INRIA

INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

Project-Team Virtual Plants

Modeling plant morphogenesis at different scales, from genes to phenotypes

Sophia Antipolis - Méditerranée

THEME BIO

Activity Report

2008

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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 and its control by genetic processes.

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

This study is performed from two complementary perspectives.

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

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

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

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

3. Scientific Foundations

3.1. Analysis of structures resulting from meristem activity

To analyse plant growth and structure, we focus mainly on methods for analysing sequences and tree-structured data. 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 analysed with combinatorial methods in order to compare them or to reveal particular types of organisation. We investigate a family of techniques to quantify distances between branching systems based on non-linear structural alignment (similar to edit-operation methods used for sequence comparison). Based on these techniques, we study the notion of (topology-based) self-similarity of branching structures in order to define a notion of degree of redundancy for any tree structure and to quantify in this way botanical notions, such as the physiological states of a meristem, fundamental to the description of plant morphogenesis.
- *Statistical modeling*: We investigate different categories of statistical models corresponding to different types of structures.
  - Longitudinal data corresponding to plant growth follow up: the statistical models of interest are equilibrium renewal processes and generalized linear mixed models for longitudinal count data.
  - Repeated patterns within sequences or trees: the statistical models of interest are (hidden) variable-order Markov chains and lumped processes constructed from Markov chains. Variable-order Markov chains are in particular applied to identify complex branching patterns resulting from local inhibition phenomena.

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

  We investigate both estimation methods and diagnostic tools for these different categories of models. In particular we focus on diagnostic tools for Markovian and hidden Markovian models (in this latter case to explore the hidden state sequence or tree space).

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

3.2. Meristem functioning and development

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

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

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

OpenAlea is a component based, open-software platform for interdisciplinary research in plant modeling and simulation. This platform is used for the integration and comparaison of different models and tools provided by the research community. It is based on the Python language that aims at being both a *glue* language for the different modules and an efficient modeling language for developing new models and tools. *OpenAlea* currently includes modules for plant simulation, analysis and modeling at different scales (*V-Plants* modules), for modeling ecophysiological processes such as radiative transfer, transpiration and photosynthesis (*RATP*, *Archimed*, *Caribu*, *Adel*) 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 are more particularly in charge of the development of the kernel and of some main data structures such as multiscale tree graph and statistical sequences.

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

4. Software

4.1. V-Plants

Participants: Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal [coordinator], Florence Chaubert-Pereira, David Da Silva, Szymon Stoma, Jérôme Chopard, Samuel Dufour-Kowalski, Jean-Baptiste Durand, Pascal Ferraro.

Other participant: Aida Ouangraoua (LaBRI, Bordeaux).

Computer algorithms and tools developed by the Virtual Plants team are integrated in a common software suite *V-Plants*, dedicated to the modeling and analysis of plant development at different scales (e.g. cellular tissue, whole plant, stand). The architecture of *V-Plants* is based on the Python language and is designed to be modular and scalable.

In 2008, the *V-Plants* packages have been integrated as components of the *OpenAlea* platform (see Section 4.2). Some components are distributed with he OpenAlea platform and usable through the visual programming environment (see figure 2).

One of a key component, PlantGL [20], provides a set of graphical tools and algorithms for geometrical plant modeling and simulation at different scales. It is used by many other components to represent the geometry of biological shapes from 3D meristems (see [19], [22]), plant architectures (see [20]) to plant populations (see [31], [45]). PlantGL is built around a scene-graph datastructure and provides efficient algorithms and original geometrical shapes (parametric surfaces, dedicated envelops) usefull for plant modeling.

4.2. OpenAlea

Participants: Frédéric Boudon, Christophe Godin, Yann Guédon, Christophe Pradal [coordinator], Florence Chaubert-Pereira, David Da Silva, Szymon Stoma, Jérôme Chopard, Samuel Dufour-Kowalski, Christian Fournier, Hervé Sinoquet.

This research theme is supported by an INRIA ODL Grant.
Other participant: Nicolas Donès (INRA - UMR PIAF, Clermont Ferrand).

OpenAlea [21] is an open source project primarily dedicated to the plant research community, with a particular focus on plant architecture, ecophysiology and meristem simulation. It is a distributed collaborative effort to develop Python libraries and tools which address the needs of current and future work in plant architecture.

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

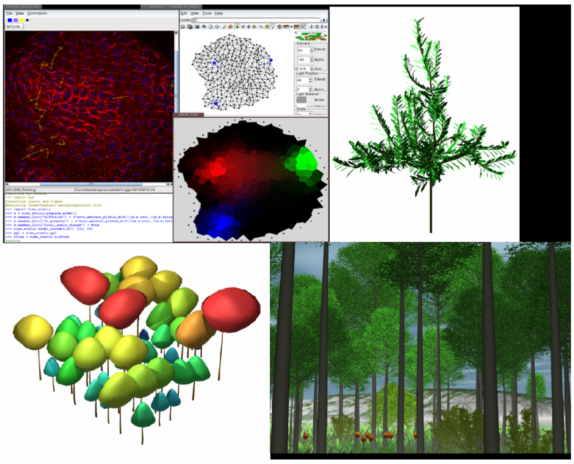
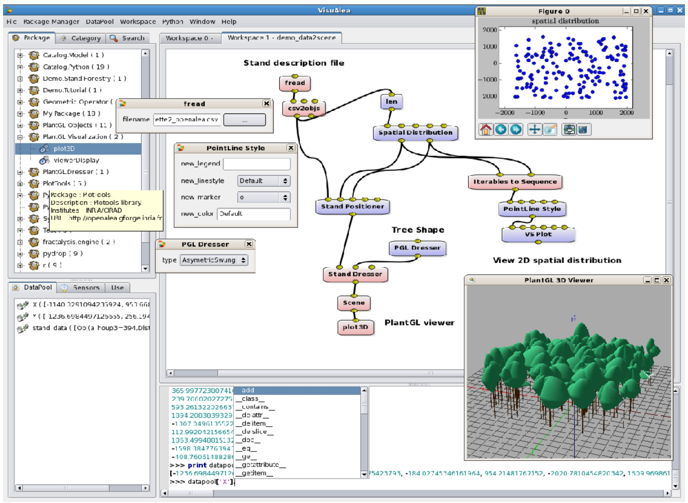


Figure 1. V-Plants components of the OpenAlea platform: simulating plant processes at different scales. Top Left: Reconstruction of a virtual meristem, analysis and simulation of the auxin fluxes inside the meristem. Top Right: Reconstruction of a virtual apple tree from digitized data. Bottom: Simulation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



Package : PlotTools
Description : Plotools library
Institutes : INRIA/CIRAD
URL : http://openalea.gforge.inria.fr

filename: ette2_openalea.csv

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

In 2008, the following steps have been performed:

1. Develop and extend the component platform architecture
    - OpenAlea.Core is the kernel of OpenAlea. It provides a component architecture, a package manager and a dataflow to build models by interconnecting components in a directed graph.
    - OpenAlea.Visualea is a visual programming application allowing us to build intuitively new models by connecting available components together. For each component, a graphical user interface is automaticaly generated based on the type of its interfaces (see figure 2).
    - OpenAlea.Deploy : Deploy extends the python setuptools package to simplify the deployment and the installation of the different OpenAlea packages. It is able to research available OpenAlea packages on different web repositories (like GForge), and provides an uniform way to the user to install and update components on different platforms.
2. Integrate existing models and provide functionalities
    - Provide common tools (basic data structure, statistics, visualization...)
    - Integrate ecophysiological models (Caribu, RATP, Drop [INRA])
    - Integrate V-Plants models (meristem, plant structure analysis, 3D modeling)
3. Animation and diffusion
    - Developers and modelers of different teams start collaboration and work together in pairs on a common objective during coding and modeling sprint sessions. In 2008, three coding sprint and two modeling sprints have been organised.
    - Software demonstrations have been held in the FSPM conference [21] and in the INRIA 40 ans, presenting a set of plant modeling scenarii provided by differents modelers of the OpenAlea community.

