Activity Report 2011

Project-Team VIRTUAL PLANTS

Modeling plant morphogenesis at different scales, from genes to phenotype

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

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Keywords: Multiscale Models, Plant Growth, Computer Graphics, Cellular Networks, Markovian Model, Biological Images

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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 develop a detailed analysis of apical meristem processes, based on advanced mathematical and computational methods and tools, to get a deeper and better understanding of plant development.

This study is performed from two complementary perspectives.

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

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

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

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

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

3. 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. Theses methods range from algorithms for computing distance between sequences or tree-structured data to statistical models.

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

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

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

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

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

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

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

3.2. Meristem functioning and development

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

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

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

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

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

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

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

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

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

OpenAlea is the result of a collaborative effort associating 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.).
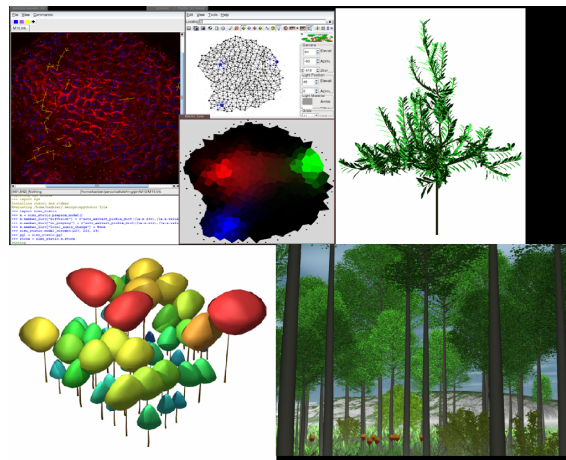
4. Software

4.1. V-Plants

Participants: Frédéric Boudon, Christophe Godin [coordinator], Yann Guédon, Christophe Pradal [software architect], Daniel Barbeau, Thomas Cokelaer, David Da Silva, Jean-Baptiste Durand, Pascal Ferraro, Eric Moscardi.

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

- Multi-scale geometric modeling and visualization. VPlants.PlantGL is a geometric library which provides a set of graphical tools and algorithms for 3D plant modeling at different scales [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 now available in OpenAlea. They provide different models and algorithms for plant architecture analysis and simulation.

- Meristem functioning and development. A first set of components has been created in the last 4-years period to model meristem development in OpenAlea. These tools are currently being integrated thoroughly in the platform so that modelers and biologists can use them, and reuse components easily (for meristem 3D reconstruction, cell tracking, statistical analysis of tissues, creating and manipulating atlases, creating or loading models of growth that can further be run on digitized structures, etc).

- Standard data structure for plants. A new implementation of the MTG formalism for representing and manipulating multiscale plant architecture has been developed. It provides a central data-structure to represent plants in a generic way in OpenAlea. This implementation is available through the packages OpenAlea.MTG. These components make it possible to share plant representations between users and fosters the interoperability of new models.

- Simulation system. The study of plant development requires increasingly powerful modeling tools to help understand and simulate the growth and functioning of plants. In the last decade, the formalism of L-systems has emerged as a major paradigm for modeling plant development. Previous implementations of this formalism were made based on static languages, i.e. languages that require explicit definition of variable types before using them. These languages are often efficient but involve quite a lot of syntactic overhead, thus restricting the flexibility of use for modelers. We developed L-Py [26] an adaptation of L-systems to the Python language (basis of OpenAlea). Thanks to its dynamic typing property, syntax is simple, code execution is made easy and introspection property of the language makes it possible to parameterize and manipulate simply complex models. Independent L-systems can be composed to build-up more complex modular models. MTG structures (that are a common way to represent plants at several scales) can be translated back and forth into L-system data-structure and thus make it easy to reuse in L-systems tools for the analysis of plant architecture based on MTGs. Extensions to integrate multiscale dynamic models are currently being developed in collaboration with P. Prusinkiewicz and his team from the University of Calgary. A paper presenting L-Py has been submitted to Frontiers in Technical Advances in Plant Sciences.

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, Thomas Cokelaer, Christian Fournier, Eric Moscardi.

This research theme is supported by an INRIA ADT Grant and by a RTRA Grant.
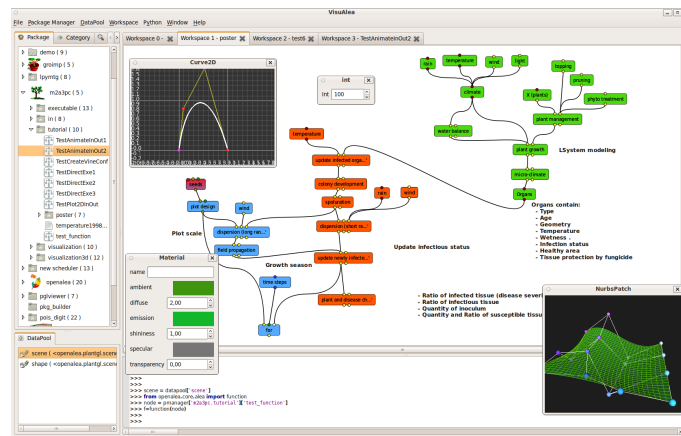
Figure 2. OpenAlea.Visualea: Visual programming interface. The package manager shows the available components. The components can be interconnected on a workspace to form a data-flow. The python interpreter allows low level interaction with the system.

OpenAlea [9] 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 2011, one major release was done : Openalea 1.0. The following progresses were accomplished:

1. Develop and extend OpenAlea and Visualea:

   – The standard library of components has been extended with useful scientific packages such as a flexible data plotting package (Openalea.Pylab), 2D and 3D image manipulation (Openalea.Image) and linear algebra operations (Openalea.Numpy).

   – Several models of computation have been implemented on the data-flow data-structure to enable discrete event simulation and control flow inside OpenAlea.

2. Animation and diffusion

   – The first OpenAlea Workshop have been held in Montpellier and has been attended by more than 60 scientists. A scientific board has been defined to manage the development and diffusion of OpenAlea. It is composed by 12 scientists.

