

INSTITUT NATIONAL DE RECHERCHE EN INFORMATIQUE ET EN AUTOMATIQUE

Project-Team Virtual Plants

Modeling plant morphogenesis at different scales, from genes to phenotypes

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Table of contents

1.	Team	1
2.	Overall Objectives	1
	2.1. Overall Objectives	1
3.	Scientific Foundations	2
	3.1. Analysis of structures resulting from meristem activity	2
	3.2. Meristem functioning and development	3
	3.3. OpenAlea: An open-software platform for plant modeling	3
4.	Software	4
	4.1. VPlants	4
	4.2. OpenAlea	4
5.	New Results	5
	5.1. Analysis of structures resulting from meristem activity	5
	5.1.1. Analysis of the relative extents of preformation and neoformation in tree shoots by a	
	deconvolution method	5
	5.1.2. Analysis of longitudinal count data and underdispersion	6
	5.1.3. Changes in branching structures within the whole plants	6
	5.1.4. Growth components in trees	7
	5.1.5. Markov switching models	7
	5.1.6. Diagnostic tools for hidden Markovian models	7
	5.1.7. Methods for exploring the segmentation space for multiple change-point models	8
	5.1.8. Hidden Markov tree models for investigating physiological states within plants	9
	5.1.9. Branching processes for plant development analysis	9
	5.1.10. Self-similarity in plants	9
	5.1.11. Reconstruction of plant foliage density from photographs	10
	5.1.12. Fractal analysis of plant geometry	11
	5.1.13. Light interception by canopy	11
	5.1.14. Heritability of architectural traits	12
	5.1.15. Lumped processes constructed from Markov chains	13
	5.1.16. Multivariate dynamic model for ordinal outcomes	13
	5.1.17. An integrated model of apple tree development	13
	5.2. Meristem functioning and development	13
	5.2.1. 3D surface reconstruction and cell lineage detection in shoot meristems	13
	5.2.2. Simulation of auxin fluxes in the meristem	15
	5.2.3. Dynamic model of phyllotaxy based on auxin fluxes	15
	5.2.4. Mechanical model of a tissue	16
	5.2.5. Modeling axillary root initiation	16
6.	Other Grants and Activities	
		17
	6.1.1. New interfaces of mathematics ACI grant: Arborescences	17
	6.1.2. ANR NatSim Grant	17
	6.1.3. ANR CarpVirtuel Grant	18
	6.1.4. ATP CIRAD Meristem Grant	18
	6.2. UE Grants	18
	6.2.1. RTN SY-STEM Grant	18
_	6.3. International Bilateral Relations	19
7.		. 19
	7.1. Services to the scientific community	19
	7.2. Academic teaching	20
	7.2.1. Master Biostatistics	20

7.2.2. Master Computer Science	20
7.2.3. Master Biotraçabilité, Biodétection, Biodiversité	20
7.2.4. Master Course	20
7.2.5. Statistics Courses	20
7.2.6. High School class	20
7.3. Participation to workshops, seminars and miscellaneous invitations	20
7.4. Theses and Internships	21
7.4.1. Ongoing Theses	21
7.4.2. Internships	21
8. Bibliography	

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2. Overall Objectives

2.1. Overall Objectives

The Virtual Plants team is a joint team between INRIA, CIRAD and INRA. It is 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 variableorder Markov chains and lumped processes constructed from Markov chains. Variableorder 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 and Markov switching linear mixed 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 architecture analysis and modeling (*V-Plants* modules), for modeling radiative transfer, transpiration and photosynthesis (*RATP*, *Archimed*, *Canestra*) 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 CIRAD, INRA, INRIA, LaBRI, INPG 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. VPlants

Participants: Christophe Pradal [coordinator], Samuel Dufour-Kowalski, Frédéric Boudon, Pierre Barbier de Reuille, Jean-Baptiste Durand, Christophe Godin, Yann Guédon.

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

The V-Plants packages are integrated as component of the OpenAlea platform (see Figure 1).

In 2006, the *PlantGL* component has been finalized. **PlantGL** is an open source graphic library for the creation, simulation and analysis of 3D virtual plants. PlantGL is designed to be:

- *Portable* : PlantGL is available on major operating systems (GNU Linux, Microsoft Windows). It is also compatible with various plant modeling systems (L-studio, AMAP, etc.) and graphic toolkits (Pov-Ray, Vrml, etc.).
- *Simple* : the targeted audience is composed of researchers in the plant modeling community with no *a priori* knowledge in computer graphics. Examples of use are depicted in [30],[31].
- *Modular* : PlantGL is composed of several independent modules like a geometric library, GUI components and Python wrappers. They can be used alone or combined in a specific application.
- *Hybrid system* : Core computational components of PlantGL are implemented in the C++ compiled language for performance. In addition for flexibility of use, these components are also exported in the Python interpreted language.

PlantGL is a key component of the OpenAlea platform and is used by many other modelling components (see Figure 1).

4.2. OpenAlea

Participants: Christophe Pradal [coordinator], Samuel Dufour-Kowalski, Frédéric Boudon, Christophe Godin, Nicolas Donès [INRA], Hervé Sinoquet, Christian Fournier [INRA], Frédéric Théveny [CIRAD].

This research theme is supported by an INRIA ODL Grant.

OpenAlea is an open source project primarily aimed at the plant research community, with a particular focus on Plant Architecture and Ecophysiology. It is a distributed collaborative effort to develop Python libraries and tools which address the needs of current and future work in Plant Architecture.[25].

OpenAlea is designed as a component framework to dynamically glue together models from different plant research labs (see Figure 2).

In 2006, the following steps have been performed:

- 1. Set up of the collaborative infrastructure of OpenAlea:
 - Software engineering tools (use of gforge at INRIA),
 - E-tools for communication (Instant Messaging for distant meetings),
 - Coordination (e-meetings, e-forum, organisation of Coding Sprints for developers),
 - Training session for developers and modelers on the intergration of components in OpenAlea.
- 2. Developper tools to ease the integration of new components.
 - SConsX : SConsX simplify the build of complex multi-platform softwares. It allows to
 describe what needs to be built in high-level terms, and works with several compilers on
 Linux and Windows. It is based on SCons construction tool.

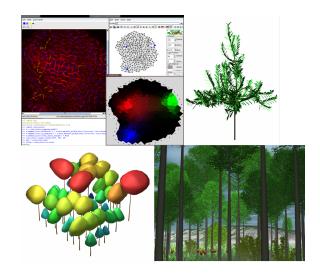


Figure 1. VPlants components of the OpenAlea platform: simulating plant processes at different scales. Top Left: Reconstruction of a virtual meristem, analysis and simulation of the auxin fluxes inside the meristem. Top Right: Reconstruction of a virtual apple tree from digitized data. Bottom: Simulation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

- DistX : It is an OpenAlea package which extends Python Distutils library to ease the installation of components in OpenAlea. It provides a uniform interface for building and installing complex packages as well as automatically creating Windows installers and Linux rpm in one command and in a platform independent way.
- 3. Assistance to the development and integration of new components in OpenAlea:
 - Module for digitizing root systems grown in rhizotrons (collaboration with C. Jourdan, CIRAD),
 - Module for the simulation of maize architecture and light interception computation. Integration of components ADELE-maïs and *Caribu* (collaboration with C. Fournier, M. Chelles, INRA).