5. New Results

5.1. Analysis of structures resulting from meristem activity

5.1.1. Acquisition and design of plant geometry

Participants: Chakkrit Preuksakarn, Christophe Pradal, Frédéric Boudon, Christophe Godin, Hervé Sinoquet.

This research theme is supported by ANR project NatSim.

Virtual 3D model of plants are required in many areas of plant modelling. They can be used for instance to simulate physical interaction of real plant structures with their environment (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 architecture in 3D [42], [34]. These methods are based on direct measurements of position and shape of every plant organ in space. Although they provide accurate results, these methods are particularly time consuming. More rapid and automated methods are now required in order to collect plant architecture data of various types and sizes in a systematic way. In this topic, we explore the use of laser scanner and direct sketching. Resulting models should be parsimonious to be machine readable. We also consider the definition of methods to post process these complex representations into compact ones and apply them on streaming.

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

In this work, we investigate the possibility to use 3D laser scanners to automate plant digitizing. In collaboration with the GALAAD EPI, we are currently designing algorithms to reconstruct branching systems without leaves from scanner data simulated on plant mock-up obtained using different digitizing method. In its current state, our reconstruction pipeline is made up of three main steps: segmentation, reconstruction and modeling. Based on a variational k-means clustering algorithm, cylindrical components and branching regions of data points are identified and located. An adjacency graph is then built from neighborhood information of components. Simple heuristics allow us to extract a tree structure and identified branches from the graph. Finally, a B-spline model is computed to give a compact and accurate reconstruction of the branching system. This preliminary work has lead us to submission of a first article and a proposal to the 2008 ARC INRIA call, where several reconstruction methods will be investigated in collaboration with the project-teams GALAAD (based on algebraic geometry), EVASION (based on implicit convolution surface) and various lab from INRA (PIAF-Clermont Ferrand, LEPSE- and AFEF-Montpellier and Lusignan).

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

  Modeling natural elements such as trees in a plausible way, while offering simple and rapid user control, is a challenge. In collaboration with the Evasion EPI, we developed a method based on the design of plants from silhouettes. This sketching paradigm allows quicker and more intuitive specification of foliage at multiple scales than having to sketch each branch of a tree. This choice allows us to incorporate botanical knowledge to infer branches that connect in a plausible way to their parent branch and have a correct distribution in 3D. We illustrate these ideas by building a seamless sketch-based interface, used for sketching foliage silhouettes from the scale of an entire tree to the scale of a leaf. Each sketch serves for inferring both the branches at that level and construction lines to serve as support for sub-silhouette refinement. When the user finally zooms out, the style inferred for the branching systems he has refined (in terms of branch density, angle, length distribution and shape) is duplicated to the unspecified branching systems at the same level. Meanwhile, knowledge from botany is again used for extending the branch distribution to 3D, resulting in a full, plausible 3D tree that fits the user-sketched contours. As our results show, this system can be of interest to both experts and novice users: while experts can fully specify all parts of a tree and over-sketch specific branches if required, any user can design a basic 3D tree in one or two minutes, as easily as sketching it with paper and pen, as illustrated on Figure 3. This work has been accepted at the Eurographics 2009 conference and will be published in Computer Graphics Forum [44].

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

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

  Much effort has been made in realistic modeling of plants for instance as support of physical simulation. As the trend moves towards networked and distributed virtual environment, however, the current models are inadequate as they are not designed for progressive transmissions. In this work, we fill in this gap by proposing a progressive representation for plants based on generalized cylinders. We proposed a differential coding of plants: an average branch is computed for any chosen group of branches and then, for each branch, we only need to code some transformations for instantiation and differences for geometry refinement. To be able to stream, we identify and take advantage of two types of dependencies: topological and dependencies due to differential coding. We obtain a progressive model that makes it possible to select a lightweight representation of a plant while preserving branch density. To facilitate the transmission of the plants in the network, we quantify the visual contribution of each branch and use this weight in packet scheduling. We show the efficiency of our representations and effectiveness of our packet scheduler through simulations. This work has been presented at 2008 ACM Multimedia Conference [25] and received the Best Paper Award.

5.1.2. Modeling the plant ontogenic programme

Participants: Christophe Godin, Yann Guédon, Evelyne Costes, Jean-Baptiste Durand, Pascal Ferraro.

This research theme is supported by a PhD programme.

The remarkable organization of plants at macroscopic scales may be used to infer particular aspects of meristem functioning. The fact that plants are made up of the repetition of many similar components at different scales, and the presence of morphological gradients, e.g. [29], [36], [37], [6], provides macroscopic evidence for the existence of regularities and identities in processes that drive meristem activity at microscopic scales. Different concepts have been proposed to explain these specific organisations such as "morphogenetic programme" [39], "age state" [33] or "physiological age" [30]. 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 [33], [30]. Here we develop computational methods to decipher these rules.

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

  In the context of a collaboration with Claudia Negron and Ted DeJong, stochastic models (hidden semi-Markov chains) for the branching and axillary flowering structures of different categories of peach and almond shoots were built. These stochastic models will be integrated in simulation systems which combine stochastic models with different mechanistic models of biological function, in particular carbon partitioning functions. This collaboration extends the work initiated on apple trees [41], [15]; see 5.1.3.

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

  During the past years, a set of methods was proposed to characterize the growth components (mainly ontogenetic and environmental components) of forest trees [35] on the basis of main axes measured at the growth unit/annual shoot scale. We started to study axis structure of fruit trees. The agronomic context (grafted cultivars, irrigated orchard) renders very rapid the ontogenetic changes and reduces the environmental influence compared to forest trees. We studied in particular the structures of apple tree cultivars at growth unit (GU) scale over six consecutive years. Hidden variable-order Markov chains were applied to identify repeated patterns in sequences of GUs. In these models, GU categories are deduced from morphological characteristics (number of nodes and presence/absence of flowering) and their succession modeled by a non-observable variable-order Markov chain. Repeated patterns were organized in three successive stages, identified as three groups of "memories" (i.e. succession of GU categories of a given length) in the models. These stages correspond to vegetative GUs with decreasing vigor separated by flowering occurrence. Flowering GUs represented a preferential pathway between vegetative GUs of decreasing vigor and generated patterns that were interpreted with respect to regular versus alternate bearing of the cultivars. This approach led us to propose a synthetic scheme of apple tree ontogeny that combines polycyclism, flowering and morphogenetic gradients. It demonstrates the key role of shoot apical meristem flowering, during tree ontogeny for sympodial species.

- *Hidden Markov tree models for investigating physiological states within plants.* (Yann Guedon, Evelyne Costes, Jean-Baptiste Durand, Yves Caraglio (UMR AMAP), Patrick Heuret (UMR AMAP))

  Plant architecture is the result of repetitions that occur throughout growth and branching processes. During plant ontogeny, changes in the morphological characteristics of plant entities such as growth units or annual shoots, are interpreted as the indirect effect of the meristems being in different physiological states. Thus, connected entities can exhibit either similar or very contrasted characteristics. We designed a statistical model to reveal and characterise homogeneous zones and transitions between zones within tree-structured data: the hidden Markov tree (HMT) model. This model enables us to assign the entities to classes sharing a same "physiological state" [3]. The ability of hidden Markov tree models (HMTs) to discriminate classes of entities that make biological sense was investigated using diverse temperate and tropical forest species.