   – StandAlone binary installers have been released on Windows and Mac to ease the installation of a large number of packages without relying on a web server. A Ubuntu repository has been set up on Launchpad.

   – A continuous integration server has been set up (link http://vp-continuous.cirad.fr) to test the reliability of all the components after every commit.

– 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 500,000 times during the last two years. OpenAlea is the first project at Inria Gforge in term of number of downloads and of page views.

4.3. Alinea

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

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

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

Different components have been integrated into the OpenAlea platform:

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

In 2011, 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, maïze and other species like vine, rose or apple tree.

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 (ligth, rain, wind, pests, ...), to set up initial conditions of growth models or to assess their output against real data. In the past decade, methods have been developed to digitize plant architectures in 3D [42], [33]. These methods are based on direct measurements of position and shape of every plant organ in space. Although they provide accurate results, they are particularly time consuming. More rapid and automated methods are now required in order to collect plant architecture data of various types and sizes in a systematic way. In this aim, we explore the use of pictures, video, laser scanner and direct sketching.

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

  We investigate the possibility to use 3D laser scanners to automate plant digitizing. We are developing algorithms to reconstruct branching systems without leaves or foliage from scanner data or from scan simulated on plant mock-up obtained using different digitizing method. For this we collaborate with the EPI Galaad from Sophia-Antipolis, the EPI Imagine from Grenoble, different INRA teams, UMR PIAF in Clermont Ferrand, UMR LEPSE and AFEF team in Montpellier and Lusignan, the University of Helsinki, Finland and the CFCC in England.

  We developed a reconstruction pipeline composed of several procedures. A contraction procedure, first aggregates points at the center of the point cloud. The team proposed a simple adaptive scheme to contract points. In parallel, the Galaad team explored uses of detection of circular patterns to be contracted toward their center. Comparison of these approaches has been carried out. In a second step, a skeleton procedure uses a Space Colonization Algorithm [41] to build the skeleton of the shape from the contracted point set. This method is adaptive to the local density of the point set. Then a pipe-model based procedure makes it possible to estimate locally diameters of the branches. Finally, an evaluation procedure has been designed to assess the accuracy of the reconstruction. Results Publication of this work is in progress.

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

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

  Modeling natural elements such as trees in a plausible way, while offering simple and rapid user control, is a challenge. In a first collaboration with the EPI Evasion we developed a method based on the design of plants from silhouettes [43]. This sketching paradigm allows quick and intuitive

specification of foliage at multiple scales. On this topic, we started a collaboration with S. Longuay and P. Prusinkiewicz who develop iPad tools to design plants based on SCA. Combination of multitouch interface, sketching paradigm and powerfull adaptive procedural model that generate realistic trees offer intuitive and flexible design tools. This work is part of the INRIA associated team with the University of Calgary.

- *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 [21].

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

  Understanding the controlling factors of fruit quality development is challenging, because fruit quality is the result of the interplay between physical and physiological processes that are under the control of genes and the environment. Although process-based models have been used to make significant progress in understanding these factors, they to a large extent ignore the shape and internal structure of the fruit. To help characterizing effects of fruit shape and internal structure on quality, the creation of a 3D virtual fruit model that integrates fruit structure and function with growth governed by environmental inputs has been investigated. For this purpose, a modelling pipeline has been created that includes the following steps: creation of a 3D volumetric mesh of the internal and external fruit structure, calculation of the fruit's physical properties from the resulting mesh, and integration of aspects of fruit physiology into the 3D structure. This pipeline has been applied to study tomato fruit (Solanum lycopersicum) by constructing 3D volumetric meshes from two images of perpendicular fruit slices and from MRI data, and integrating water and carbon transport processes into one of these meshes. To illustrate the tomato model, a simulation of one season's of the fruit's growth has been performed and its results compared with an already published process-based tomato fruit model. The results of the two models were in general agreement, but our model provided additional information on the internal properties of the fruit, such as a gradient in sugar concentration. Once the model is calibrated and evaluated, our approach will be suitable for studying the effects of internal fruit heterogeneity and overall shape on fruit quality development [18].

5.1.2. Modeling the plant ontogenic programme

Participants: Christophe Godin, Yann Guédon, Evelyne Costes, Jean-Baptiste Durand, Pascal Ferraro, Anaëlle ambreville, Christophe Pradal, Catherine Trottier, Jean Peyhardi, Yassin Refahi, Etienne Farcot.

This research theme is supported by two PhD programmes.

The remarkable organization of plants at macroscopic scales may be used to infer particular aspects of meristem functioning. The fact that plants are made up of the repetition of many similar components at different scales, and the presence of morphological gradients, e.g. [23], [35], [36], [32], 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" [38], "age state" [31] or "physiological age" [24]. 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 [31], [24]. 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], Anna Davidson [UC Davis], Ted DeJong [UC Davis], Claudia Negron [UC Davis]).

  In the context of a collaboration with Claudia Negron, Anna Davidson, 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 corresponding to different genetic backgrounds, environment conditions and horticultural practices 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 [40], [3]; see 5.1.3.

- *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 [34], [27]). To characterize genetic determinisms of the alternation of flowering in apple tree progenies at annual shoot (AS) scale, a model of the transitions between ASs was built. The ASs were of two types: flowering or vegetative. Two replications of each genotype were available. Our model operated on tree-structured data and relied on a second-order Markov tree. Generalized Linear Mixed Models (GLMMs) were used to model the effet of year, replications and genotypes (with their interactions with year or memories of the Markov model) on the transition probabilities. This work was the continuation of the Master 2 internship of Jean Peyhardi (Bordeaux 2 University) and was carried out in the contex of the PhD thesis of Baptiste Guitton.