5. New Results

5.1. Analysis of structures resulting from meristem activity

5.1.1. Analysis of the relative extents of preformation and neoformation in tree shoots by a deconvolution method

Participants: Yann Guédon, Javier G. Puntieri [INRA], Sylvie Sabatier [CIRAD], Daniel Barthélémy [INRA].

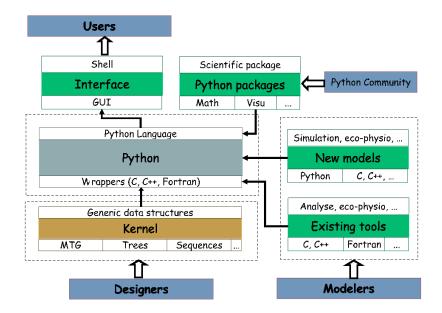


Figure 2. OpenAlea architecture: the kernel, based on Python, provides the user with various modules and data structures written in python C or C++ and dedicated to plant modeling. A graphic interface makes it possible to manipulate all the modules with a visual programming approach.

Neoformation is the process by which organs not preformed in a bud are developed on a growing shoot, generally after preformation extension. The aim of this study was to apply a deconvolution method to estimate the neoformation distributions (rather than simply the mean number of neoformed organs) of shoots of five woody species known to develop both preformed and neoformed organs. For each of eight data sets, the distribution of the number of neoformed organs was estimated from two independent samples, one corresponding to the distribution of the total number of organs (in fully extended shoots of the first sample), and the other to the distribution of the number of preformed organs (in dissected buds of the second sample). It was shown that neoformation contributed more than preformation to explain full-size differences between shoots developed in different positions within the architecture of each tree species and that, for a given position, the dispersion of the number of preformed organs is higher (due to differences of growth cessation times) than the dispersion of the number of preformed organs [18].

5.1.2. Analysis of longitudinal count data and underdispersion

Participants: Catherine Trottier, Mariem Zouch [Ecole Polythechnique de Tunisie], Yann Guédon.

The elongation of leafy axes is influenced by environmental conditions such as for instance rainfall. In the context of plant growth follow-up, measurement is made of the number of newly elongated leaves during successive observation periods. These count data are often underdispersed with reference to the Poisson distribution. Incorporating the rainfall covariate within a statistical model requires to take into account both the delayed response of the plant to a water stress and the difference in time step between the rainfall covariate (daily data) and the plant response (observation period of several days). Statistical models studied for analysing these longitudinal count data belong to the classes of generalized linear mixed models. We are studying particular models based on weighted Poisson distributions where weighted Poisson distributions define a two-parameter exponential family.

5.1.3. Changes in branching structures within the whole plants

Participants: Evelyne Costes, Yann Guédon, Christophe Godin, Michael Renton [INRA].

The objective of this study was to model the changes in growth unit branching structures during tree ontogeny. A single statistical model was estimated from around 700 branching sequences measured on two six-year-old apple trees, cultivar "Fuji". This statistical model is a hidden semi-Markov chain were the underlying semi-Markov chain represents the succession and the lengths of branching zones along the growth units while the observation distributions represent the branching type composition within each zone. The main output of this study was to show that, while the succession and the lengths of branching zones change during ontogeny, the compositions of branching zones remain unchanged. In particular the composition of the flowering shoot zone is not affected by the alternation of flowering and non-flowering years [21].

5.1.4. Growth components in trees

Participants: Yann Guédon, Yves Caraglio, Patrick Heuret, Emilie Lebarbier [INA-PG], Céline Meredieu [INRA].

Observed growth, as given for instance by the length of successive annual shoots along a tree trunk, is mainly the result of two components: an ontogenetic component and an environmental component. An open question is whether the ontogenetic component along an axis at the growth unit or annual shoot scale takes the form of a trend or of a succession of phases. Various methods of analysis ranging from exploratory analysis (symmetric smoothing filters, sample autocorrelation functions) to statistical modeling (multiple change-point models, hidden semi-Markov chains and hidden hybrid model combining Markovian and semi-Markovian states [34]) were applied to extract and characterize both the ontogenetic and environmental components using contrasted examples. This led us in particular to favor the hypothesis of an ontogenetic component structured as a succession of stationary phases and to highlight phase changes of high magnitude in unexpected situations (for instance when growth globally decreases). These results shed light in a new way on botanical concepts such as "morphogenetic gradient" and "physiological age of meristem".

5.1.5. Markov switching models

Participants: Florence Chaubert, Yann Guédon, Christian Lavergne, Catherine Trottier, Yves Caraglio.

Incorporating both the influence of explanatory variables and inter-individual heterogeneity in a hidden Markov vian model is a challenging problem. We are studying different families of Markov switching models including Markov switching linear mixed models, i.e. models that combine linear mixed models in a Markovian manner and Markov switching generalized linear mixed models. In the case of a Markov switching linear mixed model, the underlying Markov chain represents the succession of growth phases while the linear mixed models attached to each state of the Markov chain represent both the trend, the influence of the explanatory variables (mainly climatic variables which are time-dependent explanatory variables measured at a scale different from the scale of the plant response) and the inter-individual heterogeneity within a given growth phase. The EM algorithm which is the standard algorithm for estimating hidden Markovian models cannot be applied for estimating Markov switching mixed models. We are thus investigating alternative solutions relying either on numerical techniques or on algorithms for simulating state sequences and random effects (see Figure 3).

5.1.6. Diagnostic tools for hidden Markovian models

Participants: Yann Guédon, Jean-Baptiste Durand.

This research theme is partially supported by the ACI "Arborescences".

Once a hidden Markovian model has been estimated, it is generally of interest to understand the hidden state sequence (or tree) structure underlying each observed sequence (or tree). Questions of interest are:

- Is the most probable state sequence most probable by a long way or are there other state sequences with near-optimal probability?
- Do these near-optimal sequences have state structures very similar to the most probable state sequence or do they greatly differ?

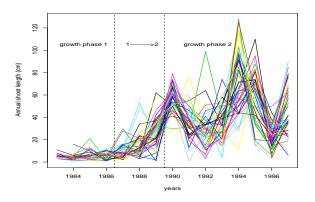


Figure 3. Segmentation of sequences of annual shoot lengths along 15-year-old sessile oak trunks using a 2-state Markov switching linear mixed model. The phase change year (between 1986 and 1990) is specific to each tree. Synchronous fluctuations highlight a year effect due mainly to climatic factors (e.g. in 1990 and 1996).

