 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, 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 4) 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 time course 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 has appeared in the journal Nature Methods [5].

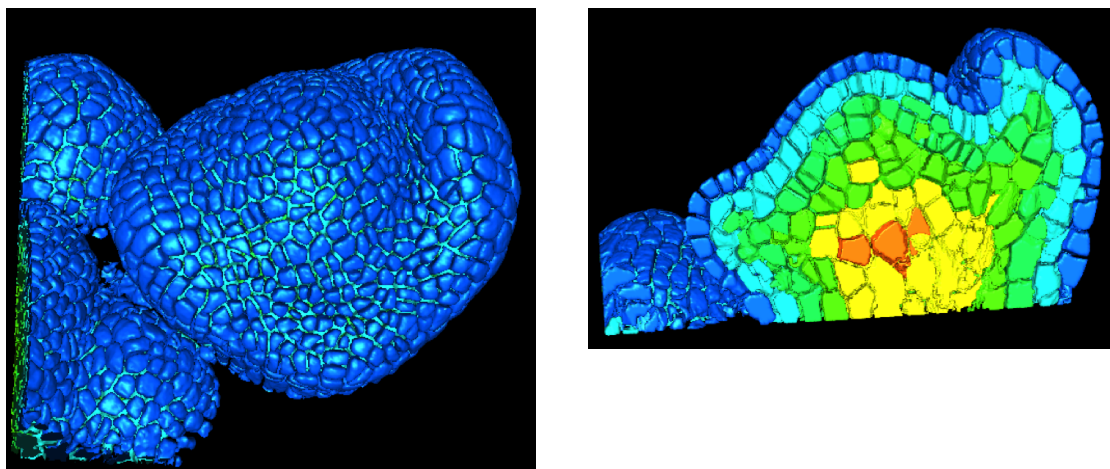


Figure 4. Surface view of a flower meristem automatically segmented using MARS at cell resolution and a transversal cut showing the inner segmented tissues

- *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 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 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 5 shows a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity, etc.)

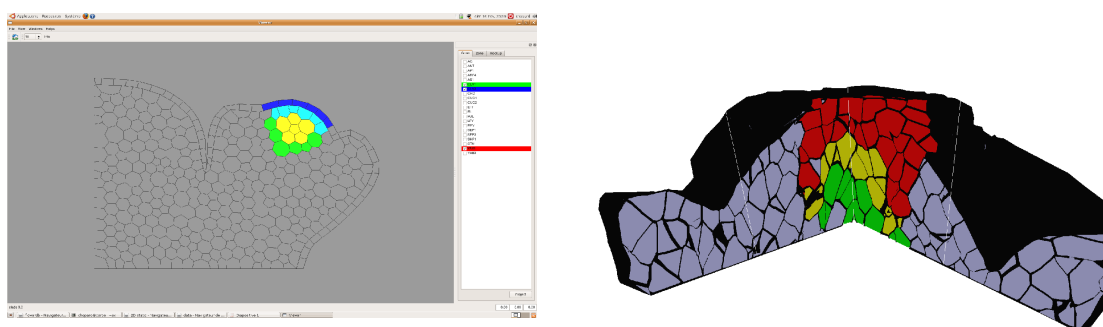


Figure 5. Prototype of a 3D database represented as a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity, ...)

### 5.2.2. Shape analysis of meristems

(Frederic Boudon, Yann Guedon, Francois Mankessi [BURST, DAP], Olivier Monteuis [BURST, DAP], Jean Luc Verdeil [BURST, DAP] )

