

# 2025 Activity Report

RESEARCH CENTRE: Inria Lyon Centre

IN PARTNERSHIP WITH: Ecole normale supérieure de Lyon, CNRS, INRAE

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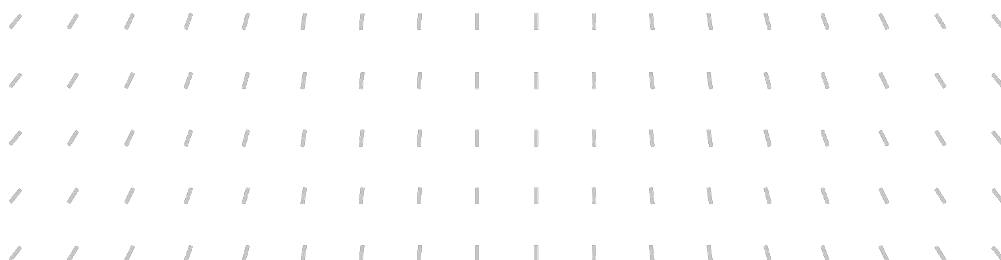
Project-Team

## MOSAIC

MOrphogenesis Simulation and Analysis In siliCo

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*In collaboration with* Réproduction et Développement des Plantes



## **Project-Team MOSAIC**

*Creation of the Project-Team: 2019 July 01*

Each year, Inria research teams publish an Activity Report presenting their work and results over the reporting period. These reports follow a common structure, with some optional sections depending on the specific team. They typically begin by outlining the overall objectives and research programme, including the main research themes, goals, and methodological approaches. They also describe the application domains targeted by the team, highlighting the scientific or societal contexts in which their work is situated. The reports then present the highlights of the year, covering major scientific achievements, software developments, or teaching contributions. When relevant, they include sections on software, platforms, and open data, detailing the tools developed and how they are shared. A substantial part is dedicated to new results, where scientific contributions are described in detail, often with subsections specifying participants and associated keywords. Finally, the Activity Report addresses funding, contracts, partnerships, and collaborations at various levels, from industrial agreements to international cooperations. It also covers dissemination and teaching activities, such as participation in scientific events, outreach, and supervision. The document concludes with a presentation of scientific production, including major publications and those produced during the year.

## Keywords

### Computer sciences and digital sciences

- A3.4. – Machine learning and statistics
- A6.1. – Methods in mathematical modeling
- A6.2. – Scientific computing, Numerical Analysis & Optimization
- A6.3. – Computation-data interaction
- A6.5. – Mathematical modeling for physical sciences
- A7.1. – Algorithms
- A8.1. – Discrete mathematics, combinatorics
- A8.2. – Optimization
- A8.3. – Geometry, Topology
- A8.7. – Graph theory
- A8.12. – Optimal transport
- A9.2. – Machine learning
- A9.5. – Robotics and AI
- A9.12.1. – Object recognition
- A9.12.4. – 3D and spatio-temporal reconstruction

### Other research topics and application domains

- B1.1.2. – Molecular and cellular biology
- B1.1.3. – Developmental biology
- B1.1.7. – Bioinformatics
- B1.1.8. – Mathematical biology
- B1.1.9. – Biomechanics and anatomy
- B1.1.10. – Systems and synthetic biology
- B1.1.11. – Plant Biology
- B3.5. – Agronomy
- B9.1.2. – Serious games
- B9.5.1. – Computer science
- B9.5.2. – Mathematics
- B9.5.5. – Mechanics
- B9.5.6. – Data science