  This PhD thesis also comprised the study of alternation in flowering at individual scale, with annual time step. To relate alternation of flowering at AS and individual scales, indices were proposed to characterize alternation at individual scale. 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 relied on a parametric hypothesis on the base effect (random slopes specific to genotype and replications), which translated into mixed effect modeling. Different indices of alternation were then computed on the residuals. Clusters of individuals with contrasted patterns of bearing habits were identified. Our models highlighted significant correlations between indices of alternation at AS and individual scales. The roles of local alternation and asynchronism in regularity of flowering were assessed using an entropy-based criterion, which characterized asynchronism.

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

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

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

  Formally, the shoot properties are summed up using the notion of shoot state. The number of children shoots in each state is modeled through discrete multivariate distributions. Model selection procedures are necessary to specify parsimonious distributions. We developed an approach based on probabilistic graphical models to identify and exploit properties of conditional independence between

numbers of children in different states, so as to simplify the specification of their joint distribution. The graph building stage was based on a Poissonian Generalized Linear Model for the contigency tables of the counts of joint children state configurations. Then, parametric families of distributions were implemented and compared statistically to provide probabilistic models compatible with the estimated independence graph.

This work was carried out in the context of Pierre Fernique's Master 2 internship (Montpellier 2 University and AgroParisTech). It was applied to model dependencies between short or long, vegetative or flowering shoots in apple trees. The results highlighted contrasted patterns related to the parent shoot state, with interpretation in terms of alternation of flowering. This work will be continued during Pierre Fernique's PhD thesis, with extensions to other fruit tree species (mango trees) and other strategies to build probabilistic graphical models and parametric discrete multivariate distributions including covariates and mixed effects.

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

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

- *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 want to find 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. In a previous work we showed that this problem can be solved in polynomial time and gave the corresponding algorithm [6].

Now, we continue this work along different directions:

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

  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. A publication on this topic is currently in progress.

–   *Search for the NST* (Farah Ben-Naoum, Christophe Godin, Pascal Ferraro) The NEST
    algorithm constructs a closest self-nested tree that embeds a given tree T. This means in
    particular that $T \in NEST(T)$. For some trees this definition might be too restrictive and
    one may want to get rid of the latter constraint. In this case, the closest self-nested tree
    (NST) to a tree T would be defined by:

    $$NST(T) = \arg\min_{S \in \mathcal{S}(T)} D(T, S),$$

    where $\mathcal{S}(T)$ is now the set of all self-nested trees. Although it has not yet been demon-
    strated, the computation of $NST(T)$ is likely to be a NP-complete problem. Therefore
    we decided to develop a heuristic algorithm to carry out this optimization. This algorithm
    is based on evolutionary optimization algorithms. First results obtained at the University
    of Sidi Bel Abbes by Farah Ben Naoum are very encouraging. They should contribute to
    define a general method to compress tree-like structures based on self-similarity.

–   *Stochastic NESTs* (Jean-Baptiste Durand, Christophe Godin, Pascal Ferraro, Yann Guédon)

    One of the limits of the original NEST algorithm in defining a compressed structure is
    that it does not take into account possible small variations in the identification of similar
    tree patterns in the global tree structure. In real trees, it is however seldom the case that
    similar tree parts are exactly isomrophic. They may differ by small details while keeping
    globally similar. A general compression technique should account for such variations from
    a theoretical point of view. This is what we intend to do here by developing a stochastic
    NEST approach. The idea is to extend the definition of tree compression to include the
    notion of tree distribution in compressed representations of trees. A first formalism has
    been designed for stochastic tree compression.

- *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 [29] 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 in-
  vestigate this, Fabrice Besnard and Teva Vernoux are studying *Arabidopsis thaliana ahp6* mutants,
  AHP6 being a protein known for its inhibitory effect in the cytokinin signaling pathway. At the
  macroscopic scale, this mutation induces perturbations of the phyllotaxis, barely sensible on single
  plants. In order to characterize these perturbations, we designed a pipeline of models and methods
  [20] which decompose into three steps: (i) identification of perturbation patterns, (ii) characteriza-
  tion of perturbation patterns using hidden variable-order Markov chains and combinatorial mixture

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 methods, we have shown that the perturbation patterns in both wild-type and mutant plants can be explained by permutations in the order of insertion along the stem of 2 or 3 consecutive organs. The number of successive synchronized organs between two permutations reveals unexpected patterns that depend on the nature of the preceding permutation (2- or 3-permutation). We identified significant individual deviations of the level of baseline segments with reference to 137.5°, which confirms theoretical model predictions. Finally, we highlighted a marked relationship between permutation of organs and defects in the elongation of the internodes in between these organs. All these results can be explained by the absence of a strict coupling between the timing of organ development and their angular and longitudinal position on the stem. A paper about these results is in revision for the journal Science. Another more methodological paper is in progress.

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

Participants: Jean-Baptiste Durand, Damien Fumey, Frédéric Boudon, Christophe Godin, Yann Guédon, Jean Peyhardi, Pierre Fernique, 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.* (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 [34], (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 [27] [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 [15]. 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 AGAP])

  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. In the PhD of Damien Fumey we explored 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'. Results of this experiment [30] 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 [28]. A paper describing this model is currently in progress.

5.2. Meristem functioning and development

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

5.2.1. *Data acquisition and design of meristem models*

Participants: Frédéric Boudon, Christophe Godin, 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, Jan Traas, Pradeep Das, Vincent Mirabet.