In this study we made an attempt to characterize a relation between the age of a Shoot apical meristem (SAM) and the shape of its dome. For this, we considered a set of SAM derived from five different outdoor and in vitro sources of juvenile and mature *Eucalyptus urophylla* x *Eucalyptus grandis* akin genotypes were compared. Overall measurements of SAM dome height  $H$  and diameter  $D$  ranged from 2 to 35  $\mu\text{m}$  and 20 to 80  $\mu\text{m}$ , notwithstanding significant differences according to the various physiological origins of plant material investigated. SAM domes from the mature trees "Mat" were taller than those from the rejuvenated ministock plants "Rej": from the in vitro microcuttings "IVM" of the same clone, and also from the in vitro juvenile seedlings "IVJ", whereas outdoor seedlings "Juv" SAM domes exhibited intermediate height. SAM domes from the rejuvenated material "Rej", from the in vitro mature "IVM" and juvenile "IVJ" origins were also narrower than those from the outdoor seedlings "Juv" and to lesser extent than those from the mature trees "Mat". Overall the mature source "Mat" displayed bigger and somehow sharper hemispherical domes than those from "Rej" and "Juv", physiologically more juvenile, or those from the in vitro origins "IVM" and "IVJ" which looked flatter and smaller. SAM dome height, diameter  $D$  and  $H/D$  values varied also significantly according to shoot apex status. More specifically,  $H$ ,  $D$  and  $H/D$  SAM differences between the five origins were not significant when SAM were in their more organogenic stage, to become more salient as leaf structures started to elongate and to differentiate. This was particularly obvious for mature tree "Mat" SAM dome shapes

which showed at this stage much higher  $H/D$  values than the other SAM sources. Additionally, a shape index  $S$  used for characterizing more accurately dome shapes confirmed these trends. These observations provide additional arguments to the view that juvenility in trees become more and more time and space restricted as ageing increases, to be ultimately confined to the more organogenic phases of SAM, from which shoot characteristics derive [15].

### 5.2.3. Transport models

**Participants:** Mikaël Lucas, Jérôme Chopard, Christophe Godin, Michael Walker.

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

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 [55] [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 their different PIN allocations. For example [41] used the so-called 'up-the-gradient' model in the L1 to recreate the depletion zone around a maximum, and a 'flux-mediated' model to produce the midvein growing through the L2. A more unified approach was that of Stoma *et.al.* [10] who used the flux-mediated model in both tissues, but with different powers of the auxin flux, *i.e.* with a linear function in the L1 and a quadratic one in the L2.

We seek a truly unified model with no difference in the PIN allocation model. Our approach is based on inherent differences between the L1 and L2, specifically their dimensionality and the distribution of sources and sinks. We also use a flux-feedback function whose power is intermediate between one and two. For powers close to but slightly higher than one, the diffuse PIN distribution is retained in the L1 but a canalized one is formed in the L2. Hence a unified model seems within reach.

We are also comparing two and three dimensional simulations to test the common approximation of three-dimensional tissues being modeled as two-dimensional. We find that source-sink models are well-approximated in two dimensions while sink- and source-driven systems show qualitatively different behavior.

In collaboration with colleagues at ENS-Lyon, we are working towards running simulations on digitized realistic tissues at different stages of growth. By scanning at multiple stages of growth and tracking lineages we hope to study the interplay of growth and PIN dynamics. We can run the simulation on successive growth stages while ensuring that daughter cells inherit auxin and PIN concentrations from their mothers.

This work is done as part of the Geneshape project, whose general aim is to compare the invagination of the carpel in *Arabidopsis thaliana* to that of the ascidian organism, *Ciona intestinalis*.

- *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 Laplace, Malcolm Bennett [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 [52], [53]. 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 this research further.

#### 5.2.4. Mechanical model

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

*This research theme is supported by the ANR 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 through 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 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 [21]. 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 2011.

#### 5.2.5. Cell cycle model

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

*This research theme is supported by the ANR 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 meristems 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.

#### 5.2.6. Gene regulatory networks

Modeling 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, Yann Guédon, Jonathan Legrand, François Parcy, Jan Traas, Teva Vernoux)

In the continuity of previous years, work on gene network modeling has concerned both methodological and applied developments.

On the methodological side, numerical tools for the simulation of gene network models have been further developed, in the context of Y. Refahi's thesis. First, in order to propose efficient simulation methods, an existing cellular automata approximation of differential equations has been tested on simplified (1D) meristem structures, with promising results. This preliminary study will now be extended to realistic 3D and 4D structures, reconstructed from microscopy data using the methods



in [14]. To this aim, a first set of generic tools have been developed by Y. Refahi to perform and analyze simulations on these structures. The focus will now be put on the effect of time, and thus growth of the meristem, on the patterns that simple models can generate.

Another methodological work was to continue the analysis of the piecewise-linear formalism. The publication [13] accepted last year has appeared. Recent developments, using tools from control theory to ensure (or preclude) stable periodic solutions in a gene network, have been shown in an international conference [24]. A new development, based on an approximation of piecewise-linear models by Markov chains, has also been presented in an international conference [20].