## Contents

<b>Project-Team MOSAIC</b>	<b>1</b>
<b>1 Team members, visitors, external collaborators</b>	<b>5</b>
<b>2 Overall objectives</b>	<b>6</b>
<b>3 Research program</b>	<b>6</b>
3.1 Axis 1: Representation of biological organisms and their forms <i>in silico</i> . . . . .	6
3.2 Axis 2: Data-driven models of form development . . . . .	7
3.3 Axis 3: Plasticity and robustness of forms . . . . .	7
3.4 Key modeling challenges . . . . .	8
3.4.1 A new paradigm for modeling tree structures in biology . . . . .	8
3.4.2 Efficient computational mechanical models of growing tissues . . . . .	8
3.4.3 Realistic integrated digital models . . . . .	8
3.4.4 Development of a computational environment for the simulation of biological form development . . . . .	8
<b>4 Application domains</b>	<b>8</b>
<b>5 Highlights of the year</b>	<b>9</b>
<b>6 Latest software developments, platforms, open data</b>	<b>9</b>
6.1 Latest software developments . . . . .	9
6.1.1 bvpy . . . . .	9
6.1.2 dxtr . . . . .	10
6.1.3 TimageTK . . . . .	10
6.1.4 vt . . . . .	11
6.1.5 vt-python . . . . .	11
6.1.6 TimageTK_geometry . . . . .	12
6.1.7 cellcomplex . . . . .	12
6.1.8 tides . . . . .	13
6.1.9 Collects . . . . .	13
6.1.10 Riemannian L-systems . . . . .	14
6.1.11 Gnomon . . . . .	14
<b>7 New results</b>	<b>16</b>
7.1 Dynamical characterization of morphogenesis at cellular scale . . . . .	16
7.2 Reconstruction of macroscopic forms from images and characterization of their variability	19
7.3 Analysis and simulation of tree data . . . . .	21
7.4 Mechanics of tissue morphogenesis . . . . .	22
7.5 Signaling and transport for tissue patterning and growth . . . . .	26
7.6 Integration of processes for morphogenesis . . . . .	29
7.7 New computational approaches for morphogenesis . . . . .	29
7.8 Preparation of a new team: TRABOULE . . . . .	31
<b>8 Bilateral contracts and grants with industry</b>	<b>31</b>
8.1 CIFRE PhD thesis with ACOREL . . . . .	31
<b>9 Partnerships and cooperations</b>	<b>32</b>
9.1 National initiatives . . . . .	32

<b>10 Dissemination</b>	<b>35</b>
10.1 Promoting scientific activities	35
10.1.1 Journal	35
10.1.2 Invited talks	36
10.1.3 Leadership within the scientific community	36
10.1.4 Scientific expertise	36
10.1.5 Research administration	36
10.2 Teaching - Supervision - Juries - Educational and pedagogical outreach	37
10.2.1 Supervision	37
10.2.2 Juries	37
10.2.3 Educational and pedagogical outreach	37
10.2.4 Participation in Live events	38
<b>11 Scientific production</b>	<b>38</b>
11.1 Major publications	38
11.2 Publications of the year	39
11.3 Cited publications	41

# 1 Team members, visitors, external collaborators

## Research Scientists

- Christophe Godin [Team leader, INRIA, Senior Researcher, HDR]
- Olivier Ali [INRIA, Researcher, HDR]
- Romain Azais [INRIA, Researcher, HDR]

## Faculty Member

- Julien Derr [ENS DE LYON, Professor, HDR]

## Post-Doctoral Fellows

- Guillaume Mestdagh [INRIA, Post-Doctoral Fellow, until Jan 2025]
- Justina Stark [INRIA, Post-Doctoral Fellow, from Feb 2025]
- Gauthier Weissbart [CNRS, Post-Doctoral Fellow, from Nov 2025]

## PhD Students

- Jeanne Abitbol Spangaro [CNRS, until Jun 2025]
- Elsa Gascon [INRIA]
- Adrien Marion [INRIA, from Oct 2025]
- Henri Pechoux [INRIA]
- Lucie Poupardin [INRIA]
- John Thampi [CNRS]

## Technical Staff

- Guillaume Cerutti [INRAE, Engineer]
- Annamaria Kiss [INRAE]
- Jonathan Legrand [CNRS, Engineer]
- Guillaume Mestdagh [INRIA, Engineer, from Feb 2025 until Mar 2025]
- Manuel Petit [INRIA, Engineer]
- Gonzalo Revilla Mut [INRIA, Engineer]

## Interns and Apprentices

- Ritish Verma [ENS DE LYON, Intern, from Feb 2025 until Apr 2025]

## Administrative Assistant

- Leslie Dussollier [INRIA]

## Visiting Scientist

- Aurèle Boussard [SORBONNE UNIVERSITE, from Apr 2025]

## External Collaborators

- Frédéric Boudon [CIRAD, HDR]
- Ibrahim Cheddadi [UGA]
- Emmanuel Faure [LIRMM, HDR]
- François Parcy [CNRS, HDR]
- Samuel Vernoux [CNRS, HDR]

## 2 Overall objectives

Our general aim in MOSAIC is to identify key principles of organism development in close collaboration with biologists by constructing a new generation of models based on explicit mathematical and computational representations of forms. For this we will develop a dual modeling approach where conceptual models will be used to identify self-organizing principles and realistic models will be used to test non-trivial genetic and physical hypotheses *in silico* and assess them against observations. This will contribute to extend the domain of systems biology to developmental systems and help interpret where possible the vast amount of geometric, molecular and physical data collected on growing forms. The main originality of the project lies in its integrated approach: we want to face the complexity of living organisms by developing an integrated view of form development, relying on the study of the interaction between coupled processes.