  (i) Analysis of *Symphonia globulifera*(Clusiaceae) (a tree species of the rain forest in French Guyana). The overall context of this study is to identify underlying rules that govern plant construction. One phenomenon of particular importance is the synchronous character of growth: growth units that developed at the same time tend to be similar. To assess how synchonism is affected by the light conditions, trees growing in a greenhouse under various light treatments were compared with forest trees using HMT models. Synchronicity of the development of children and parent shoots was assessed by resorting to tree comparison methods [32]. Separated models were built for each forest population, and for the greenhouse individuals. Then a global model was built for all individuals, and the impact of population on the model states was assessed. As a perspective, the last step of the study is to analyse how the local dependencies accounted for in the HMTs affect the classes estimated using this model, compared to classes obtained with an independent mixture model where no dependency is modelled between connected entities. This should lead to assess the importance of the context in the clustering obtained by HMTs.

  (ii) Analysis of beech trees (*Fagus Sylvatica L.*). The aim of this study is to highlight ordered stages in the differentiation sequence of the meristems, and to assess the effect of population diversity (age and conditions of growth) on the number, the nature and the dynamics of the stages. The former study, which involved two sets of beech trees (30-year-old individuals and tree tops of 100-year-old individuals), was completed by a third set composed of individuals with various social status. The first question was to check that adding further individuals should not result into indefinitely adding new classes to the model, since the concept of "physiological state" requires that the states are ordered and comprise a final absorbing state (oldest possible age). This hypothesis is consistent with the obtained results, since adding new individuals for HMT estimation did not modify the number of classes, but only changed the transition probability between classes (and also slighltly the distribution of the characteristics for each class). The final model reinforced the hypothesis of two flowering stages characterised by different patterns of entities with different levels of vigor, as highlighted by a variable-order Markov chain estimated on all the paths along the (oldest) trees. As a perperpective, we plan to discriminate the individuals using some particular patterns they exhibit during flowering.

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

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

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

where T is a tree, $D(\cdot,\cdot)$ is a distance on the set of trees (chosen so as to preserve certain structural properties between the compared trees) and $\mathcal{S}^+(T)$ is the set of self-nested trees that contain T, i.e. that can be obtained from T by inserting nodes only.
To solve this optimization problem, we designed a polynomial-time algorithm that makes it possible to quantify the degree of self-nestedness of a tree in a precise manner. The distance to this nearest embedding self-nested tree (NEST) is then used to define compression coefficients that reflect the compressibility of a tree. In the context of the structural analysis of botanical plants, it is possible to give a strong biological interpretation of the NEST of a tree based on the hypothesis that isomorphic tree structures at macroscopic levels are actually produced by meristems in identical physiological states (scaling hypothesis). This makes it possible to show that the reduction graph of the NEST of a plant may be interpreted as the maximum sequence of differentiation states that any meristem of a plant may go through. We characterized this approach on both a database of artificial plants with degraded degree of self-nestedness and on a real plant (a rice panicle) whose structure was completely measured, see Figure 4. We showed that the NEST of this plant may be interpreted in biological terms and reveals important aspects of the plant growth. This work has been submitted to IEEE Transactions on Computational Biology and Bioinformatics (IEEE/ACM TCBB), and is currently under revision.

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

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

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

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

- *Analyzing growth components in trees.* (Florence Chaubert-Pereira, Yann Guédon, Yves Caraglio, Christian Lavergne, Catherine Trottier)

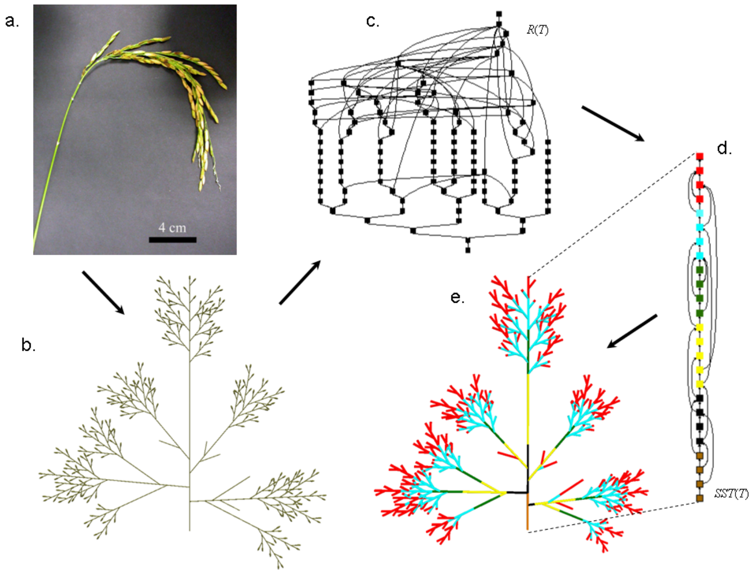

Figure 4. (a) Photo of a rice panicle (b) tree representing the topological structure of the panicle (c) Reduced graph of the panicle tree (d) Corresponding NEST that can be interpreted as the maximal sequence of differentiation states that a meristem can go through when building the panicle (e) color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

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 [35], (ii) a time-varying environmental component assumed to take the form of fluctuations that are synchronous between individuals, (iii) an individual component corresponding to the local environment of each tree. This environmental component is thus assumed to be a "population" component as opposed to the individual component. In order to identify and characterize these three components, we proposed to use semi-Markov switching linear mixed models [11], [27], [23], i.e. models that combine linear mixed models in a semi-markovian manner. The underlying semi-Markov chain represents the succession of growth phases (endogenous component) while the linear mixed model attached to each state of the underlying semi-Markov chain represents -in the corresponding growth phase- both the influence of time-varying climatic explanatory variables (environmental component) as fixed effects, and inter-individual heterogeneity (individual component) as random effects. We investigated the estimation of Markov and semi-Markov switching linear mixed models in a general framework. The difficulty of this task comes from the two latent structures within the model, namely the underlying (semi-) Markov chain and the random effects. We proposed a MCEM-like algorithm (MCEM, or Monte Carlo EM algorithms, are EM (Expectation-Maximization) algorithms where the E step is performed via a simulation) whose iterations decompose into three steps (sampling of state sequences given random effects, prediction of random effects given state sequences and maximization). Concerning the application to forest trees, we showed that growth phases are not only defined by average growth level but also by growth fluctuation amplitudes in response to climatic fact ors and inter-individual heterogeneity. The proposed statistical modeling approach relies on the availability of climatic data. In the case where climatic data are not available, we are studying Markov and semi-Markov switching linear mixed models with year random effects common to all the trees to model the synchronous part of the growth fluctuations With semi-Markov switching linear mixed models, the response variable is constrained to be approximately normally distributed. We are now studying the statistical methodology for semi-Markov switching generalized linear mixed models to take into account non-normally distributed response variables (e.g. number of growth units, apex death/life, non-flowering/flowering character). It should be noted that the estimation algorithms proposed for (semi-)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.

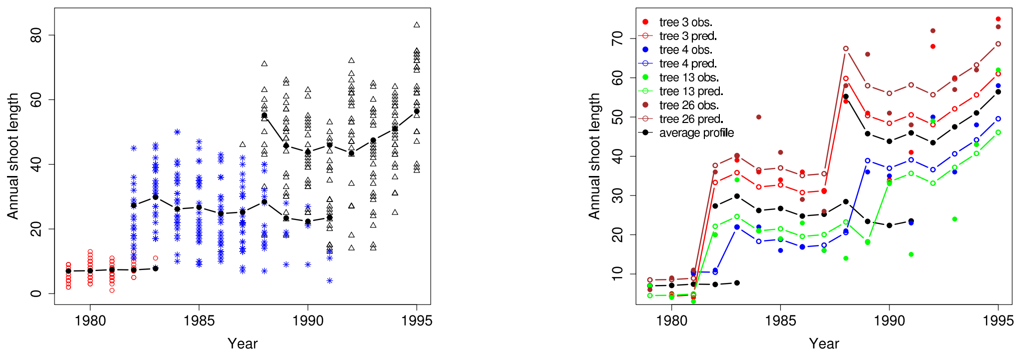

Figure 5. Corsican Pine : on the left, estimated cumulated rainfall effect for each state (state 0: red; state 1: blue; state 2: black) represented by point lines and observed annual shoot lengths (points). On the right, estimated cumulated rainfall effect for each state represented by black point lines (average profile), observed annual shoot lengths (points) and predicted annual shoot lengths (point lines).