  In previous work [5], 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. In 2011, we worked to improve the robustness of the MARS-ALT pipeline. The software pipeline was completely re-engineered so as to be easily available in OpenAlea with documentation. We also designed new tests to improve the method and get high-quality results on different types of organisms.
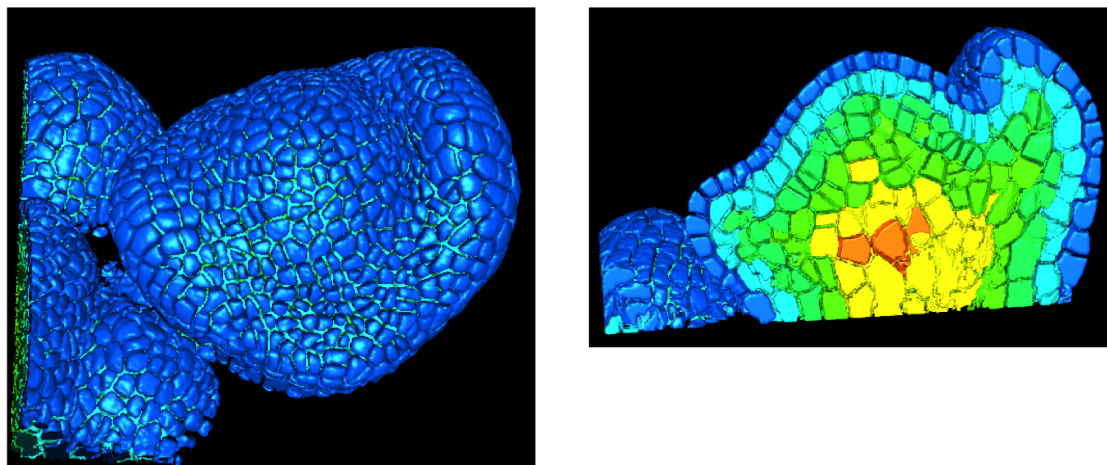

Figure 4. Surface view of a flower meristem automatically segmented using MARS at cell resolution and a transversal cut showing the inner segmented tissues

- *Design of 3D virtual maps 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 3D virtual map is mainly descriptive. However, like for classical databases, specific tools make it possible to explore the virtual map according to main index keys, in particular spatial and temporal keys. Both a dedicated language and a 3D user interface are being designed to investigate and query the 3D virtual map.

  A prototype version of this 3D virtual map is currently being built and is integrated in *V-Plants*, see figure 5 where a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity, etc...).

  Using this 3D virtual map prototype, along with piecewise-linear models of gene networks, and optimization techniques, our colleagues from ENS/Lyon have been able to develop a model of the gene network regulating sepal polarization in *A. thaliana*. This model, which is consistent with a very comprehensive literature data set, also include new predictions for certain gene interactions, and will appear next year in Plant Cell .[14]
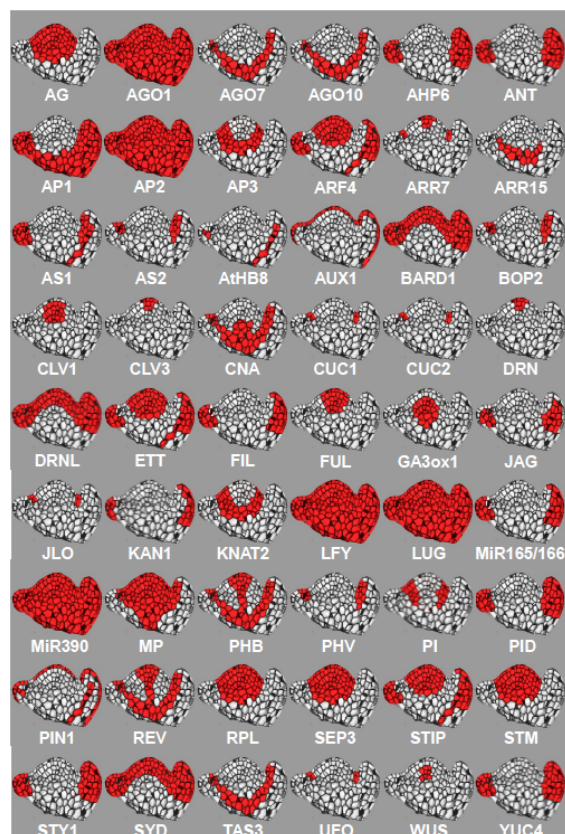
Figure 5. A 3D database represented as a cell-based map that can contain different types of information (cell lineage, cell size, cell identity, ...), from [14].

5.2.2. *Shape analysis of meristems*

(Jean-Baptiste Durand, Frederic Boudon, Yann Guedon, Francois Mankessi [BURST, DAP], Olivier Monteuuis [BURST, DAP], Jean Luc Verdeil [PHIV, DAP])

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

5.2.3. *Transport models*

Participant: 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 [39] [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 [25] 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 completely 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.

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.

A paper on this unified model is being written. This work is done in the context of the Geneshape and iSAM projects.

5.2.4. *Mechanical model*

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

This research theme is supported by the ANR VirtualFlower and Geneshape projects.

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 . 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. *Gene regulatory networks*

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

- *The auxin signaling pathway* (Etienne Farcot, Yann Guédon, Christophe Godin, Yassin Refahi, Jonathan Legrand, Jan Traas, Teva Vernoux)

  The auxin signalling network involves about 50 potentially interacting factors. We applied a graph clustering method [16] that relies on 0/1 interactions between factors deduced from yeast two-hybrid (Y2H) data. The Y2H analysis involves two independent tests (X-gal and HIS3 tests). Each possible interaction was tested in the two possible configurations, where each protein was alternatively the bait and the prey protein. A binary interaction is thus a summary of the four outputs of the X-gal and HIS3 tests. In order to limit the loss of information, we designed a standardization procedure to summarize the outputs of the X-gal and HIS3 tests as a distance defined on a continuous scale. This opens the possibility to studies the influence of phylogenetic distances between factors on their interactions using an extension of the mixture model for random graphs that incorporate explanatory variables. This work is the object of a collaboration with Jean-Benoist Leger and Stéphane Robin (MIA, AgroParisTech/INRA).

  As an output to this interaction extraction, it was possible to apply a clustering procedure (work of Y. Guédon and J. Legrand), based on a mixture model of random graphs. This allowed us to determine a well-founded simplified network, which was then used to develop a differential equation model. 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 sensor. The combination of computational techniques and novel experimental tools and data that were developed in this project have led to a new view of the meristem behavior, where auxin signaling, and not only its transport, plays a crucial role. These results have appeared in a systems biology journal with wide readership [16].