While our approach will mainly focus on plant development at different scales, the MOSAIC project will also consider the morphogenesis of model animal systems, such as ascidians<sup>1</sup>, to cross-fertilize the approaches and to open the possibility to identify abstractions and principles that are relevant to morphogenesis of living forms in general. Our work will focus on how physical and chemical processes interact within the medium defined by the form and feedback on its development. We will seek to integrate both mechanistic and stochastic components in our models to account for biological variability in shape development. In the long run, the team's results are expected to contribute to set up a new vision of morphogenesis in biology, at the origin of a new physics of living matter, and based on a more mechanistic understanding of the link between genes, forms and their environment.

To achieve the team's objectives, we will develop over the next 12 years a project focused on the definition of a consistent mathematical framework to formalize form growth and on the development of corresponding computational algorithms. The mathematical framework will extend classical dynamical systems to dynamical systems with a dynamical state-structure, i.e. to dynamical systems whose state is represented as a graph of components that may change in time. A similar approach was successfully developed in the last two decades in the restricted context of branching organisms and plant development. We now want to extend it to more general forms, and address the diversity of associated new and stimulating computational challenges. For this, we will organize our research program into three main research axes.

## 3 Research program

### 3.1 Axis 1: Representation of biological organisms and their forms *in silico*

The modeling of organism development requires a formalization of the concept of form, *i.e.* a mathematical definition of what is a form and how it can change in time, together with the development of efficient algorithms to construct corresponding computational representations from observations, to manipulate them and associate local molecular and physical information with them. Our aim is threefold. First, we will develop new computational structures that make it possible to represent complex forms efficiently in space and time. For branching forms, the challenge will be to reduce the computational burden of the current tree-like representations that usually stems from their exponential increase in size during growth. For tissue structures, we will seek to develop models that integrate seamlessly continuous representations of the cell

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<sup>1</sup>A large class of marine animals (also called sea-squirt) in the phylum of Tunicates that is close to vertebrates, shares a particularly well conserved developmental program and that is a good model to study the development of chordates.

geometry and discrete representations of their adjacency network in dynamical and adaptive framework. Second, we will explore the use of machine learning strategies to set up robust and adaptive strategies to construct form representations in computers from imaging protocols. Finally, we will develop the notion of digital atlases of development, by mapping patterns of molecular (gene activity, hormones concentrations, cell polarity, ...) and physical (stress, mechanical properties, turgidity, ...) expressions observed at different stages of development on models representing average form development and by providing tools to manipulate and explore these digital atlases.

The computational approach developed by the team is well illustrated for instance by the works on the geometric reconstruction of ascidian embryos development at cell resolution based on time-lapse light-sheet microscopy imaging [7], and on the construction of digital atlases of the young growing flower [9]. The proximity of our approach from the biological data is also reflected by the construction and analysis of hormone maps such as in [5]. On a more mathematical side, [8] and [2] illustrate the combinatorial approaches developed by the team on branching structures.

### 3.2 Axis 2: Data-driven models of form development

Our aim in this second research axis will be to develop models of physiological patterning and bio-physical growth to simulate the development of 3D biological forms in a realistic way. Models of key processes participating to different aspects of morphogenesis (signaling, transport, molecular regulation, cell division, etc.) will be developed and tested *in silico* on 3D data structures reconstructed from digitized forms. The way these component-based models scale-up at more abstract levels where forms can be considered as continuums will also be investigated. Altogether, this will lead us to design first highly integrated models of form development, combining models of different processes in one computational structure representing the form, and to analyze how these processes interact in the course of development to build up the form. The simulation results will be assessed by quantitative comparison with actual form development. From a computational point of view, as branching or organ forms are often represented by large and complex data-structures, we aim to develop optimized data structures and algorithms to achieve satisfactory compromises between accuracy and efficiency.