- *Analyzing the impact of arboricultural practices on fruit tree branching structures.* (Damien Fumey, Christophe Godin, Yann Guédon, Evelyne Costes, Pierre-Eric Lauri (UMR DAP))

  Arboricultural practices such as pruning, artificial bending or fruit thinning are crucial interventions in orchard management and are used for controlling tree size, penetration of light into the canopy and the equilibrium between vegetative and reproductive growth. The aim of the PhD of Damien Fumey is to explore the possibility of integrating such practices in a model of apple tree development. To this end, a field experiment was designed to study the effects of pruning (thinning or heading cuts) on two apple cultivars with contrasted architecture, 'Fuji' and 'Braeburn'. The first results of this experiment [24] showed that thinning cuts of laterals tended to be compensated by an increase in lateral branching.

  We are investigating the influence of artificial bending on the branching structure of apple tree cultivars in different contexts (bending in winter during the plant resting period or in spring during shoot elongation). To achieve this, a hidden semi-Markov chain that represents the branching structure is built on the basis of a sample of shoot not subject to bending. Then, we explore the space of state sequences for a given observed shoot subject to bending on the basis of the estimated hidden semi-Markov chain. In this way, it is possible to characterize the branching structure of shoots subject to bending.

  We are also studying the influence of the elongation speed (indirectly represented by internode length) on the immediate branching (i.e. offspring shoots developing without delay with respect to the parent node establishment date). For this, we build semi-Markov switching generalized linear models (i.e. semi-Markovian combination of multinomial models) where the influence of internode length is modeled as a fixed effect.

- *Coupling stochastic models with mechanistic models for plant development simulation.* (Yann Guédon, Christophe Godin, Evelyne Costes, Michael Renton (Univ. Western Australia), Przemek Prusinkiewicz (Univ. Calgary), Colin Smith (INRA), Ted de Jong (UC Davis))

  The MAppleT model aim to bring together models of topology and geometry in a single simulation such that the architecture of an apple tree may emerge from process interactions [15]. This integration was performed using L-systems. A mixed approach was developed based on stochastic models to simulate plant topology and mechanistic model for the geometry. The succession of growth units (GUs) along axes and their branching structure were jointly modeled by a hierarchical hidden Markov model. A biomechanical model was used to calculate stem form at the metamer scale, taking into account the intra-year dynamics of primary, secondary and fruit growth. Outputs consist of 3-D mock-ups - geometric models representing the progression of tree form over time. To assess these models, a sensitivity analysis was performed and descriptors were compared between simulated and digitized trees, including the total number of GUs in the entire tree, descriptors of shoot geometry (basal diameter, length), and descriptors of axis geometry (inclination, curvature). Despite some limitations, MAppleT constitutes a useful tool for simulating development of apple trees in interaction with gravity.

  The strategy developed in MAppleT for combining stochastic models with mechanistic models of biological functions was applied to the L-PEACH system [18]. In this case, the stochastic models of plant topology were combined with a carbon partitioning model for simulating peach tree development.

  We are currently working on a new extension of MAppleT that takes into account arboricultural practices such as pruning, artificial bending or fruit thinning. These methods are crucial interventions in the management of orchards and are used to control tree size, light penetration within the canopy and the equilibrium between vegetative and reproductive growth. The PhD of D. Fumey aims at developing a stochastic formalization of the competition between the meristems in the plant, to be integrated in a model of growth reactive to pruning interventions. This model will be based on field experiments which recently provided first results for assessing the rules underlying tree responses to pruning, on two apple cultivars with contrasted architecture, Fuji and Braeburn. The first experimental results showed that thinning and heading cuts promoted local activation of lateral latent meristems but also increased the branching on un-pruned axes. They also raise new questions with respect to growth distribution in trees, in terms of number of shoots, branch positions along the parent shoot and priority between shoots.

- *Fruit tree phenology in relation to global warming.* (Yann Guédon, Jean-Michel Legave (INRA))

  Over the last 40 years, perceptible advances in dates of flowering stages have been observed in fruit trees and in particular for apple and pear trees growing in different cropping areas in Western Europe. The time-course variation of dates of flowering stages was established for eight chronological sequences. Our aim was to propose a statistical modeling framework for such sequences with the objective of characterizing the relationship between flowering advances in fruit trees and global warming [17]. After an exploratory analysis, change-point models were applied to univariate and multivariate sequences [28]. In the multivariate case, the variables correspond to different cropping areas or to different cultivars. The results clearly support the occurrence of a significant abrupt change in the time-course variation of flowering dates at the end of the 1980s toward more frequent early dates, the most probable change instant being between 1988 and 1989. The coincidence between this abrupt change in phenological variations and marked increases in temperature recorded particularly in France at the end of the 1980s led us to consider the flowering advances in apple and pear trees as impacts of global warming. The suddenness in the response to global warming could be explained by changes in rates for completion of chilling and heat requirements, successively essential to the development of floral primordia within buds. Marked temperature increases during the heat phase would have suddenly resulted in more frequent years with relatively short duration for completion of the heat requirements and consequently more frequent early flowering years, despite some years with relatively long duration of chilling requirements.

- *A multiscale model of light interception.* (David Da Silva, Frederic Boudon, Christophe Godin, Hervé Sinoquet)

  Light capture by plants is an essential process for plant growth and survival since light provides plants with energy which can be used for transpiration and carbon fixing. In particular, the local light environment in the canopy during plant development is a major component of the meristem fate [12]. In ecophysiology, the most common approach to model light interception abstracts the plant canopy as a turbid medium, i.e. a medium made of infinitely small foliage particles randomly dispersed in the vegetation volume. In such medium, light penetration can be expressed by the Beer-Lambert law, which defines the probability p_0 that a photon crosses the vegetation volume without any interception as:

  $$p0 = \exp(G.LAD.l) \tag{1}$$

  where LAD is the leaf area density of the canopy, l is the distance travelled by a ray of light in the canopy ad G is a geometric constant. This equation is only valid for homogeneous and random foliages. For clumped foliages, that augment the self-shading effect, or for foliages whose regularity decreases the self shading effect, a correction has to be introduced in the original Beer-lambert equation by adding a new empirical coefficient μ that depends on the foliage dispersion. This modification is usually sufficient to adapt the initial model satisfactorily. However, how the coefficient μ is related to the plant architecture is still unknown.

  To address this issue, we designed a multiscale model of light interception based on the Beer-Lambert original equation. In this model, we consider that a plant canopy may be recursively decomposed into sub-canopies corresponding to clusters at different scales. The probability that a ray is stopped by the vegetation volume is then expressed recursively as a function of the multiscale structure of the plant:

  $$p_{i,j} = 1 - p_{0_{i,j}} = 1 - \prod_{k=1}^{n_j} [1 - p_{i+1,k}] \tag{2}$$

  where $p_{i,j}$ is the opacity of the jth subcanopy at scale i. This expression generalizes the Beer-Lamber equation to multiscale structures and makes it possible to interpret the μ coefficient. The approach was illustrated and tested on the multiscale structure of digitized plants (mango trees). This model has been published in the journal Multiscale Modeling and Simulation [16].