  As a follow up, extensions of the differential equation model are under study, with the aim of better understanding this system in more general contexts than the shoot apical meristem development.

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

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

At the single cell level, new results were obtained in the framework of piecewise-linear models. Since their introduction in the late 1960's, these models have been believed to present chaotic behavior in some parameter regimes. However, this was mostly observed numerically, based on intensive generation of random networks. In a collaboration between E. Farcot and R. Edwards (Univ. Victoria, Canada), with recent input from one of his students, E. Foxall, we have introduced a method to explicitly build piecewise affine models having a return map which is conjugate to a topological horseshoe. A paper presenting these results is currently in revision.

At a higher scale, we have also continued the study of gene regulation in meristematic tissues. Numerical tools for the simulation of gene network models have been further developed, in the context of Y. Refahi's thesis. Using realistic 3D and 4D structures, reconstructed from microscopy data using the methods in [5], we have defined putative gene expression patterns in collaboration with biologist colleagues in Lyon (P. Das). We then have constructed an adimensionalized model with only 3 parameters, based on the existing literature [37]. Using standard optimization procedures to fit these parameters we were able to reproduced the in silico patterns with great accuracy. Moreover, alternative patterns were found, based on hypotheses of continuous deformation of gene patterns under tissue growth. These predictions remain to be tested, and this will constitute a large part of Y. Refahi's post-doctoral project (INRA/INRIA CJS fund), in collaboration with ENS Lyon and the team of Henrik Jönsson in Lund, Sweden.

A related study has been initiated during a visit of E. Farcot at the Memorial University of Newfoundland, funded by the INRIA "Explorateur" program (see international relations section). This visit has allowed to initiate a mathematical study of gene regulated patterning in plants, with the aid of tools from equivariant dynamical systems theory, and more generally by relying on symmetry properties. Some first results have been obtained concerning homogeneous patterns in regular tissues, and their bifurcations.

5.2.6. Model integration

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

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

Our approach consists 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.

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

At a scale involving organs and their geometric arrangement, 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. This coupled model has led us to hypothesize some interactions between genes and a particular plant hormone, and experiments are currently being made to verify this prediction.

6. Partnerships and Cooperations

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 2011 two-day workshop was devoted to Models at whole plant scale. The invited speakers were Winfried Kurth (University of Göttingen), Mathieu Javaux (Université Catholique de Louvain), Yann Guédon, Renaud Bastien (INRA, PIAF), Frédéric Mothe (INRA, LERFoB), Annikki Mäkelä (University of Helsinki), David Da Silva (UC Davis), Michaël Chelle (INRA, EGC), Jochem B. Evers (Wageningen University), Brian Enquist (University of Arizona, Tucson), François Tardieu (INRA, LEPSE). The seminar is organized by Yann Guédon, Christine Granier (INRA, LESPE) and Soazig Guyomarc'h (Montpellier 2 University, DIADE) with the support of Agropolis International and Agropolis Foundation.

6.1.2. *OpenAlea*

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

Funding: Agropolis foundation (Contractors for Virtual Plants: CIRAD and INRA from 2009 to 2012)

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. *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: CIRAD (INRIA sub-contractor) 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 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).

6.1.5. *Fruit3D*

Participants: 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 ecophysiologists. Physical and biological laws involved in tissue differentiation and cell growth, in relation to fruit growth and compartmentalization, and a number of related traits of quality (e.g. size, composition and texture) are modeled and integrated within the virtual tomato. 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.

6.1.6. *PlantScan3D*

Participants: Frédéric Boudon, Chakkrit Preuksakarn, Jean-Baptiste Durand, 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.

6.1.7. *GeneShape*

Participants: Jérôme Chopard, Michael Walker, Etienne Farcot, Christophe Godin.

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 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, CRBM, Montpellier.

6.2. International Bilateral Relations

6.2.1. ANR-BBSRC Grant

Participants: Christophe Godin, Jan Traas, Etienne Farcot, Yassin Refahi, Frédéric Boudon, 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 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 use live imaging and sector analysis to produce quantitative models of growth for these organs. We then integrate information on regulatory genes with spatial information to produce in silico models of the regulatory network controlling sepal and petal development. The results of the project consist of:

- Capturing quantitative data on sepal and petal morphogenesis
- Analyzing and model the regulatory networks underlying sepal and petal development
- Linking morphogenesis to regulatory networks
- Creating 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. It is part of a wider program, the ERASysBio initiative, a consortium of European funding bodies, ministries and project management agencies. The purpose of this consortium is to develop fundamental and strategic collaboration in the funding of systems approaches to biological research. The iSAM project is one of the 16 transnational consortia that have been selected out of 51 proposals; in total they comprise 85 working groups from 14 countries. Four partners are involved in iSAM: the group of J. Murray will focus on mutants of cell cycle regulation, the group of Y. Helariutta is specialized in several aspects of cytokinin regulation, while the group of J. Traas in Lyon provides input regarding auxin regulation and transport, and Virtual Plants is in charge of the modeling aspects, in synergy with the three other groups.

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

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

The team of Pr. Prusinkiewicz at the University of Calgary (Canada) is an *associated team* of *Virtual Plants*. In this context, F. Boudon spent 5 weeks in Calgary, and Wojtek Palubicki, PhD student, came for a 3 months visits to work on plant architecture simulation models.

Yann Guédon is working with Claudia Negron (PhD student), Anna Davidson (PhD student), David Da Silva (post-doctoral fellow) and Ted DeJong (University of California, Davis) on the analysis of the development and the branching and axillary flowering structures of peach and almond shoots. Claudia Negron, Anna Davidson, David Da Silva and Ted DeJong visited the Virtual Plants and the AFEF teams (Evelyne Costes) in September 2011.

6.3. International Initiatives

6.3.1. *INRIA Associate Teams*

The team of Pr. Prusinkiewicz at the University of Calgary (Canada) has been an *associated team* of *Virtual Plants* from 2009 to 2011. see http://www-sop.inria.fr/virtualplants/wiki/doku.php?id=projects:eqass-vp-uc.