On the more applied side, a paper in collaboration with teams in Marseilles has appeared, as a result of E. Farcot's work as a post-doc in 2007 [12], on the modeling of T cell differentiation.

As a second aspect, the work on the auxin signaling pathway, in collaboration with T. Vernoux, has led to a publication recently submitted to a journal, as well as a presentation in the FSPM conference [25]. From a methodological point of view, this work involves a first clustering procedure applied by Y. Guédon and J. Legrand, of statistical nature, which has allowed us to determine a well-founded simplified network, based on newly acquired protein-protein interaction data. This simplified network has been used to study a differential equation model. Based on a combination of analytical and numerical investigations, this model showed that the meristem could present well differentiated buffering abilities in its role of auxin perception, a prediction that was corroborated by experiments using a newly developed auxin signaling sensor.

Finally, we have developed a first model of the control of floral initiation by genes, and in particular the situation of cauliflower mutants, in which the meristem 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. It involves C. Godin, E. Farcot and F. Parcy.

This work constitutes a first step towards unifying the two main axes of the team research project.

### 5.2.7. Model integration

**Participants:** Mikaël Lucas, Michael Walker, Jérôme Chopard, Frédéric Boudon, Christophe Godin, Mahmoud Omidvar, Christophe Fiorio, 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 in 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.

- *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 foundation (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 2010 two-day workshop, organized jointly with IFR Daphné, was devoted to imaging, phenotyping and modeling plant organ morphogenesis. The invited speakers were Henrik Jönsson (Lund University, Sweden), Gregoire Malandain (Asclepios, INRIA Sophia Antipolis), Nathalie Wuyts (LEPSE, Montpellier), Richard Smith (University of Bern, Switzerland), Jos A. Feijó (Lisbon University), Malcolm J. Bennett (University of Nottingham, UK), Asuka Kuwabara (University of Sheffield, UK), Hendrik Poorter (FZJ Jülich, Germany), Patrick Lemaire (IBDML, Marseilles), Jérôme Chopard (INRIA, Virtual Plants) and Arezki Boudaoud (ENS Lyon). The seminar is organized by Yann Guédon, Christine Granier (INRA, LEPSE) and Laurent Laplaze (IRD, DIAPC) with the support of Agropolis International and Agropolis Foundation.

#### 6.1.2. *OpenAlea*

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

Funding: Agropolis foundation (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 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, ...

#### 6.1.3. *vTissue*

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

Funding: INRIA ADT (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 modeling in our teams. More precisely, we aim at building 3D models of meristem development at cellular resolution based on images obtained with confocal or multiphoton microscopy. This set of components will be used by biologists and modelers making it possible to build such meristem structures, to explore and to program them. This platform is embedded in the OpenAlea framework and is based on the imaging components of the platform MedINRIA.

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

#### 6.1.4. *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 Cible 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 2010, this action was relayed by the launching of three new projects with the teams that participate to ARC :

- Phenomena, funded by Agropolis foundation, that aims at integrating Nitrogen dynamic between leaves, as a function of their local illumination in the canopy. This resulted in the port of Nema model under Alinea.Nema and a first coupling, under the platform with Alinea.Adel and Alinea.Caribu [18]
- the launch of the Op-Op ARC INRIA that aim at improving the Alinea.Caribu package for light illumination of virtual crops.
- the launch of the ECHAP project (funded by Ministere de l'Agriculture) for the development, under OpenAlea of a set of tools for simulating the effect of pesticide on disease development.

This toolbox will use the ALinea.ADEL module and import new modules from Septo 3D model [17]. Currently, only the prototype has been designed.

Besides these actions, the group created by the ARC continued to develop Alinea, by improving the geometric model of leaves in ADEL [11], include a package for leaf optical properties computation from leaf nitrogen content (Alinea.LeafOpticals), develop a link between Alinea.Adel and the crop model Ecomeristem [37] and finally propose some guidelines for porting modular models under OpenAlea [26].

#### 6.1.5. Phenomena

**Participants:** Christophe Pradal, Christian Fournier [INRA, LEPSE], Benoit de Solan [Arvalis/INRA, Avignon], Frédéric Baret [INRA, UMMAH], Elmer Ccopa-Rivero [INRA, UMMAH], Bruno Andrieu [INRA, EGC], Michel Chelle [INRA, EGC].