Methods for exploring the state sequences that explain a given observed sequence for a known hidden Markovian model may be divided into three categories: (i) enumeration of state sequences, (ii) state profiles i.e. state sequences summarized in a $J \times \tau$ array where J is the number of states and τ the length of the sequence, (iii) computation of a global measure of the state sequence uncertainty (entropy of the state sequence that explains an observed sequence for a known hidden Markovian model). Various methods belonging to these three categories have been developed for different families of hidden Markovian models including hidden semi-Markov chains, hidden hybrid model combining Markovian and semi-Markovian states [34] and different categories of hidden Markov tree models. In particular, we propose a new type of state profiles that can be viewed as the superposition of all the state sequences from the less probable to the most probable [17]. Due to their multidimensional nature, state profiles are difficult to visualize and interpret on trees. Hence, we propose to compute in a first stage a unidimensional profile of conditional entropies that summarize for each vertex the state uncertainty. In a second stage, the usual state profiles are visualized on selected paths of interest within the tree.

5.1.7. Methods for exploring the segmentation space for multiple change-point models Participant: Yann Guédon.

The retrospective or off-line change-point detection problem is addressed. From an algorithmic point of view, this research theme is closely connected to the preceding theme restricted to hidden semi-Markov chains. The studied algorithms share a common structure with similar algorithms recently proposed for exploring the state sequence space structure for hidden semi-Markov chains [17]. The separability of the computations at change points corresponds to conditional independence at jump times for hidden semi-Markov chains. A key difference between a hidden semi-Markov chain and a multiple change-point model lies in the fact that the hidden semi-Markov chain parameters are fixed parameters (previously estimated) for state sequence or state profile computation while change-point model parameters (for instance mean and variance for each segment in the Gaussian case) are "contextual" parameters that depend on the change points. This explains the specific behaviour of the proposed diagnostic tools in connection with the determination of the optimal number of change points. Methods for exploring the segmentations, (ii) summary of the possible segmentations in change-point or segment profiles. Concerning the first category, a forward dynamic programming algorithm for computing the top L most probable segmentations and a forward-backward algorithm for sampling

segmentations are studied. Concerning the second category, a forward-backward dynamic programming algorithm and a smoothing-type forward-backward algorithm for computing two types of change-point and segment profiles are studied. The proposed methods are mainly useful for exploring the segmentation spaces for successive numbers of segments. Change-point and segment profiles may help to predict supplementary change points, highlight overestimation of the number of segments and a specific type of change-point profiles summarizes the uncertainty concerning the location of change points.

5.1.8. Hidden Markov tree models for investigating physiological states within plants

Participants: Jean-Baptiste Durand, Yann Guédon, Yves Caraglio, Evelyne Costes, Patrick Heuret.

This research theme is supported by the ACI "Arborescences".

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 to assign the entities to classes sharing a same "physiological state" [4]. 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) The analysis of branches from Aleppo pines helped to define more precisely, the connection between branching intensity, length, polycyclism and male or female sexuality (see Figure 4).
- (ii) The analysis of *Symphonia globulifera* (Clusiaceae) (a tree species of the rain forest in French Guyana) individuals highlighted a structuring of the plant into well-separated and clearly interpretable classes of entities. This work laid the basis for assessing the effect of the growth conditions (light intensity, neighbourhood of other trees) on the architecture of symphonia, and for clustering individuals with a same stage of development. As a perspective, we aim at quantifying the rate of synchronised vs. unsynchronised growth phases, using the classes as a synthetic description of the plants.
- (iii) The analysis of beech trees grown in different conditions allowed to progress towards the biological validation of classes of entities identified by the HMT model. The stability of the number and nature of the classes was investigated by increasing the diversity of the considered population, and this will be further assessed through the analysis of beech trees with various social status.

5.1.9. Branching processes for plant development analysis

Participants: Jean Bérard [U. Lyon I], Anne Perrut [U. Lyon I], Didier Piau [U. Lyon I], Evelyne Costes, Yves Caraglio, Patrick Heuret, Yann Guédon.

This research theme is supported by the ACI "Arborescences".

We are investigating multitype branching processes with dependences as a new analysis tool for plant structures. This research theme is closely connected to the preceding one concerning hidden Markov tree models since, in most cases, the types are the states restored for each entity using a previously estimated hidden Markov tree model. Our objective is twofold: First, we are testing various sub-families of branching processes (with different parameterizations and dependencies) using a set of reference data sets (apple tree, Aleppo pine, *Symphonia globulifera*) in order to determine the most useful ones. Second, branching processes focus on an unusual way of studying plant development and this generates new biological questions concerning the rules governing the generation of offspring entities from a parent entity.

5.1.10. Self-similarity in plants

Participants: Pascal Ferraro, Christophe Godin.

This research theme is supported by the ACI "Arborescences".

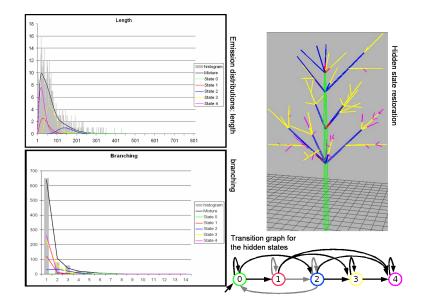


Figure 4. Modeling Aleppo pine architecture using a 5-state hidden Markov tree.

Self-similarity of plants has attracted the attention of biologists for at least 50 years [32], yet its formal treatment is rare, and no measure for quantifying the degree of self-similarity of plants was defined. To fill this gap, we recently introduced a formal definition and corresponding measures of self-similarity, tailored to axial branching plant structures (branching structures having a trunk). These measures are based on edit distance algorithms that makes it possible to compute topological distances between branching systems which are not isomorphic. The formalism was illustrated using theoretical axial branching systems, and applied to analyze self-similarity in two sample plant structures: inflorescences of *Syringa vulgaris* (lilac) (Figure 5) and shoots of *Oryza sativa* (rice) [6]. From a biological perspective, we may observe that this approach of self-similarity enables us to set up a link between the macroscopic world of branching structures and the microscopic world of meristems (from which these structures were supposedly produced). This is made possible through the following simplifying, though fundamental, scaling hypothesis: *If two branching structures in a plant are similar, they were probably produced by meristems with similar state and context.*

An extension of this first approach has been undertaken to define self-similarity for a more general class of branching structures (including structures that does not have a well defined trunk) with sound theoretical fundation. This extension is based on the systematic identification of isomorphic structures in trees. This makes it possible to define the class of self-similar trees as a class of trees with particular distribution of isomorphic subtrees. A polynomial algorithm able to compute, for any given input tree, the closest tree in the class of self-similar trees has been designed. This optimal closest self-similar tree (CST) can be viewed as a maximally compressed version of the input tree. On the one hand, this opens the way for designing new compression techniques of trees in various application domains (e.g. computer graphics). On the other hand, under the above scaling hypothesis, the CST structure is expected to provide biologically significant hierarchies of meristem states.