6.3.2. *Visits of International Scientists*

Farah Ben-Naoum, from the University of Sidi Bel Abbes, Algeria, visited the team during one month to work with Christophe Godin on the application of evolutionary algorithms to the compression of tree structures.

6.3.3. *Participation In International Programs*

During the period October 2011-January 2012, E. Farcot is a visitor at the Memorial University of Newfoundland (MUN), St. John's, Canada, to work with Pr. Yuan Yuan, in the Mathematics and Statistics department. This visit was funded by the "Explorateur" program.

7. Dissemination

7.1. Services to the scientific community

- Christophe Godin has rendered the following services in 2011:
  - he is a member of the Steering Committee of UMR AGAP,
  - he is a member since 2011 of the scientific committee of Environment-Agronomy department at INRA
  - 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)
  - he is a member of the working group on Human Resources at INRIA.
  - he was a member of the Modeling commission headed by Patrick Valduriez, in charge of inventoring modelling actions on Montpellier and providing advice on the organization of research on modeling in the region.

- – he is a member of the scientific board of 2 the Labex NUMEV axes: Modeling and Algorithms.
  - – he is associated editor of the new journal: Frontiers in technical advances in plant sciences: http://www.frontiersin.org/technical_advances_in_plant_science/editorialboard
  - – he is the regional correspondant for the national group working on the introduction of computer science in high-schools in 2012, and headed by G. Berry, R. Cabane and G. Dowek.
  - – he is a member of the MECSI working group, in charge on collecting educational contents for the introduction of computer science in high-schools in 2012.
  - – he organized with M. Lizambert from Montpellier academy the first "workshop on Education-Research and industry" for preparing the introduction of computer science in high-schools in 2012.
  - – he was member of a Jury for several young resercher positions at INRA.
  - – he was member of an AERES visiting committee for the evaluation of an INRA Unit (Lusignan)

- • Yann Guédon has rendered the following services in 2011:
  - – 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 referee for papers submitted to Journal of Computational Science, Forest Ecology and Management and the XXIIIe GRETSI conference.

- • Frederic Boudon was referee for papers submitted to SIGGRAPH, Computer Graphics Forum and Ecological Modelling.

- • Christophe Pradal has rendered the following services in 2011:
  - – he is the coordinator of the national platform for plant modeling OpenAlea
  - – he was member of the scientific board of EuroSciPy'11, and editor of an associated special issue.
  - – he was a reviewer for international conferences (EuroScipy), and journals (Annals of Botany, Journal Of Scientific Computing).

- • 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 Majecstic conference for young researchers in information and computer science, see http://majecstic2010.labri.fr/index.php.

- • The team received several visitors from exterior research groups in 2011: Farah Ben Naoum, from Sidi Bel Abbes University, Algeria, visited us last spring for 1 month. Wojtek Palubicki, from Pr. Prusinkiewicz team in Calgary, visited the team in November-December 2011.

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).
This involves 21h of M2 classes. He participated to the jury of this Master.

7.2.2. Other Master Classes

- Christophe Godin was co-responsible for a Master class on 'Ecophysiology and plant modeling' with participation of Yann Guédon, Christophe Pradal and Christian Fournier in Montpellier SupAgro (15h).
- Christophe Godin and Yann Guédon and Etienne Farcot gave 9h of lecture in visio conference for a Master (M1) on plant development and modeling in Dakar, Senegal.
- Christophe Godin gave a 4h lecture in a Master class (M2) on Plant modeling in the Master Biologie du développement des Plantes of Jussieu Paris VI.
- 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.

7.2.3. 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), Odile Sirlin (Biology) from the Lycée Georges Pompidou, Castelnau. Occupation: 2 hours every week per over two third of the year.

7.3. Participation in workshops, seminars and miscellaneous invitations

- Yann Guédon was an invited speaker at the hidden Markov model workshop organized by GdR ISIS.
- Frédéric Boudon was invited speaker at the 6th International Symposium on Intelligent Information Technology in Agriculture, held in Beijing, China in 28-30 October. He gave a talk at the Departement of Computer Sciences of the University of Calgary in December. He also presented L-Py and the work on reconstruction from laser scan of the team at the OpenAlea seminar in June. This last work was also presented at the T-LIDAR workshop organized by T. Constant (INRA, Nancy) at Montpellier in November.
- Christophe Godin was an invited speaker in 9 occasions during the year, in particular for the 20th anniversary of the computer science Lab (Labri) in Bordeaux (June), and for the launch of the Sainburry Lab on plant development in Cambridge 'September).
- Christophe Pradal presented a poster at the European Scientific Python Conference at the Ecole Normal Supérieure ULM, in Paris, in August 2011.
- Etienne Farcot gave a presentation at the mid-term meeting of the ERASysBio+ program, for the iSAM project, in Vienna, in September 2011.
- Yassin Refahi gave a talk at the "Combinatorial Pattern Matching" conference (CPM2011) in June, in Palermo, Italy [20].
- Michael Walker presented a poster at "Plant Growth Biology and Modelling 2011" in Elche, Spain. The poster title was "Towards a Unified PIN Model for the SAM in Arabidopsis Thaliana". He also gave a presentation at the first NUMEV colloquium "Solutions Numériques, Matérielles et Modélisation pour L'Environnement et le Vivant" in Montpellier, entitled "Modelling the shoot apical meristem".
- Mik Cieslak gave an oral presentation at the IXth International Symposium on Modelling in Fruit Research and Orchard Management, in June 2011, in Saint-Jean-sur-Richelieu, Québec, Canada.

7.4. Theses and Internships

7.4.1. Theses defenses

- Yassin Refahi, *"Multiscale modelling of Arabidopsis thaliana phyllotaxis perturbation"*, Montpellier 2 University; November, 15th 2011 [11].