- *Modeling of light transmission under heterogeneous forest canopy.* (David Da Silva, Frederic Boudon, Christophe Godin, Philippe Balandier (CEMAGREF))

  A major factor for heterogeneous forest management is the control of light microclimate. Indeed growth and survival of regeneration saplings and understorey vegetation development is closely related to light available below the forest trees. Manipulating the forest structure by thinning adult trees is therefore a major tool to control light transmission to the understorey.

  The transmission is related to the attenuation of light which is usually estimated with the Beer-Lambert law assuming homogeneous foliage within the canopy. However forest canopies are far from homogeneous, which requires models that can take into account the effect of clumping between and within trees. In this work we develop a model that can be readily used with both coarse or detailed parameterization to generate any type of stand and compute the distribution of light transmitted below the canopy. This work is a made in collaboration with the INRA - ONF - CEMAGREF project *ECOGER*.

- *Miscellaneous: method transfer to population dynamics models*

Participants: Yann Guédon, Jean-Michel Gaillard [Université Claude Bernard, Lyon], Roger Pradel [Centre d'Écologie Fonctionnelle et Evolutive, Montpellier], Lauriane Rouan [Centre d'Écologie Fonctionnelle et Évolutive, Montpellier].

Hidden Markov models were applied to capture-recapture data and in particular algorithms for computing counting distributions of state corresponding to the lifetime reproductive success of an individual i.e. the number of young raised during its lifespan [26].

5.2. Meristem functioning and development

5.2.1. Data acquisition and design of meristem models

Keywords: *Confocal microscopy*, *cell tracking*, *meristem*.

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

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

Studies on plant development require the detailed observation of the tissue structure with cellular resolution. In this context it is important to develop methods that enable us to observe the inner parts of the organs, in order to analyse and simulate their behaviour. Here we focus on the apical meristems, that have been extensively studied using live imaging techniques and confocal microscopy. An important limitation of the confocal microscope lies in the data anisotropy. To overcome this limitation, we need to design 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.

- *Image restoration using matching and fusion.* (Romain Fernandez, Christophe Godin, Jan Traas, Jean-Luc Verdeil, Pradeep Daas (ENS-Lyon), Grégoire Malandain (INRIA), Vincent Mirabet (ENS-Lyon))

  Images acquired by confocal laser-scanning imaging systems suffer from the shadowing effect on cell walls that are parallel to the focal plane. We designed a restoration method and an acquisition protocol that produce high-quality and isotropic images of meristems, using matching and fusion of stacks of the same meristem acquired under different orientations. The cell walls parallel to the focal plane are up to 30 % brighter after the fusion than before. This method provides images with a sufficient quality, which can be processed by automatic algorithms with few errors (cell segmentation average error ratio is close to 2 to 3%).

- *3D reconstruction of shoot and root meristems from confocal microscopy.* (Romain Fernandez, Christophe Godin, Jan Traas, Jean-Luc Verdeil, Pradeep Daas (ENS-Lyon), Grégoire Malandain (INRIA))

  In order to understand the dynamics of the meristems, 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 tracking algorithm in order to map two segmentations of the same meristem at different times. Two versions of the algorithm were developed, according to the manner the tracking problem is solved :

  - A heuristic method, that iteratively selects and locks the better correspondance between a cell of the first image and one or more cells of the second image, using a maximum likelihood criterion.
  - A global method, that solves the tracking problem using a min-cost flow algorithm.

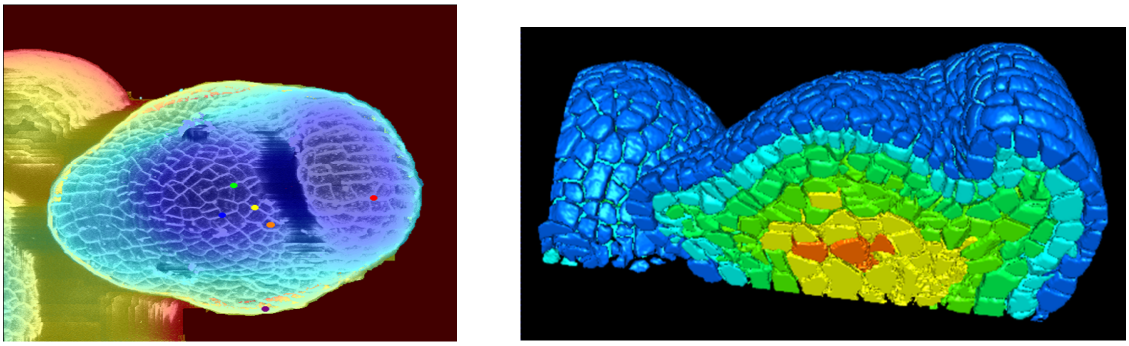

Figure 6. On the left, picture of a meristem after automated surface treatment. On the right output of automated 3D segmentation (collaboration Asclepios EPI, ENS Lyon, and PHIV team).

Results make it possible to automatically follow the cell lineages over several days. We are currently working on adding adjacency constraints between cells in order to improve the lineage recognition process. The procedures developed in this direction of work are illustrated in Figure 6.

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

  This research theme is supported the ANR Virtual Carpel project.

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

  A prototype version of such a database is currently being built and is integrated in *V-Plants*. Algorithms to explore such database at various levels of abstraction will have to be developed. Queries such as: get the number of cell of the L1 layer, get the volume ratio between two zones with different gene expression identities, perform the intersection of two expression zones, compute the curvature at the topmost cell, find the lineage of cells descending from this region, etc. would typically be carried out efficiently with such a database. The prototype of a 3D database presented on figure 7 shows a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity, etc...)

5.2.2. Transport models

Participants: Mikaël Lucas, Szymon Stoma, Jérôme Chopard, Christophe Godin, Yann Guédon, Christian Jay-Allemand, Laurent Laplaze, Jan Traas.

This research theme is supported by the ANR project Virtual Carpel project and the RN SY-STEM project.

The transport of plant hormones, proteines, water and sugars is critical to plant development. In particular, the active transport of the plant hormone auxin has been shown to play a key role in the initiation of organs at

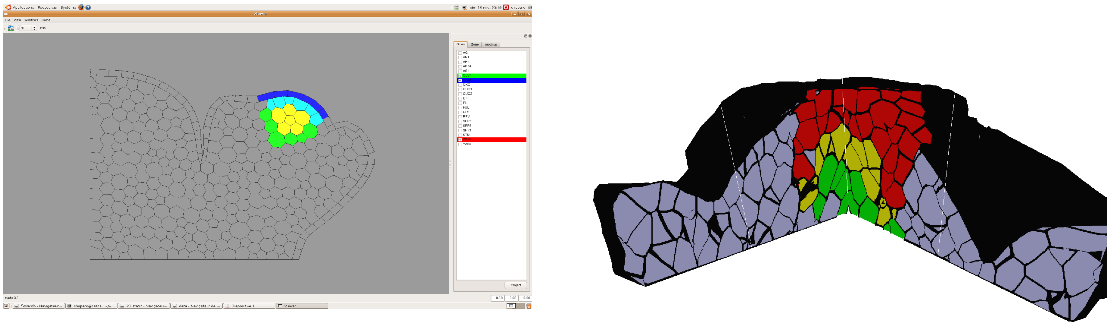

Figure 7. Prototype of a 3D database represented as a cell-based volumic tissue that can contain different types of information (cell lineage, cell size, cell identity,...)

the shoot apex. Polar localized membrane proteins of the PIN1 and AUX/LAX family facilitate this transport and recent observations and models suggest that the coherent organization of these proteins in the L1 layer is responsible for the creation of auxin maxima, which in turn triggers organ initiation close to the meristem centre [40] [1]. Here, to better understand this phenomenon, we model the transport throughout the network of cells and compare its predictions to the actual observations.