5.1.11. Reconstruction of plant foliage density from photographs

Participants: Jessada Phattaralerphong [U. Kasetsar, Bangkok, Thailand], Christophe Godin, Hervé Sinoquet.

Methods have been developed in the past decade to digitize plant architecture in 3D. These methods are based on direct measurements of position and shape of every plant organ in space. Although they provide accurate

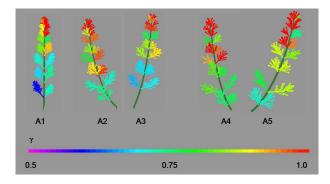


Figure 5. Quantification of self-similarity (Lilac inflorescences): the approach is based on the recursive comparison between trunks and branches. On the figure, branches structurally similar to the trunk are shown in red while branches with structures very different from the trunk are colored in blue

results, these methods are particularly time consuming. In this work, we design a method to reconstruct the 3D leaf density of the plant based on horizontal photographs of the plant crown and on foliage aggregation assumptions. The problem is formulated as an inverse problem were the model is based on different variants of Beer-Lamber model for light interception. This results in a large number of non-linear equations, which depends on several structural parameters (discretization of the image, discretization of the canopy, number of "black zones" on the image, etc.). The huge set of equations is solved using the optimization algorithm L-BFGS-B with simple bounds. This algorithm is based on the gradient projection method and uses a limited memory BFGS matrix to approximate the Hessian of the objective function. Comparisons were made between the actual leaf foliage density of plants digitized leaf by leaf and results of our methods. They show that optimal experimental parameter can be defined depending on the type of plant crown (number of photographs, size of the image zones used for discretization, size of the voxels, ...).

5.1.12. Fractal analysis of plant geometry

Participants: Frédéric Boudon, David Da Silva, Christophe Godin, Hervé Sinoquet.

Plant geometry is a key factor for the modeling of plant ecophysiological interaction with the environment. To capture and analyse the irregular nature of plant shapes we develop tools based on fractal geometry. For this purpose, a range of fractal methods is applied to various 3D digitized tree databases and on theoretical plants generated from fractal rules (Iterated Function Systems). We determined the fractal dimension of tree crowns using two different methods (see Figure 6). The first one is based on the classical box-counting estimator, adapted here to 3D scenes. The method was extensively analysed and various features and drawbacks were discussed. Possible variants of the box counting estimators of the fractal dimension with better properties have been investigated [27]. Other estimators of the fractal dimension were also considered, based on the so called "two-surface" method and on mass estimators [12]. These latter estimators are connected with the notion of lacunarity, used in fractal geometry to characterize the texture of the studied object as a function of scale. Here, we defined a notion of "centered" lacunarity that can be used to characterise the typical size of gaps at different scales in the object.

5.1.13. Light interception by canopy

Participants: Hervé Sinoquet, Christophe Godin, David Da Silva.

Light models for vegetation canopies based on the turbid medium analogy are usually limited by the basic assumption of random foliage dispersion in the canopy space. The objective of this work was to assess the effect of three possible sources of non-randomness in tree canopies on light interception properties. For this

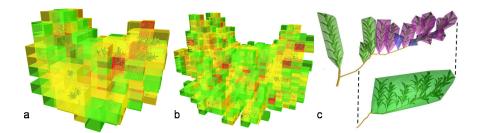


Figure 6. Two methods for estimating the hypothetical fractal dimension of plants i) The box counting estimator based on the number of voxels intercepted by the plant as voxel size is decreasing, a-b. ii) The two-surface estimator based on an allometric relationship between plant envelops at different scales, c.

purpose, four three-dimensional (3D) digitized trees and four theoretical canopies - one random and three built from fractal rules - were used to compute canopy structure parameters and light interception, namely the skyvault averaged STAR (Silhouette to Total Area Ratio). STAR values were computed from (1) images of the 3-D plants, and (2) from a 3-D turbid medium model using space discretization at different scales. For all trees, departure from randomness was mainly due to the spatial variations in leaf area density within the canopy volume. Indeed STAR estimations, based on turbid medium assumption, using the finest space discretization were very close to STAR values computed from the plant images. At this finest scale, foliage dispersion was slightly clumped, except for one theoretical fractal canopy, which showed a marked regular dispersion. Taking into account a non-infinitely small leaf size, whose effect is theoretically to shorten self-shading, had a minor effect on STAR computations. STAR values computed from the 3-D turbid medium were very sensitive to plant lacunarity, a parameter introduced in the context of fractal studies to characterize the distribution of gaps in porous media at different scales. This study shows that 3-D turbid medium models based on space discretization are able to give correct estimation of light interception by 3-D isolated trees, provided that the 3-D grid is properly defined, that is, discretization maximizes plant lacunarity.

5.1.14. Heritability of architectural traits

Participants: Christian Cilas, Evelyne Costes, Vincent Segura [INRA], Christophe Godin.

Plant development is controlled by the combined effect of gene activity and environmental constraints. At a given date, a plant architecture is thus the outcome of this combination. The question of identifying the genetic and environmental components of plant development can be addressed by studying the heritability of architectural traits. We started to investigate this issue in the context of two agronomic applications, respectively on coffee and apple tree ([13]; [22]). In these studies, architectural parameters were used to predict target traits for breeding programs: (i) yield capacity for coffee trees; (ii) adequate forms for an easy and low cost training in the field and regular bearing behaviour, for apple trees. Observation protocols for describing the architecture were applied to six clones of Coffea canephora in a comparative trial on the one hand, and on an apple progeny whose parents were chosen for their contrasted architecture, on another hand. Architectural traits, including both topological and geometric traits, were collected at different scales (trees, branching systems, axes and nodes) and were included in architectural databases which were explored using the V-Plants software (formely AMAPmod). Several traits exhibited high heritability values, for instance branching, internode length and branch orientation in apple tree. In the case of coffee tree, some of the traits displayed strong genetic correlations with cumulated yield over two cycles (14 years). In the apple tree progeny, since a genetic map was built in UMR GenHort in Angers, correlations between the phenotypic variation of a given trait and allelic variations observed in the population are currently under investigation to seek for quantitative trait loci (QTL).

5.1.15. Lumped processes constructed from Markov chains

Participants: Yann Guédon, Yves d'Aubenton-Carafa [CNRS], Claude Thermes [CNRS].