7.4.2. Ongoing Theses

- Anaëlle Dambreville, *"Determinants and modelling of mango phenology: interactions between structural and temporal components in a branching structure and temperature effect"*, Montpellier 2 University. Supervised by: F. Normand, Y. Guédon.

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

- Jonathan Legrand, *"Hormon signaling and control of morphogenesis during flower development"*, ENS Lyon. Supervised by: P. Das, Y. Guédon.

- Maryline Lièvre, *"Analysis and multiscale modelling of foliar growh in Arabidopsis thaliana in response to environmental stresses. Implication of the floral transition in the foliar expansion"*, Montpellier 2 University. Supervised by: C. Granier, Y. Guédon.

- Chakkrit Preuksakarn, *"Digitizing and assessing virtual architectural models of growing plants"*, Montpellier 2 University. Supervised by: C. Godin, F. Boudon.

- 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. Supervised by: C. Trottier, Y. Guédon.

7.4.3. Internships

- Pierre Fernique (Montpellier 2 University), *"Modelling branching properties of plants using multitype branching processes"*.

8. Bibliography

Major publications by the team in recent years

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

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

[3] E. COSTES, C. SMITH, M. RENTON, Y. GUÉDON, P. PRUSINKIEWICZ, C. GODIN. *MAppleT: simulation of apple tree development using mixed stochastic and biomechanical models*, in "Functional Plant Biology", 2008, vol. 35, n° 9 & 10, p. 936–950, http://www-sop.inria.fr/virtualplants/Publications/2008/CSRGPG08.

[4] D. DA SILVA, F. BOUDON, C. GODIN, H. SINOQUET. *Multiscale Framework for Modeling and Analyzing Light Interception by Trees*, in "Multiscale Modeling and Simulation", aug 2008, vol. 7, n° 2, p. 910-933, http://www-sop.inria.fr/virtualplants/Publications/2008/DBGS08.

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

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

[7] Y. GUÉDON, Y. CARAGLIO, P. HEURET, E. LEBARBIER, C. MEREDIEU. *Analyzing growth components in trees*, in "Journal of Theoretical Biology", 2007, vol. 248, n° 3, p. 418–447, http://www-sop.inria.fr/virtualplants/Publications/2007/GCHLM07.

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

[9] C. PRADAL, S. DUFOUR-KOWALSKI, F. BOUDON, C. FOURNIER, C. GODIN. *OpenAlea: A visual programming and component-based software platform for plant modeling*, in "Functional Plant Biology", 2008, vol. 35, n° 9 & 10, p. 751–760, http://www-sop.inria.fr/virtualplants/Publications/2008/PDBFG08a.

[10] S. STOMA, M. LUCAS, J. CHOPARD, M. SCHEADEL, J. TRAAS, C. GODIN. *Flux-based Transport Enhancement as a Plausible Unifying Mechanism for Auxin Transport in Meristem Development*, in "PLOS Computational Biology", 2008, vol. 4, n° 10, http://www-sop.inria.fr/virtualplants/Publications/2008/SLCSTG08.

Publications of the year

Doctoral Dissertations and Habilitation Theses

[11] Y. REFAHI. *Multiscale modelling of Arabidopsis thaliana phyllotaxis perturbation*, Université Montpellier 2, 2011.

Articles in International Peer-Reviewed Journal

[12] D. DA SILVA, P. BALANDIER, F. BOUDON, A. MARQUIER, C. GODIN. *Modeling of light transmission under heterogeneous forest canopy: an appraisal of the effect of the precision level of crown description*, in "Annals of Forest Science", 2011, p. 1–13, http://dx.doi.org/10.1007/s13595-011-0139-2.

[13] D. FUMEY, P. LAURI, Y. GUÉDON, C. GODIN, E. COSTES. *How young trees cope with the removal of whole or part of shoots: an analysis of local and distant responses to pruning in 1-year-old apple (Malus x domestica; Rosaceae) trees*, in "American Journal of Botany", 2011, vol. 98, n° 11, p. 1737–1751, http://www-sop.inria.fr/virtualplants/Publications/2011/FLGGC11.

[14] C. LA ROTA, J. CHOPARD, P. DAS, S. PAINDAVOINE, F. ROZIER, E. FARCOT, C. GODIN, J. TRAAS, F. MONÉGER. *A data-driven integrative model of sepal primordium polarity in Arabidopsis*, in "Plant Cell", 2011.

[15] O. TAUGOURDEAU, F. CHAUBERT - PEREIRA, S. SABATIER, Y. GUÉDON. *Deciphering the developmental plasticity of walnut saplings in relation to climatic factors and light environment*, in "Journal of Experi-

mental Botany", 2011, vol. 62, n° 15, p. 5283–5296, http://www-sop.inria.fr/virtualplants/Publications/2011/
TCSG11.

[16] T. VERNOUX, G. BRUNOUD, E. FARCOT, V. MORIN, H. VAN DEN DAELE, J. LEGRAND, M. OLIVA, P.
DAS, A. LARRIEU, D. WELLS, Y. GUÉDON, L. ARMITAGE, F. PICARD, S. GUYOMARCH, C. CELLIER,
G. PARRY, R. KOUMPROGLOU, J. DOONAN, M. ESTELLE, C. GODIN, S. KEPINSKI, M. BENNETT, L.
DE VEYLDER, J. TRAAS. *The auxin signalling network translates dynamic input into robust patterning at
the shoot apex*, in "Molecular Systems Biology", 2011, vol. 7, n° 508, http://www-sop.inria.fr/virtualplants/
Publications/2011/VBFMVLODLWGAPGCPKDEG.

International Conferences with Proceedings

[17] J. CHOPARD, C. PRADAL, D. BARBEAU, T. COKELAER, C. GODIN. *Scientific workflow for reusing
plant/FSPM models*, in "International Congress on Modelling and Simulation", 2011, http://www-sop.inria.
fr/virtualplants/Publications/2011/CPBCG11.