- *Canalization as a plausible mechanism of auxin transport in the meristem.*

  While the regulation of PIN polarization is thus a key determinant of primordia formation, very little is known about its biological or physical nature. However, two recent models have shown that such a polarization may be due to a simple mechanistic hypothesis, called "up the hill" hypothesis, which states that in each cell, PIN proteins are preferentially located on cell walls separating this cell from neighbouring cells with maximum auxin concentration. PIN proteins may thus transport auxin against the concentration gradients.

  Although this hypothesis was shown to be a plausible explanation of phyllotaxy by two teams independently [38], [43], it is not consistent with an other hypthesized auxin transport mechanism that has been proposed in the 70's by Sachs to explain the development of vascular vessels during leaf development and that is now recognized as a fairly plausible mechanism of vein formation. This hypothesis suggests that PIN proteins are polarized in the direction of the auxin flux through the cell, and thus reinforce the flux. This positive feedback mechanism is called 'canalization'.

  In [22], we showed that canalization is an alternative plausible mechanism for auxin transport in the L1 layer of the meristem. This approach unifies the models used for leaves and meristems and the mechanisms creating primordia at the meristem surface and provascular strands in the inner parts of the meristem, below the primordia.

- *Modeling axillary root initiation* (Mikael Lucas, Christophe Godin, Christian Jay-Allemand, Laurent Laplaze)

  Root architecture is a crucial part of plant adaptation to soil heterogeneity and is mainly controlled by root branching. The process of root system development can be divided into two successive steps: lateral root initiation and lateral root development/emergence which are controlled by different fluxes of the plant hormone auxin. While shoot architecture appears to be highly regular, following rules such as the phyllotactic spiral, root architecture appears more chaotic. We used stochastic modeling to extract hidden rules regulating root branching in Arabidopsis thaliana. These rules were used to build an integrative mechanistic model of root ramification based on auxin transport [19], [13]. This model was experimentally tested using plants with modified rhythm of lateral root initiation or mutants perturbed in auxin transport. Our analysis revealed that lateral root initiation and lateral root development/emergence are interacting with each other to create a global balance between the respective ratio of initiation and emergence. A mechanistic model based on auxin fluxes successfully predicted this property and the phenotype alteration of auxin transport mutants or plants with modified rythms of lateral root initiation. This suggests that root branching is controlled by mechanisms of lateral inhibition due to a competition between initiation and development/emergence for auxin.

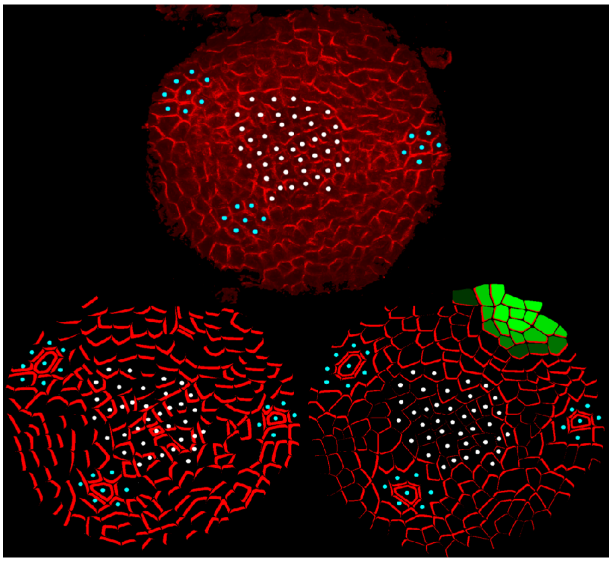

Figure 8. Transport of the plant hormone auxin in a virtual meristem: a comparison between simulations and experimental data. Top: observed distribution of auxin transporters (PIN proteins) in shoot apical meristem cells of Arabidopsis. The image was obtained by immunolabelling of the PIN1 auxin-carrier using confocal microscopy. Bottom left: Digitized version of the top image where the efflux carriers have been manually positioned. Bottom right: simulated distribution of efflux carriers (in red) emerging from a flux-based polarization hypothesis of auxin transport. This type of virtual experiments makes it possible to test in silico different hypotheses on mechanisms that are not fully accessible experimentally and to assess their plausibility by comparing predictions with experimental data. This figure was used for the cover of the Oct issue of PLoS Comp Biol [22].

5.2.3. Mechanical model

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

This research theme is supported by the ANR project Virtual Carpel project and the RN SY-STEM project.

The rigid cell walls that surround plant cells is responsible for their shape. These structures are under constraint due to turgor pressure inside the cell. To study the overall shape of a plant tissue and morphogenesis, its evolution throughout time, we therefore need a mechanical model of cells. We developed such a model, in which walls are characterized by their mechanical properties like the Young modulus which describes the elasticity of the material. Wall deformation results from forces due to turgor pressure. Growth results from an increase in cell wall synthesis when this deformation is too high. The final shape of the tissue integrate mechanicaly all the local deformation of each cell.

To model this process, we used a tensorial approach to describe both tissue deformation and stresses. Deformations were decomposed into elementary transformations that can be related to underlying biological processes. These processes can then be individually tested to study their role in plant morphogenesis. Different numerical approaches have been tested to solve the integration problem associated with the model simulation. In 2D cases, transversal cut of the meristem or representation of the surface of the meristem only, walls are treated as linear 1D elements. An efficient way to solve the problem uses a mass-spring solver in which each wall is a spring whose stiffness depends on its mechanical properties. However, for large deformations or 3D systems, this approach is no longer efficient enough. In these particular cases we use finite elements methods to integrate the local constraints at tissue scale and find overall tissue growth. These results have been presented by C. Godin and J. Chopard at the Cargèse summer school on *The Geometry and Mechanics of Growth in Living Systems* in July 2008.

5.2.4. Cell model

Participants: Szymon Stoma, Mikaël Lucas, Yassin Refahi, Jérôme Chopard, Etienne Farcot, Christophe Godin, Jan Traas.

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

A cell model is needed for different aspects. First cell growth is coupled with cell cycle since above a certain threshold cells divide. To model tissue growth, we thus need to make explicit such rules and design a model of cell growth and division that could be reused in the tissue growth. Second, we need to model the cell identity. For this, modelling the genes activities within cells is of primary importance since a stable combination of genes defines a particular cell identity and function.

- *Cell division.* (Szymon Stoma, Jérome Chopard, Christophe Godin, Jan Traas)

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

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

  Since September 2008, and the arrival of Etienne Farcot and Yassin Refahi, the development of models of gene regulation in the context of meristem growth has become a new major topic in the team. The aims of this research in the 2 to 3 years to come will be closely related to those of the *Flower Model* project 6.3.1. Currently, preliminary studies are being performed on the connections that can be made between transport models (of auxin in particular) and the effects of hormone signaling on gene networks. The main methodological challenge of this work will be to take into account spatial organisation of cells – and thus of gene network – in order to describe the role played by genes in meristem morphogenesis.

5.2.5. Model integration

Participants: Mikaël Lucas, Szymon Stoma, Jérôme Chopard, Frédéric Boudon, Christophe Godin, Laurent Laplaze, Jan Traas.

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

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

- *development of a platform for the 'programmable tissue'.* (Szymon Stoma, Jérome Chopard, Christophe Pradal, Frédéric Boudon, Etienne Farcot, Christophe Godin)

  One key aspect of our approach will the development of a computer platform dedicated to the programmable tissue. 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.

- *coupling of transport and mechanics models.* (Szymon Stoma, Jérome Chopard, Christophe Godin)

  A first coupling between a transport model and a mechanical model of cell interaction has been performed in the context of Szymon Stoma's PhD thesis. This model uses a surface representation of the L1 layer of the meristem and assumes a homogeneous internal turgor pressure directed towards the output due to inner layers. Using this integration, a first simulation of the formation of an organ at the tip of a PIN meristem could be reproduced.