The problem of formulating lumpability hypotheses for a Markov chain is addressed. In the classical approach to lumpability, this problem can be formulated as the determination of an appropriate state space (smaller than the original state space) such that the lumped chain defined on this state space retains the Markov property. We propose a different perspective on lumpability where the state space is fixed and the partitioning of this state space is represented by a one-to-many probabilistic function within a two-level stochastic process. Three nested classes of lumped processes can be defined in this way as sub-classes of first-order Markov chains. These lumped processes enable parsimonious reparameterizations of Markov chains that help to reveal relevant partitions of the state space. Characterizations of the lumped processes on the original transition probability matrix are derived. Different model selection methods relying either on hypothesis testing or on penalized log-likelihood criteria are investigated and extensions to lumped processes constructed from high-order Markov chains are proposed. These lumped processes enables to highlight differences between intronic sequences and gene untranslated region sequences in human DNA sequences [19].

5.1.16. Multivariate dynamic model for ordinal outcomes

Participants: Florence Chaubert, Frédéric Mortier [CIRAD], Laurent Saint-André [CIRAD], Yann Guédon.

Individual or stand-level biomass is not easy to measure. The current methods employed, based on cutting down a representative sample of plantations, make it possible to assess the biomasses for various compartments (bark, dead branches, leaves, ...). However, this felling makes individual longitudinal follow-up impossible. In this context, we propose a method to evaluate individual biomasses by compartments when these biomasses are taken as ordinals. Biomass is measured visually and observations are therefore not destructive. The technique is based on a probit model redefined in terms of latent variables. A generalization of the univariate case to the multivariate case is then natural and takes into account the dependency between compartment biomasses. These models are then extended to the longitudinal case by developing a Dynamic Multivariate Ordinal Probit Model. The performance of the MCMC algorithm used for the estimation is illustrated by means of simulations built from known biomass models. The quality of the estimates and the impact of certain parameters, are then discussed [29].

5.1.17. An integrated model of apple tree development

Participants: Colin Smith, Evelyne Costes, Yann Guédon, Christophe Godin.

This research theme is supported a post-doc INRA Grant.

A first integration of stochastic and mechanistic approaches has been carried out to model the development of apple trees (over the first six years of the growth). The simulation was based on two submodels: hidden semi-Markov chains described the branching patterns (type of axillary production at each node of a branch) and a biomechanical model was used to simulate the bending of branches under fruit and branch weight. The model thus attempts to capture in an integrated, developmental framework both the apple tree's topology (the branching patterns) and its form (the shape of the branches, as determined dynamically by the gravity and the wood properties). The core simulation is specified using a L-system implemented with the Ł+C language (Prusinkiewicz & Karwowski, University of Calgary) with which the stat module of VPlants has been coupled. The statistical analysis was done using the the statistic module of *VPlants* (*VPstats*) [21]. This work is the first attempt worldwide to integrate advanced stochastic descriptions of topology and mechanistic processes. This new type of structure-function model demonstrates that such an integration at tree level can now be done quantitativelly and faithfully with respect to observed tree architectures.

5.2. Meristem functioning and development

5.2.1. 3D surface reconstruction and cell lineage detection in shoot meristems

Participants: Romain Fernandez, Pierre Barbier de Reuille, Grégoire Malandain [INRIA], Christophe Godin, Isabelle Bohn-Courseau [INRA], Jean-Luc Verdeil [CIRAD], Jan Traas.



Figure 7. Top row: A tree over four years of growth. Bottom row: The same tree with the convex hull of the branches used to characterize the overall spatial occupation of the crown.

This research theme is supported by the European RTN project SY-STEM, an INRA ASC Grant and a CIRAD ATP Grant.

We developed a general protocol for observing and reconstructing in 3D and 4D the surface of shoot apical meristems from confocal microscopy at cell scale. This includes: acquisition of images, preprocessing of the images, image segmentation, three- and four-dimensional reconstruction of the meristem surface and quantitative analysis. This protocol uses both classical techniques from image processing (topological closure, watersheds) and specially designed algorithms [33]. We intend now to adapt this methodology We are currently working on an algorithm to automate the detection of cell lineage throughout time in temporal series corresponding to meristem development. These tools are being integrated in the software platform *OpenAlea* for plant modeling and analysis and are freely available for the scientific community.

5.2.2. Simulation of auxin fluxes in the meristem

Participants: Pierre Barbier de Reuille, Christophe Godin, Isabelle Bohn-Courseau [INRA], Jan Traas.

This research theme is supported by the European RTN project SY-STEM.

The active transport of the plant hormone auxin plays a major role in the initiation of organs at the shoot apex. Polar localized membrane proteins of the PIN1 family facilitate this transport and recent observations suggest that auxin maxima created by these proteins are at the basis of organ initiation. This hypothesis is based on the visual, qualitative characterization of the complex distribution patterns of the PIN1 protein in *Arabidopsis Thaliana*. To take these analyzes further, we investigated the properties of the patterns using computational modeling and extensive sensitivity analysis of the model. The simulations reveal novel aspects of PIN1 distribution (see Figure 8). In particular they suggest an important role for the meristem summit in the distribution of auxin and the emergence of phyllotactic patterns. We confirm these predictions by further experimentation and propose a detailed model for the dynamics of auxin fluxes at the shoot apex [11].

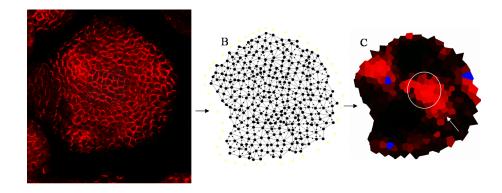


Figure 8. A. Top view of a meristem. Bright red zones denote PIN proteins (obtained by immuno-labelling). B. Transport network of auxin derived from the previous picture. C. Simulation of auxin distribution in this network showing accumulation zones (blue: already formed organ location, arrow: futur organ location, circle: auxin accumulation in the center of the meristem)

5.2.3. Dynamic model of phyllotaxy based on auxin fluxes

Participants: Szymon Stoma, Pierre Barbier de Reuille, Christophe Godin, Isabelle Bohn-Courseau [INRA], Jan Traas.

This research theme is supported by the European RTN project SY-STEM.

We integrated the previous results (organization of the PIN transporters, auxin fluxes, accumulation of auxin in the meristem center) in a dynamic model of the meristem development. The meristem structure is represented by a Voronoï diagram and the changes over time of the meristem structure were described using declarative rules using the *MGS* language (language dedicated to the modeling of dynamic systems with dynamic structures (DS)2, developed at the University of Evry by J.L. Giavitto and O. Michel). The complete model relies on i) a model of cell growth and division, ii) a spring-mass description of the mechanical interaction between cells, iii) a magnetic polarisation of PIN transporters towards the primordia and the center iv) assumptions for auxin transport identical to the static case. Based on these models and assumptions, we showed that phyllotactic patterns emerge from cell growth and cell-cell interactions [11]. This cell-centered model is a first step towards the development of a 3D mechanical and dynamic model of the *Arabidopsis Thaliana* meristem based on cell-cell interaction.