**Funding:** Agropolis foundation (Contractors for Virtual Plants: INRIA from 2010 to 2012)

The aim of this project is to combine a 4D plant model with a functioning model as a support to improve field high throughput phenotyping with remote sensors. This is a critical need to enhance interpretation of large amount of genotypic data made available by sequencing methods in constant improvement. Collecting more frequent and more accurate plant and stand measurements may lead to a better characterization of cultivar response to stresses.

Plant breeding appears to be a major component in the way to solve the new challenges that agriculture in Mediterranean areas is facing. New techniques allowing to access specific traits of cultivars have to be developed based on non destructive and rapid measurements such as those offered by close range remote sensing known as proxidetection.

This work is based on two existing models, the NEMA model for nitrogen dynamic between leaves [18] and the Alinea.ADEL architectural model. Implementation use the modeling platform OpenAlea, dedicated to functional structural modeling of plants. The coupled model is then be used to simulate reflectance and gap fraction with a radiative transfer model (Baret et al., 2007).

#### 6.1.6. M2A3PC

**Participants:** Christophe Pradal, Yann Guédon, 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.*

**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 Gotheron [INRA Avignon].



The aim of this project (see <http://www.sm.u-bordeaux2.fr/M2A3PC/>) is to develop a methodology to model plant-pathogen interactions at several spatio-temporal scales. We explored more in depth two particular scales: the plant individual and the plot scales, on two patho-systems, vine-powdery mildew and apple-scab.

The spread of a pathogen within a strongly anthropized perennial vegetable cover depends on many factors acting at contrasted spatio-temporal scales. This is of paramount importance for vine and apple trees and their airborne parasites, namely the powdery mildew, and the apple scab respectively, that strongly rely on the susceptibility and status of their hosts. Both crop systems require from 7 to 20 fungicide treatments per year. Sustainable crop management relies on a better understanding of the dynamics of these epidemics at various spatio-temporal scales.

The generic M2A3PC model [31] was built in the OpenAlea platform in order to compare the effect of plant architecture and growth on the two diseases. Pertinent output variables from the plant individual scale were built to assess the plant infection status, and some of them were used as input at plot scale. A model describing plants-pathogen interactions at the plot scale was also proposed, whose output must still be compared with experimental data.

### 6.1.7. Fruit3D

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

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

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 ecophysicists. 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. 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 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 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:** Jérôme Chopard, Michael Walker, Etienne Farcot, 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, they also have 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, Marseilles.

## 6.2. International Bilateral Relations

### 6.2.1. ANR-BBSRC Grant

**Participants:** Christophe Godin, Jan Traas, Etienne Farcot, Yassin Refahi, Frédéric Boudon, Andrew Bingham [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 behavior 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 expertises on imaging, floral development and quantitative modeling, to focus on a comparative analysis of sepal and petal growth in *Arabidopsis thaliana*. 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. 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. More information can be found at <http://www.erasysbio.net/index.php?index=277>.

### 6.2.3. EU 2WAYS Grant

**Participants:** Etienne Farcot, Frédéric Boudon, Christophe Godin, Nicola Buckley [Cambridge University, UK], Jim Haseloff [Cambridge University, UK], Tim Rudge [Cambridge University, UK].

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

*Hands on Synthetic Biology* is one of the 17 teams involved in the 2WAYS project, and is composed by Virtual Plants and collaborators from Cambridge University. It is created and coordinated by EUSCEA (European Science Events Association), and supported by the European Commission, as a Science in Society project under FP7. Its aim was to communicate about science in an interactive manner. One aspect of the project was to develop presentations for the public, and the other was to organize events where the main actors would be young students. It led to the development of interactive programs usable by a very wide audience on a computer or a touch-screen, to illustrate the role of genes in flower development. The project culminated in a Final Event, held in the European Parliament in Brussels, from November 29 to December 2. See <http://www.twoways.eu/> for more detailed information.

#### 6.2.4. Other bilateral relations

There is currently an active connection with the group of Malcolm Bennett, at the Centre 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 Mikaël 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 Palubicki and Steven Longuay, respectively PhD and Masters students, have come for 5 week visits each.

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. He visited the UC Davis team in September.