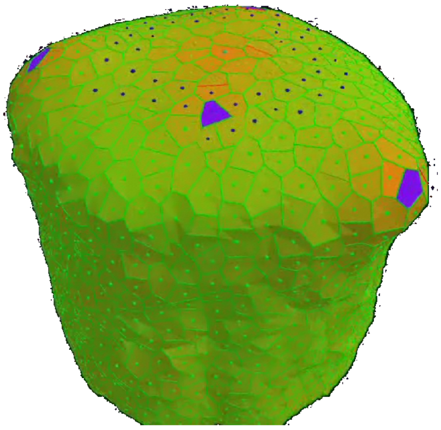

Figure 9. First simulation attempting to integrate transport and mechanical processes within a growing tissue at cell level. The emerging phyllotaxy is very unstable.

- *coupling of transport and genetic network models.* (Yassin Refahi, Jérome Chopard, Etienne Farcot, Christophe Godin, Jan Traas)

  This is coming in the next years.

- *coupling of transport, mechanical and growth models.* (Szymon Stoma, Jérome Chopard, Christophe Godin)

  An attempt to integrate both a mechanical and a transport models in a growing meristem was made by Szymon Stoma to simulate emerging phyllotactic patterns Fig. 9. Many technical problems were encountered and partially solved. The overall simulation could show the emergence of a growing axis, however, the phyllotaxy was very unstable. Further developments are required on such a complete, cell-based integration.

6. Other Grants and Activities

6.1. National Grants

6.1.1. Agropolis computational plant seminar

(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 seminars and a yearly one-day workshop at Agropolis. This workshop is devoted to a specific topic selected each year and keynote speakers are invited. The seminar is organized by Yann Guédon, Christine Granier (INRA, LESPE) and Laurent Laplaze (IRD, DIAPC) with the support of Agropolis International and Agropolis Foundation.

6.1.2. Advanced Markovian techniques in population dynamics.

(Contractor for Virtual Plants: CIRAD. From 2008 to 2009)

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

6.1.3. ANR NatSim Grant

Participants: Christophe Pradal, Frédéric Boudon, Christophe Godin.

(Contractor for Virtual Plants: CIRAD. From December 2005 until December 2008)

Nature simulation (NATSIM) : hybrid representation for modeling, simulation, visualisation and streaming of animated natural scenes. In this project, our goal is to create models of natural scenes containing vegetals (trees, forests, prairies), watercourses (rivers, rivulets, waterfalls) and clouds (clouds, mist, fog). On the one hand, the botanic, biologic and physics communities acquire and store huge data sets representing each single natural entity with a dedicated model. On the other hand, the user community is willing to smoothly navigate in realistic virtual environments or to easily create complex virtual landscapes. The project NatSim addresses this huge amount of data in terms of data structure, techniques and algorithms, in a unifed framework able to adapt both to the content (e.g. the internal representation) and to the navigation context (e.g. view point, devices etc.). We focus on the models, the evolution, the adaptive transmission and the visualization, but also on the composition of several natural entities in a complex virtual environment. The project gathers partners whose expertise covers botany, modeling and simulation (DAP: CIRAD-INRIA-SophiaAntipolis in Montpellier, LIAMA : Academy of Sciences of China, INRIA, CIRAD, Evasion: INRIA-Rhne Alpes), graphics (Evasion, IRIT: Univ.Toulouse-CNRS, Iparla: INRIA-Futur) as well as adaptive streaming (IRIT, Iparla).

6.1.4. ANR CarpVirtuel Grant

Participants: Jérôme Chopard, Christophe Godin.

(Contractor for Virtual Plants: INRIA. From December 2005 until December 2008)

The virtual carpel (CarpVirtuel): building of a predictive model of the development of the female sexual organ of the flower. The carpel is the precursor of the fruit in the flowering plants and is therefore of capital socio-economic importance. The early phase of carpel development is crucial regarding final morphology. The objective of the project is to understand cellular and molecular mechanisms behind the early phase of carpel development. For this purpose, we combine experimental and modeling approaches. During the first year we have gathered first quantitative morphometric data of carpel growth using live imaging to build a 3D computer model and even a 4D model if we include developmental stages: the virtual carpel. In parallel, transcriptomic data have been collected in such a way to have homogeneous samples of tissues and stages of development. Information will be extracted from these data to construct a gene interactions network controlling carpel development. This analysis will be achieved in both wild type and mutant plants affected in carpel development. All these data will be processed and integrated into the virtual carpel model, which will then in turn, help to predict the effect of a given gene or of a defined cellular process on carpel development in planta. For this model, we are currently studying a mechanical model of cell-cell interaction in 3 dimensions. The project is carried out in collaboration with teams of biologists and computer scientists from ENS-Lyon (Jan Traas and Michel Morvan).

6.1.5. ATP CIRAD Meristem Grant

Participants: Romain Fernandez, Christophe Godin, Olivier Devillers [INRIA], Grégoire Malandain [INRIA], Jean-Luc Verdeil [CIRAD].

(Contractor for Virtual Plants: CIRAD. From December 2005 until December 2008)

Meristem : 3D imagery and geometrical modeling of meristems. The aim of this Action Thématique Programme of CIRAD is twofold. We first intend to design 3D visualization techniques of the meristem architecture cellular and molecular levels. Second, we aim at developing a generic geometric model of the meristem able to support various treatments and modeling processes at cell scale (characterization of meristem geometry, cell growth, mechanical forces, circulation of hormone fluxes ...). Data will be collected from bi-photon microscopy at CIRAD (in the context of the RIO imaging platform) on rice, a model plant for agronomy, and on other perennial species to characterize the state of the meristem at different phenological states or for different environmental constraints. The project includes several teams from CIRAD, INRA and IRD and 3 INRIA projects Asclepios, Geometrica and Virtual Plants.

6.1.6. INRA: Alinea

Participants: Christophe Pradal, Christophe Godin, Michael Chelle [INRA, EGC Grignon], Christian Fournier [INRA, LEPSE], Gaetan Louarn [INRA, EPFA Lusignan].

(Collaboration with UMR LEPSE INRA. From June 2008 until December 2009)

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

6.2. EU Grants

6.2.1. RTN SY-STEM Grant

Participants: Szymon Stoma, Christophe Godin.

(Contractor for Virtual Plants: INRIA. From January 2005 to December 2008)

SY-STEM: Systems biology of stem cell function in Arabidopsis Thaliana. SY-STEM is a Marie Curie european Research Training Network (RTN) from the 6th European Framework Research Program. Significant progress has been made in the understanding of meristem development during the last few years, but the complexity and lack of completeness of the available data is such, that an integrated view of meristem function is not yet possible. Therefore, not only additional data, but also adapted mathematical and informatics approaches are now required to integrate the growing body of knowledge in such a way that it can advance the level of understanding in the field. To address these issues, SY-STEM will pursue the following objectives:

- provide extensive training in biological sciences, informatics and mathematics and create an environment that favours the interaction and integration of these disciplines,
- provide new technology platforms to study meristem function,
- address key questions on meristem function and plant developmental biology using novel systems biology and modeling approaches.

The integration of the unprecedented amount of data generated in this way will involve the expertise of the participating mathematicians and computer scientists, who will create new modeling tools. This network gathers 10 european research groups that will use genetic, molecular and cellular approaches, imaging techniques, as well as large-scale genomic techniques applied to the reference plant *Arabidopsis Thaliana*. In the project, Virtual Plants is responsible for the development of a 3D dynamic model of the meristem integrating knowledge obtained by the other teams in a coherent picture of the meristem growth and functioning. The project is offering 360 fellow-months for PhD students (36 for INRIA).