5.2.4. Mechanical model of a tissue

Participants: Jérôme Chopard, Szymon Stoma, Christophe Godin, Jan Traas.

This research theme is supported by the ANR project Virtual Carpel.

From a mechanical point of view, a meristem may be represented by a set of sheets (the walls) on which pressure is acting (called turgor pressure). In the special case of a transversal cut of the meristem, the sheets appear as segments whose mechanical properties may be described using a set of springs of stiffness K and rest length l_0 . That kind of model allows the computation of the shape of the meristem as the arrangement in space of the cells that minimizes mechanical constraints or deformations. The previously mentioned chemical molecules interact with the system by changing K values. Growth is modeled by increasing l_0 proportionally to the wall deformation above some threshold. Replacing walls by springs is sufficient to model a slide of the meristem or its external shape. This approximation reaches its limits for structures with great constraints. In that case, an explicit representation of cells as 3D volumes is required. This representation (see Figure 9) use tensor mechanics to compute the shape of the meristem as a minimum of energy. The problem must be solved using finite elements methods, thus increasing computer simulation time and complexity.

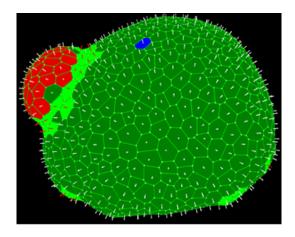


Figure 9. Simulation of a primordium formation due to the mechanical deformation of a tissue in a region (red cells) where cells elongate more rapidly than elsewhere

5.2.5. Modeling axillary root initiation

Participants: Mikaël Lucas, Christophe Godin, Yann Guédon, Christian Jay-Allemand, Laurent Laplaze.

This research theme is supported by an ENS-Lyon PhD Grant.

In this work, our aim is to understand the genetic and physiological determinants of axillary root initiation in *Arabidopsis Thaliana*. As in the case of primordia initiation of the shoot apical meristem, auxin plays a crucial role in root initiation. Organ initiation is correlated to high concentrations of auxin. However, in both systems, organ initiation is very different. In particular, in the root development, lateral organs initiation is observed at a long distance from the root meristem, with no apparent spatial or temporal structure. Our main assumption is that this system is governed by a mechanism of competition for auxin while the root system is developing. To understand this complex dynamic interaction, we develop a sink-source dynamic model of the root system development in which the transport of auxin is controlled by active carriers of the PIN family (a first prototype has been developed using L-Systems). First experimental protocols were carried out on *Arabidopsis Thaliana*, with accuracy ranging from macroscopic to cellular levels. We obtained complete data about the developmental sequence in the primary root and its laterals. This extensive database is explored using tools for sequence analysis (distance between sequences, different types of Markovian models). First results show structures and correlations between positions and stages of development of lateral organs which can now be exploited for the design of the dynamical model.

6. Other Grants and Activities

6.1. National Grants

6.1.1. New interfaces of mathematics ACI grant: Arborescences

Participants: Yann Guédon, Yves Caraglio, Evelyne Costes, Jean-Baptiste Durand, Christophe Godin, Patrick Heuret, Christophe Pradal.

(Contractor for Virtual Plants: CIRAD. From November 2004 until November 2007)

Arborescences: Mathematical and computer methods for the study of plants structure and development. The aim of this project is to propose a set of consistant methods for analyzing tree-structured data and to apply these methods to plant structures. Three main categories of methods or models are investigated: algorithms for computing distances between tree structures, hidden Markov tree models for finding homogeneous zones (or change points) within tree structures and multi-type branching processes with dependencies for analysing the generative growth process. This three-year grant started in November 2004. This project is coordinated by Yann Guédon (UMR AMAP) and the participants are the Institut Camille Jordan (University Claude Bernard Lyon 1), the LaBRI (Bordeaux), the UMR BEPC (Montpellier) and the LMC (University Joseph Fourier, Grenoble). See Sections 5.1.8, 5.1.9 and 5.1.10.

6.1.2. ANR NatSim Grant

Participants: Frédéric Boudon, Christophe Pradal, 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 (AMAP: CIRAD-INRIA-SophiaAntipolis in Montpellier, LIAMA : Academy of science of China, INRIA, CIRAD, EVASION: INRIA-Rhône Alpes), graphics (EVASION, IRIT: Univ.Toulouse-CNRS, IPARLA: INRIA-Futur) as well as adaptive streaming (IRIT, IPARLA).

6.1.3. 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. 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).

6.1.4. ATP CIRAD Meristem Grant

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

(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 Programmée of CIRAD is twofold. We first intend to design 3D visualization technics 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.

6.2. UE Grants

6.2.1. RTN SY-STEM Grant

Participants: Szymon Stoma, Pierre Barbier de Reuille, Christophe Godin.

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 computing scientists, who will create new modeling tools. This network started in January 2005 and 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* for 4 years. 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

E. Costes made a visit to Ted de Jong's Lab at the U. of Davis (USA). The possibility to start a joint project on the simulation of peach tree development, integrating stochastic and physiological components was investigated.

Christophe Godin was visiting Pr. Prusinkiewicz at the University of Calgary (Canada) to work on multiscale models of plants in November 2006. This work is carried out in the context of an long-going collaboration between both teams (visits, exchange of students, joint projects and publications).

7. Dissemination

7.1. Services to the scientific community

Christophe Godin is member 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). He was a member of the UMR AMAP board between and headed the Mathematics and Computer Science group (MIA) at UMR AMAP between 2002 and 2005. Since 2006, he has been the team leader of the joint INRIA-CIRAD-INRA Virtual Plant team located in UMR DAP, Montpellier. He is a member of the board of the new Fédération de Recherche DAPHNE, coordinating joint actions of UMRs working in Plant Sciences in the region Languedoc Roussillon. He is a member of the INRA Tree Ecophysiology Network (REA) advisory board since 2001. In 2006, he was a referee for a PhD thesis in plant modeling. He was a referee for several journal papers (Planta, Annals of Botany, Comptes Rendus de l'Académie des Sciences, Technique et Science Informatiques, Journal of Theoretical Biology, Nature). He is member of the international board of the Functional-Structural Plant Models conference (he was chair of this board between 2001-2005).

Yann Guédon is a member of the editorial board of Annals of Botany. He was a member of Jury for the selection of an engineer in Statistics at University Montpellier I. He was a referee for papers submitted to Physical Review E and Journal of Mathematical Biology. He reeviewed a "'Discovery"' Grant proposal for the Natural Sciences and Engineering Research Council of Canada.

Christophe Pradal coordinates the national platform for plant modeling: OpenALEA.