## 7. Dissemination

### 7.1. Services to the scientific community

- Christophe Godin has rendered the following services in 2010:
  - 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 representative 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 1 PhD thesis (Li Qi Han, University of Queensland, Australia) and 1 HDR (D. Rousseau, University of Angers))
  - 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 (FSPM), and journals (PloS Computational Biology, Annals of Botany, Computer Graphics Forum).
- Yann Guédon has rendered the following services in 2010:
  - he is a member of the editorial board of Annals of Botany and a member of the ERCIM working group "Computing & Statistics".
  - he evaluated a research project for the University Paris Descartes.

- he was a member of the program committee of the 6th International Workshop on Functional-Structural Plant Models and reviewed communications for this conference.
- he was a referee for papers submitted to Computational Statistics & Data Analysis.
- Frederic Boudon was referee for papers submitted to Computer Graphics Forum and Sensors.
- Christophe Pradal has rendered the following services in 2010:
  - he is the coordinator of the national platform for plant modeling OpenAlea
  - he was member of the scientific board of EuroSciPy'10, and editor of an associated special issue.
- Etienne Farcot served as a referee for papers submitted to Biosystems, Journal of Mathematical Biology, PLoS One, and for a project submitted to the ANR.
- Yassin Refahi was in the scientific board of the Majestic conference for young researchers in information and computer science, see <http://majestic2010.labri.fr/index.php>.
- The team received several visitors from exterior research groups in 2010: Farah Ben Naoum, from Sidi Ben Abes University visited us last spring. Wojtek Palubicki and Steve Longuay, from Pr. Prusinkiewicz team in Calgary, visited the team in November-December 2010.

## 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 ( <http://www.agro-montpellier.fr/um2/um1/masterbiostatistique>).

He participated to the jury of this Master.

### 7.2.2. Master Computer Science

University Montpellier 2.

Frederic Boudon teaches a course in the module supervised by Christophe Godin and Christophe Fiorio from LIRMM on plant modeling and computational geometry, entitled *computational plant modeling* <http://www-sop.inria.fr/virtualplants/wiki/doku.php?id=training:plantmodeling>.

### 7.2.3. Other Master Classes

- *Christophe Godin taught the Master classes 'An introduction to plant modeling' in the module 'Systems biology and plant development' coordinated by Jan Traas in the BioScience Master of ENS-Lyon.*
- *Christophe Pradal and Christian Fournier taught the Master classes "Impact de l'architecture de la végétation sur l'interception de la lumière" in the module 'Démarches de modélisation' in Montpellier SupAgro.*

### 7.2.4. High School class

- *C. Godin, F. Boudon and E. Farcot gave classes about plant modeling in the context of a joint one-year project together with Yves Caraglio (UMR AMAP) and high school teachers: Marc Béziz (Mathematics), Didier Lacour (Physics), Odile Sirlin (Biology) from the Lycée Georges Pompidou, Castelnau, and M. Lizambert (inspecteur d'académie). Occupation: approximately 2 afternoons per month over two third of the year.*
- *C. Godin and E. Farcot, gave a one day intervention with software demonstrations and a presentation at the CIRAD day for the "Fête de la Science", on October 21.*

- C. Godin, with interventions from M. Bezig and F. Boudon, gave a formation on L-system for high school teachers in October 22 and November 5, in Carcassonne. This is part of the organization of teaching of computer science in high schools, currently scheduled for 2012.
- in the context of the 2WAYS project, see 6.2.3, a local Science Parliament was organized in the Lycée Pompidou in Castelnau-le-Lez. About 70 pupils aged 16 to 18, had to discuss about 4 ethical issues raised by biological research, and write resolution proposals, similar to those proposed to the European Commission. A similar event was held in Brussels, from November 29 to December 2, gathering 60 pupils from all over Europe.