[18] M. CIESLAK, M. GÉNARD, S. KENOUCHE, C. GOZE-BAC, C. GODIN, N. BERTIN. *Towards a 3D virtual
fruit model integrating fruit architecture and physiology*, in "9th International Symposium on Modelling in
Fruit Research and Orchard Management", 2011, http://www-sop.inria.fr/virtualplants/Publications/2011/
CGKGGB11.

[19] L. HAN, J.-C. SOULIÉ, F. BOUDON, D. DA SILVA, T. COKELAER, C. PRADAL, L. ROUAN, E. COSTES.
*Sensitivity Analysis of Light Interception to Geometrical Traits of Apple Trees: an in silico Study based on
MAppleT model*, in "9th International Symposium on Modelling in Fruit Research and Orchard Management",
2011, http://www-sop.inria.fr/virtualplants/Publications/2011/HSBDCPRC11.

[20] Y. REFAHI, E. FARCOT, Y. GUÉDON, F. BESNARD, T. VERNOUX, C. GODIN. *A Combinatorial Model
of Phyllotaxis Perturbations in Arabidopsis thaliana*, in "22nd Annual Symposium on Combinatorial Pat-
tern Matching, Palermo, Italy", LNCS, 2011, vol. 6661, p. 323–335, http://www-sop.inria.fr/virtualplants/
Publications/2011/RFGBVG11.

National Conferences with Proceeding

[21] J. GUENARD, G. MORIN, F. BOUDON, P. GURDJOS, V. CHARVILLAT. *Reconstruction de modèles virtuels
de vignes à partir d'images*, in "Orasis - Congrès des jeunes chercheurs en vision par ordinateur", Inria, 2011,
http://www-sop.inria.fr/virtualplants/Publications/2011/GMBGC11.

Conferences without Proceedings

[22] F. BOUDON, C. PRADAL. *L-Py: L-Systems in Python*, in "EuroSciPy 2011", 2011, http://www-sop.inria.fr/
virtualplants/Publications/2011/BP11.

References in notes

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

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

[25] E. BAYER, R. SMITH, T. MANDEL, N. NAKAYAMA, M. SAUER, P. PRUSINKIEWICZ, C. KUHLEMEIER. *Integration of transport-based models for phyllotaxis and midvein formation*, in "Genes Dev", 2009, vol. 23, p. 373–384.

[26] F. BOUDON, T. COKELAER, C. PRADAL, C. GODIN. *L-Py, an open L-systems framework in Python*, in "6th International Workshop on Functional-Structural Plant Models", T. DEJONG, D. D. SILVA (editors), 2010, p. 116–119, http://www-sop.inria.fr/virtualplants/Publications/2010/BCPG10.

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

[28] T. COKELAER, D. FUMEY, Y. GUÉDON, E. COSTES, C. GODIN. *Competition-based Model of Pruning: Applications to Apple Trees*, in "6th International Workshop on Functional-Structural Plant Models", T. DEJONG, D. D. SILVA (editors), 2010, p. 87–89, http://www-sop.inria.fr/virtualplants/Publications/2010/CFGCG10.

[29] 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", Jun 2005, vol. 166, n° 3, p. 813–825, http://dx.doi.org/10.1111/j.1469-8137.2005.01405.x.

[30] 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.

[31] L. E. GATSUK, O. V. SMIRNOVA, L. I. VORONTZOVA, L. B. ZAUGOLNOVA, L.A. ZHUKOVA. *Age states of plants of various growth forms: a review*, in "Journal of Ecology", 1980, vol. 68, p. 675-696.

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

[33] C. GODIN, E. COSTES, H. SINOQUET. *A method for describing plant architecture which integrates topology and geometry*, in "Annals of Botany", 1999, vol. 84, p. 343-357.

[34] Y. GUÉDON, Y. CARAGLIO, P. HEURET, E. LEBARBIER, C. MEREDIEU. *Analyzing growth components in trees*, in "Journal of Theoretical Biology", 2007, vol. 248, n° 3, p. 418–447, http://www-sop.inria.fr/virtualplants/Publications/2007/GCHLM07.

[35] F. HALLÉ, R. A. A. OLDEMAN, P. B. TOMLINSON. *Tropical trees and forests. An architectural analysis*, Springer-Verlag, New-York, 1978.

[36] J. L. HARPER, B. R. ROSEN, J. WHITE. *The growth and form of modular organisms*, The Royal Society, London, UK, 1986.

[37] 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", 2005, vol. 21, n° 1, p. 232–240, http://dx.doi.org/10.1093/bioinformatics/bti1036.

[38] R. NOZERAN. *Integration of organismal development*, in "Positional controls in plant development", P. BARLOW, D. CARR (editors), 1984, p. 375-401.

[39] D. REINHARDT, E.R. PESCE, P. STIEGER, T. MANDEL, K. BALTENSPERGER, M. BENNETT, J. TRAAS, J. FRIML, C. KUHLEMEIER. *Regulation of phyllotaxis by polar auxin transport*, in "Nature", November 2003, vol. 426, n° 6964, p. 255–260, http://www.nature.com/nature/journal/v426/n6964/abs/nature02081.html.

[40] 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", 2006, vol. 57, n° 12, p. 3131–3143, http://www-sop.inria.fr/virtualplants/Publications/2006/RGGC06.

[41] A. RUNIONS, B. LANE, P. PRUSINKIEWICZ. *Modeling Trees with a Space Colonization Algorithm*, in "Eurographics Workshop on Natural Phenomena", 2007, p. 63-70 [*DOI :* 10.2312/NPH/NPH07/063-070], http://www.eg.org/EG/DL/WS/NPH/NPH07/063-070.pdf.

[42] H. SINOQUET, P. RIVET, C. GODIN. *Assessment of the three-dimensional architecture of walnut trees using digitizing*, in "Silva Fennica", 1997, vol. 3, p. 265–273.

[43] J. WITHER, F. BOUDON, M.-P. CANI, C. GODIN. *Structure from silhouettes: a new paradigm for fast sketch-based design of trees*, in "Eurographics", 2009.