Evelyne Costes is the scientific leader of "Fruit tree Architecture and Functions" (AFEF) team composed of 13 scientists (8 INRA researchers, 2 Agro-M professors and 3 assistant-professors). She participates to the scientific board of the UMR BEPC where she represents the INRA AFEF team which is associated to other institutions (CIRAD, IRD and Montpellier 2 University). Since 2004, she participates to the INRA scientific board of the INRA center in Montpellier. At the national level, E. Costes is involved in the scientific coordination of the working group "Achitecture" for the "Genetics and Breeding" Department (DGAP) of INRA. She also participates to the scientific board of this department. At an international level, she is member of the International Society for Horticultural Research. In 2006, she participated to the Rosaceae Genomics Conference in New-Zealand and is member of the Genomics Database for Rosaceae network (GDR).

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 jointly with Guy Mélançon (Professor at Lirmm) the course on Multiscale structures and their algorithms.

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 Course

Agro-Montpellier and Horticultural National School in Angers.

Evelyne Costes teaches a Master course in the optional module "Tree".

7.2.5. Statistics Courses

Institut National Polytechnique de Grenoble (INPG) - Ecole Nationale Supérieure d'Informatique et de Mathématiques Appliquées de Grenoble (ENSIMAG).

Jean-Baptiste Durand teaches the probability theory course, the statistical principles and methods course and the multidimensional statistical analysis course.

7.2.6. High School class

Lycée Pompidou, Castelnau le Lez.

Christophe Godin gave two 3-hours classes to pupils with scientific option on plants and fractals (jointly with Yves Caraglio).

7.3. Participation to workshops, seminars and miscellaneous invitations

Christophe Godin was invited to give seminars at ENS Lyon, INRA Paris, Institut Henri Poincaré (conference organized by Pour La Science) and at the University of Calgary (Canada). He also participated in the organization of the spring school: "Modélisation et simulation de processus biologiques dans le contexte de la génomique", Bordeaux, Avril 2006.

Yann Guédon was invited to give a seminar at Montpellier 2 University and presented a communication at the XXIIIrd International Biometric Conference (Montréal, Canada). He organized the first two internal workshops of Virtual Plants (February and June 2006).

Jean-Baptiste Durand was invited to give a seminar at TIMC-IMAG (Grenoble).

Frédéric Boudon was invited to give a seminar at Bordeaux 1 University.

7.4. Theses and Internships

7.4.1. Ongoing Theses

- Florence Chaubert, "Modèles linéaires généralisés mixtes multiphasiques", Université Montpellier II.
- David Da Silva, "Quantification de la structure autosimilaire des plantes par des méthodes de la géométrie fractale", Université Montpellier II.
- Mikaël Lucas, "Etude et modélisation des déterminismes de mise en place et de développement des racines latérales chez Arabidopsis Thaliana", Université Montpellier II.
- Szymon Stoma, "A mechanical based model of Arabidopsis Thaliana meristem development", Université Montpellier II.
- Romain Fernandez, "3D Reconstruction of meristems from+ bi-photon images", Université Montpellier II.

7.4.2. Internships

• Mariem Zouch, "Modèle de Poisson pondéré pour des données longitudinales de comptage sous- et sur-dispersées : Application aux données de suivis de croissance de plantes", Ecole Polytechnique de Tunisie.

8. Bibliography

Major publications by the team in recent years

- [1] P. BARBIER DE REUILLE, I. BOHN-COURSEAU, K. LJUNG, H. MORIN, N. CARRARO, C. GODIN, J. TRAAS. Computer simulations reveal novel properties of the cell-cell signaling network at the shoot apex in Arabidopsis, in "PNAS", vol. 103, 2006, p. 1627-1632, http://www-sop.inria.fr/virtualplants/Publications/2006/BBLMCGT06.
- [2] F. BOUDON, P. PRUSINKIEWICZ, P. FEDERL, C. GODIN, R. KARWOWSKI. Interactive design of bonsai tree models, in "Computer Graphics Forum. Proceedings of Eurographics", vol. 22, n^o 3, 2003, p. 591-599.
- [3] J.-B. DURAND, P. GONÇALVÈS, Y. GUÉDON. *Computational methods for hidden Markov tree models An application to wavelet trees*, in "IEEE Transactions on Signal Processing", vol. 52, n^o 9, 2004, p. 2551-2560.
- [4] J.-B. DURAND, Y. GUÉDON, Y. CARAGLIO, E. COSTES. Analysis of the plant architecture via tree-structured statistical models: the hidden Markov tree models., in "New Phytol", vol. 166, n^o 3, Jun 2005, p. 813–825, http://dx.doi.org/10.1111/j.1469-8137.2005.01405.x.
- [5] P. FERRARO, C. GODIN. An edit distance between quotiented trees, in "Algorithmica", vol. 48, 2003, p. 385-406.
- [6] P. FERRARO, C. GODIN, P. PRUSINKIEWICZ. *Toward a quantification of self-similarity in plants*, in "Fractals", vol. 13, n^o 2, 2005, p. 91-109, http://www-sop.inria.fr/virtualplants/Publications/2005/FGP05.
- [7] C. GODIN, Y. CARAGLIO. A multiscale model of plant topological structures, in "Journal of Theoretical Biology", vol. 191, 1998, p. 1-46, http://www-sop.inria.fr/virtualplants/Publications/1998/GC98.

- [8] C. GODIN, E. COSTES, H. SINOQUET. Plant architecture modelling virtual plants and complex systems, in "Plant Architecture and its Manipulation", C. TURNBULL (editor)., Annual plant reviews, vol. 17, Blackwell, 2005, p. 238-287, http://www-sop.inria.fr/virtualplants/Publications/2005/GCS05.
- [9] Y. GUÉDON, D. BARTHÉLÉMY, Y. CARAGLIO, E. COSTES. Pattern analysis in branching and axillary flowering sequences, in "Journal of Theoretical Biology", vol. 212, 2001, p. 481-520.
- [10] Y. GUÉDON. *Estimating hidden semi Markov chains from discrete sequences*, in "Journal of Computational and Graphical Statistics", vol. 12, n^o 3, 2003, p. 604-639.