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

- several members of the team participated to the FSPM conference, held in UC Davis, California. Namely, Frédéric Boudon, Thomas Cokelaar, Anaëlle Dambreville, Etienne Farcot, Christian Fournier, Christophe Godin, Yann Guédon, Christophe Pradal, Chakkrit Preuksakarn, Yassin Refahi were present.
- Frédéric Boudon presented a poster at the INRIA ARC days. He also attended to les journées de l'AFIG in November 2010.
- Christophe Godin was an invited speaker in the following events in 2010:
  - at the Catholic University of Louvain, in January 2010.
  - at the Vegetal Biology department of INRA Versailles, in April 2010.
  - at the scientific seminar of the Symbiose EPI in Rennes, in April 2010.
  - XVII Congress of the Federation of European Societies of Plant Biology (FESPB) in Valencia, Spain, 4-9 July, 2010.
  - International Workshop on Plant Systems Biology, in Freiburg, Germany, 2-5 September, 2010.
  - Plant Morphodynamics Workshop (27-29 September) at the John Innes Center in Norwich, UK.
- Frédéric Boudon, Christophe Godin and Etienne Farcot attended the International Workshop on Plant Systems Biology, in Freiburg, Germany, 2-5 September, 2010. They also attended the Plant Morphodynamics Workshop (27-29 September) held as a final event for the *Flower Model* ANR-BBSRC in Norwich, UK.
- Christophe Pradal was an invited speaker at Environment and Agronomy department of INRA, in December 2010. He gave a talk at the European Scientific Python Conference at the Ecole Normal Supérieure ULM, in Paris, in July 2010. He gave an other talk at the Agropolis computational plant seminar, in Montpellier, in September 2010
- Thomas Cokelaar gave a talk at the International Horticulture Conference, in Lisbon, Portugal, in August 2010
- Yassin Refahi attended the graduate school "Spatio Temporal Modeling in Biology", 8-11 June 2010, organized by the Ecole doctorale ED474 "Frontières du vivant", at the Centre de Recherches Interdisciplinaires Université Paris Descartes. He also gave a talk entitled "A Combinatorial Approach for Analyzing Perturbations in Phyllotaxis of *Arabidopsis thaliana*" at the Workshop "Algorithmique, combinatoire du texte et applications en bio-informatique", in January 2010, in Montpellier.
- Michael Walker attended the Evry Spring school on "Modelling Complex Biological Systems in the Context of Genomics", 3-7 May 2010.

### 7.4. Theses and Internships

#### 7.4.1. Theses defenses

- Romain Fernandez, 3D reconstruction and cell lineaging from laser microscopy images: Application to vegetal tissues, Montpellier 2 University, November the 3rd, 2010.

#### 7.4.2. Ongoing Theses

- Anaëlle Dambreville, "3D modelling of mango phenology", Montpellier 2 University .
- Jonathan Legrand, "Hormon signaling and control of morphogenesis during flower development", ENS Lyon.
- Chakkrit Preuksakarn, "Digitizing and assessing virtual architectural models of growing plants", Montpellier 2 University.
- 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.
- Yassin Refahi, "Modeling the growth of floral organs", Montpellier 2 University.

#### 7.4.3. Internships

- Jonathan Legrand (Montpellier 2 University), 'Mixture models for random graph: Application to the auxin signaling network'.
- Jean Peyhardi (Bordeaux 2 University) 'Mixed transition models'.
- Mahmoud Omidvar (Montpellier 2 University), 'Combinatorial map for modelling vegetal tissues'.
- Jonathan Marin (Montpellier 2 University), 'Specification of tree growth with sketching'.

## 8. Bibliography

### Major publications by the team in recent years

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## Publications of the year

### Articles in International Peer-Reviewed Journal

- [11] T. DORNBUSCH, J. WATT, R. BACCAR, C. FOURNIER, B. ANDRIEU. *A comparative analysis of leaf shape of wheat, barley and maize using an empirical shape model*, in "Annals of Botany", 2010, published online, <http://www-sop.inria.fr/virtualplants/Publications/2010/DWBFA10>.
- [12] E. FARCOT, M. BONNET, S. JAEGER, S. SPICUGLIA, B. FERNANDEZ, P. FERRIER. *TCRb Allelic Exclusion in Dynamical Models of V(D)J Recombination Based on Allele Independence*, in "Journal of Immunology", 2010, vol. 185, n<sup>o</sup> 3, p. 1622–1632, <http://www-sop.inria.fr/virtualplants/Publications/2010/FBJSFF10>.
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- [17] R. BACCAR, C. FOURNIER, T. DORNBUSCH, B. ANDRIEU, C. ROBERT. *Assessing the effect of canopy architecture as affected by sowing density on epidemics using a virtual wheat plant model coupled with a Septoria tritici epidemic model*, in "6th International Workshop on Functional-Structural Plant Models", T. DEJONG, D. D. SILVA (editors), 2010, p. 58–60, <http://www-sop.inria.fr/virtualplants/Publications/2010/BFDAR10>.
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