6.3. International Bilateral Relations

6.3.1. ANR-BBSRC Grant

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

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

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

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

6.3.2. Other bilateral relations

Christophe Godin visited Jacques Dumais at the Harvard University in August during one week. They worked together on a problem related to the characterization of phyllotactic patterns. Future exchanges between both teams have been discussed.

Christophe Pradal and Samuel Dufour-Kowalski were visiting Pr. Prusinkiewicz at the University of Calgary (Canada) to develop a connection between OpenAlea and LStudio/VLab platforms in March 2008.

For the year to come, the team of Pr. Prusinkiewicz at the University of Calgary (Canada) will be an *associated team* of *Virtual Plants*. This will imply certain visits from and to members of this group, tightening the collaboration that already exists.

Two students from Pr. Kurth's lab at the University of Cottbus (Germany) visited Christophe Pradal in July 2008 to develop a connection between OpenAlea and GroIMP, a platform dedicated to the simulation of plants and, more generally, to the dynamic development of graph structures.

Christophe Godin helps supervising the PhD work of Farah Ben-Naoum (University of Sidi Bel Abes, Algeria) on L-System learning algorithms.

7. Dissemination

7.1. Services to the scientific community

- Christophe Godin has rendered the following services in 2008:
  - he is a member of the Steering Committee of UMR DAP,
  - he is a member of the board of the Fédération de Recherche (IFR) DAPHNE, coordinating joint actions of UMRs working in Plant Sciences in the region Languedoc Roussillon,
  - he is the representant of the IFR at the doctoral school of the University of Montpellier II, SIBAGH, in Plant Biology,
  - he is a member (for 4 years) of two expert scientific commissions (CSS): at INRA (CSS Ecophysiologie, génétique et biologie intégrative des plantes) and of Montpellier 3 University (CSS mathematics, statistics and computer sciences),
  - in 2008, he was a member of the evaluation committee of UMR EGC in Paris-Grignon and referee for 1 PhD thesis (F. Corson, ENS) and one HDR in plant modeling (A. Escobar, 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 was a reviewer for several papers and gave 5 invited talks in conferences and summer schools during the year.
- Yann Guédon has rendered the following services in 2008:
  - in 2008, he was a jury member for a PhD thesis in statistics,
  - 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 Annals of Botany, Atmospheric Environment, Communications in Statistics - Theory and Methods, Computational Statistics & Data Analysis, Functional Plant Biology (2 papers), Journal of Machine Learning Research, Trees - Structure and Function, SIGGRAPH 2008 and for a book proposal submitted to Springer.
- Frédéric Boudon was referee for papers submitted to Eurographics 08, Siggraph 08, Visual Computer, Functional Plant Biology (x2) and Journal of Theoretical Biology. He also evaluated a project of Associated Team for Inria.
- Florence Chaubert-Pereira and David Da Silva have been reviewers for the DOCTISS 08 event, organized by the Ecole Doctorale de Montpellier "Information, Structures et Systèmes", a conference devoted to PhD students presentations and posters, in April 2008.
- Christophe Pradal coordinates the national platform for plant modeling *OpenAlea*.

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.

7.2.2. Master Computer Science

University Montpellier 2.
Christophe Godin teaches a course on Plant modeling and multiscale structures. computational plant modeling.

7.2.3. Master Biotraçabilité, Biodétection, Biodiversité

Montpellier 2 University.
Yann Guédon teaches a course on statistics in the context of plant biology.

7.2.4. Master Classes

Jérôme Chopard taught a Master class ’An introduction to plant modeling’ of the module ’Systems biology and plant development’ coordinated by Jan Traas in the BioScience Master of ENS-Lyon.

7.2.5. High School class

Lycée , Jules Fil, Carcassonnes.
Christophe Godin gave an invited class on plants and fractals for the ’Fête de la science’ in November 2008.

7.3. Participation in workshops, seminars and miscellaneous invitations

- Christophe Godin participated in the following events in 2008:
  - he was an invited speaker at the Advanced Workshop on Understanding and Modeling of Auxin Transport in Plants, Nottingham, May 14-16 2008 events: for a talk on "Is root branching also governed by inhibitory fields ?"
  - he was an invited speaker at the FASEB summer conference on "Mechanisms in Plant Development", 10-15 August 2008, Saxton River, Vermont, NY, USA.
  - he was also invited at the Cargèse Summer School on "Geometry and Mechanics of Growth in biological systems", 14-26 Juillet 2008,
  - he was also invited to the FORMOD summer school on "Functional-structural models of plants", 18-13 September 2008, Le Tholy, Epinal,
  - he was an invited speaker for the awards of the "Olympiades de mathématiques de la région Languedoc-Roussillon", on the subject "La face fractale des plantes"
- Yann Guédon was an invited speaker at the workshop "Change-Point Detection Methods and Applications", AgroParisTech, Paris, 11-12 September 2008.
- Jérôme Chopard, Etienne Farcot and Christophe Godin attended the kick-off workshop of the *Flower Model* ANR-BBSRC project, in Norwich in September 2008.
- Florence Chaubert-Pereira presented a communication at the XXIVth International Biometric Conference, in July 2008 in Dublin (Ireland), and another one at the COMPSTAT symposium in Porto, Portugal, on August 24th-29th 2008.
- Jérôme Chopard, Christophe Godin, Szymon Stoma and Mikaël Lucas attended the CPIB workshop, May 14-16, Nottingham, on the theme *The understanding and modeling of auxin transport in plants*.
- Jérôme Chopard attented the following summer school: Cargèse, CNRS, "The Geometry and Mechanics of Growth in Biological Systems", 14-26 July 2008.
- Szymon Stoma presented the poster "Canalization-based model of phyllotaxis" at two conferences: Meet08, 06/2008, Berlin, and IBSB08, 06/2008, Berlin.
- Christophe Pradal was an invited speaker at the INRIA workshop ’Journées de développement et d’experimentation’ in Arcachon 21-22 May 2008 for a talk on ’Feedback on the development of the open source platform OpenAlea’.

7.4. Theses and Internships

7.4.1. Theses defenses

- Florence Chaubert-Pereira: *"Combinaisons markoviennes et semi-markoviennes de modèles de régression. Application à la croissance d'arbres forestiers"*, University Montpellier 2, November 5th, 2008.
- David Da Silva: *"Caractérisation de la nature multi-échelles des plantes par des outils de géométrie fractale, application à l'interception de la lumière"*, University Montpellier 2, November 24th, 2008.
- Mikaël Lucas, *"Etude et modélisation des déterminismes de mise en place et de développement des racines latérales chez* Arabidopsis Thaliana*"*, ENS Lyon/University Montpellier 2, July 3rd, 2008.

7.4.2. Ongoing Theses

- Romain Fernandez, *"3D Reconstruction of meristems from bi-photon images"*, University Montpellier 2.
- Chakkrit Preuksakarn, *"Acquisition et validation de modèles architecturaux virtuels de plantes en croissance."*, University Montpellier 2.
- Yassin Refahi, *"Modélisation de la croissance des organes floraux"*, University Montpellier 2.
- Mohamad Saad, *"Impact des opérations sylvicoles sur les broussins et picots du chêne. Modélisation statistique de la séquence de différenciation et de la répartition le long des troncs"*, University Henri Poincaré Nancy 1.
- Szymon Stoma, *"A mechanical based model of* Arabidopsis Thaliana *meristem development"*, University Montpellier 2.

7.4.3. Internships

- Guillaume Pérouel, *"Base génétique de l'architecture de caféiers arabica - Exploration d'une base de données architecturales*, Master 2 Recherche Biostatistique, Montpellier 2 University.
- Tristan Bitard-Feidel, *"Auxin fluxes in an apoplastic model"*, Master 1 Bio-informatique, Rennes University, March to August 2008.

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