Year Publications

Articles in refereed journals and book chapters

- [11] P. BARBIER DE REUILLE, I. BOHN-COURSEAU, K. LJUNG, H. MORIN, N. CARRARO, C. GODIN, J. TRAAS. Computer simulations reveal novel properties of the cell-cell signaling network at the shoot apex in Arabidopsis, in "PNAS", vol. 103, 2006, p. 1627-1632, http://www-sop.inria.fr/virtualplants/Publications/2006/BBLMCGT06.
- [12] F. BOUDON, C. GODIN, C. PRADAL, O. PUECH, H. SINOQUET. Estimating the fractal dimension of plants using the two-surface method: An analysis based on 3D-digitized tree foliage, in "Fractals", vol. 14, n^o 3, 2006, p. 149-163, http://www-sop.inria.fr/virtualplants/Publications/2006/BGPPS06.
- [13] C. CILAS, A. BAR-HEN, C. MONTAGNON, C. GODIN. Definition of architectural ideotypes for good yield capacity in Coffea canephora, in "Annals of Botany", vol. 97, n^o 3, March 2006, p. 405-411, http://wwwsop.inria.fr/virtualplants/Publications/2006/CBMG06.
- [14] E. COSTES, E. GARCIA-VILLANUEVA, C. JOURDAN, J. REGNARD, Y. GUÉDON. Coordinated growth between aerial and root systems in young apple plants issued from in vitro culture., in "Annals of Botany", vol. 97, n^o 1, 2006, p. 85-96, http://www-sop.inria.fr/virtualplants/Publications/2006/CGJRG06.
- [15] C. GODIN, H. SINOQUET, E. COSTES, J. TRAAS. *Des plantes virtuelles pour comprendre les plantes réelles*, in "Pour la Science", n⁰ 52, jul 2006, http://www-sop.inria.fr/virtualplants/Publications/2006/GSCT06.
- [16] C. GODIN, J. TRAAS, I. BOHN-COURSEAU, P. BARBIER DE REUILLE. La modélisation comme outil d'analyse pour la biologie du développement, in "médecine/sciences", vol. 22, nº 10, October 2006, p. 29-31.
- [17] Y. GUÉDON. Exploring the state sequence space for hidden Markov and semi-Markov chains, in "Computational Statistics and Data Analysis", vol. 51, n^o 5, 2007, p. 2379–2409, http://www-sop.inria.fr/virtualplants/Publications/2007/Gue07/CSDAguedon2006.pdf.
- [18] Y. GUÉDON, J. G. PUNTIERI, S. SABATIER, D. BARTHÉLÉMY. *Relative extents of preformation and neoformation in tree shoots: Analysis by a deconvolution method*, in "Annals of Botany", vol. 98, n^O 4, 2006, p. 835–844, http://www-sop.inria.fr/virtualplants/Publications/2006/GPSB06.
- [19] Y. GUÉDON, Y. D'AUBENTON-CARAFA, C. THERMES. Analysing grouping of nucleotides in DNA sequences using lumped processes constructed from Markov chains., in "Journal of Mathematical Biology", To appear, vol. 52, n^o 3, March 2007, p. 343-372, http://www-sop.inria.fr/virtualplants/Publications/2006/GAT06.

- [20] J. LEGAVE, V. SEGURA, D. FOURNIER, E. COSTES. *The effect of genotype, location and their interaction on early growth and branching in apricot trees*, in "Journal of Horticultural Science & Biotechnology", vol. 81, n^o 2, 2006, p. 189-198, http://www-sop.inria.fr/virtualplants/Publications/2006/LSFC06.
- [21] M. RENTON, Y. GUÉDON, C. GODIN, E. COSTES. Similarities and gradients in growth-unit branching patterns during ontogeny in Fuji apple trees: A stochastic approach., in "Journal of Experimental Botany", vol. 57, n^o 12, 2006, p. 3131–3143, http://www-sop.inria.fr/virtualplants/Publications/2006/RGGC06.
- [22] V. SEGURA, C. CILAS, F. LAURENS, E. COSTES. Phenotyping progenies for complex architectural traits: a strategy for 1-year-old apple trees (Malus x domestica Borkh.), in "Tree Genetics & Genomes", vol. 2, n^o 3, 2006, p. 140-151, http://www-sop.inria.fr/virtualplants/Publications/2006/SCLC06.
- [23] A. THIERRY, F. KEPES, P. AMAR, G. BARLOVATZ, G. BERNOT, M. BEURTON- AIMAR, M. DUTREIX, J.-L. GIAVITTO, J. GUESPIN, J.-P. MAZAT, V. NORRIS, V. SCHAFTER, P. TRACQUI, F. GODIN. Modelling of complex biological systems in the context of genomics: an account of a multidisciplinary thematic seminar held in Montpellier (France) in April 2005, in "Journal of Biological Physics and Chemistry", vol. 6, 2006, p. 103-107.

Publications in Conferences and Workshops

- [24] F. BOUDON, G. LE MOGUEDEC. Déformation asymétrique de houppiers pour la génération de représentations paysagères réalistes, in "Journées Francophones d'Informatique Graphique (AFIG)", 2006, http://wwwsop.inria.fr/virtualplants/Publications/2006/BL06.
- [25] C. PRADAL, F. BOUDON, N. DONES, J.-B. DURAND, C. FOURNIER, H. SINOQUET, C. GODIN. OpenAlea - A platform for plant modelling, analysis and simulation, in "EuroPython 2006, Geneva", CERN, July 2006, http://www.europython.org/.
- [26] M. RENTON, E. COSTES, Y. GUÉDON, C. GODIN. Integrating Markov chain models and L-systems to simulate the architectural development of apple trees, in "7th International Symposium on Modelling in Fruit Research and Orchard Management, Copenhagen, Denmark", vol. 707, Acta Horticulturae, 2006, http://wwwsop.inria.fr/virtualplants/Publications/2006/RCGG06.
- [27] D. DA SILVA, F. BOUDON, C. GODIN, O. PUECH, C. SMITH, H. SINOQUET. A Critical Appraisal of the Box Counting Method to Assess the Fractal Dimension of Tree Crowns, in "Lecture Note in Computer Sciences (Proceedings of ISVC 2006)", G. BEBIS (editor). vol. 4291, Springer, 2006, p. 751–760, http://wwwsop.inria.fr/virtualplants/Publications/2006/DBGPSS06.

Internal Reports

- [28] F. BOUDON, A. MEYER, C. GODIN. Survey on Computer Representations of Trees for Realistic and Efficient Rendering, Rapport de recherche, n^o 2301, LIRIS, Université Paul Sabatier, Toulouse, 2006.
- [29] F. CHAUBERT, F. MORTIER, L. SAINT ANDRÉ. Multivariate dynamic model for ordinal outcomes, Research Report, n⁰ 5999, INRIA, 10 2006, http://www-sop.inria.fr/virtualplants/Publications/2006/CMS06.

Miscellaneous

[30] F. BOUDON. Fractals Cover Image 14(3), September 2006.

[31] F. DANJON, D. BERT, C. PRADAL. New Phytologist cover image 170(2), 2006.

References in notes

- [32] A. ARBER. Natural philosophy of plant form, University Press, Cambridge, 1950.
- [33] P. BARBIER DE REUILLE, I. BOHN-COURSEAU, C. GODIN, J. TRAAS. A protocol to analyse cellular dynamics during plant development, in "Plant Journal", vol. 44, n^o 6, 2005, p. 1045-1053.
- [34] Y. GUÉDON. *Hidden hybrid Markov/semi-Markov chains.*, in "Computational Statistics and Data Analysis", vol. 49, n^o 3, 2005, p. 663-688, http://www-sop.inria.fr/virtualplants/Publications/2005/Gue05a.