On the patterning side, the team has for example developed work to understand how genes and gene perturbation regulate phyllotaxis, with breakthrough results for instance on cauliflower fractal curds [3]. On the mechanical side, we developed models illustrating how the coupling between mechanics and gene regulation result in various emerging properties (control of organ flatness [10], of size [4], of differential growth [1]).

### 3.3 Axis 3: Plasticity and robustness of forms

In this research axis, building on the insights gained from axes 1 and 2 on the mechanisms driving form development, we aim to explore the mechanistic origin of form plasticity and robustness. At the ontogenetic scale, we will study the ability of specific developmental mechanisms to buffer, or even to exploit, biological noise during morphogenesis. For plants, we will develop models capturing morphogenetic reactions to specific environmental changes (such as water stress or pruning), and their ability to modulate or even to reallocate growth in an opportunistic manner.

At the phylogenetic scale, we will investigate new connections that can be drawn from the use of a better understanding of form development mechanisms in the evolution of forms. In animals, we will use ascidians as a model organism to investigate how the variability of certain genomes relates to the variability of their forms. In plants, models of the genetic regulation of form development will be used to test hypotheses on the evolution of regulatory gene networks of key morphogenetic mechanisms such as branching. We believe that a better mechanistic understanding of developmental processes should shed new light on old evo-devo questions related to the evolution of biological forms, such as understanding the origin of *developmental constraints*<sup>2</sup> how the internal rules that govern form development, such as chemical interactions and physical constraints, may channel form changes so that selection is limited in the phenotype it can achieve?

Work in this axis is illustrated for instance by our theoretical synthesis of phyllotaxis processes, [6], which suggests that the conspicuous arrangements of organs in plants are actually canalized to very specific and robust patterns during plant ontogenesis.

<sup>2</sup>Raff, R. A. (1996). *The Shape of Life: Genes, Development, and the Evolution of Form*. Univ. Chicago Press.

### 3.4 Key modeling challenges

During the project lifetime, we will address several computational challenges related to the modeling of living forms and transversal to our main research axes. During the first phase of the project, we concentrate on 4 key challenges.

#### 3.4.1 A new paradigm for modeling tree structures in biology

There is an ubiquitous presence of tree data in biology: plant structures, tree-like organs in animals (lungs, kidney vasculature), corals, sponges, but also phylogenetic trees, cell lineage trees, *etc.* To represent, analyze and simulate these data, a huge variety of algorithms have been developed. For a majority, their computational time and space complexity is proportional to the size of the trees. In dealing with massive amounts of data, like trees in a plant orchard or cell lineages in tissues containing several thousands of cells, this level of complexity is often intractable. Here, our idea is to make use of a new class of tree structures, that can be efficiently compressed and that can be used to approximate any tree, to cut-down the complexity of usual algorithms on trees.

#### 3.4.2 Efficient computational mechanical models of growing tissues

The ability to simulate efficiently physical forces that drive form development and their consequences in biological tissues is a critical issue of the MOSAIC project. Our aim is thus to design efficient algorithms to compute mechanical stresses within data-structures representing forms as the growth simulation proceeds. The challenge consists of computing the distribution of stresses and corresponding tissue deformations throughout data-structures containing thousands of 3D cells in close to interactive time. For this we will develop new strategies to simulate mechanics based on approaches originally developed in computer graphics to simulate in real time the deformation of natural objects. In particular, we will study how meshless and isogeometric variational methods can be adapted to the simulation of a population of growing and dividing cells.

#### 3.4.3 Realistic integrated digital models

Most of the models developed in MOSAIC correspond to specific parts of real morphogenetic systems, avoiding the overwhelming complexity of real systems. However, as these models will be developed on computational structures representing the detailed geometry of an organ or an organism, it will be possible to assemble several of these sub-models within one single model, to figure out missing components, and to test potential interactions between the model sub-components as the form develops.

Throughout the project, we will thus develop two digital models, one plant and one animal, aimed at integrating various aspects of form development in a single simulation system. The development of these digital models will be made using an agile development strategy, in which the models are created and get functional at a very early stage, and become subsequently refined progressively.

#### 3.4.4 Development of a computational environment for the simulation of biological form development

To support and integrate the software components of the team, we aim to develop a computational environment dedicated to the interactive simulation of biological form development. This environment will be built to support the paradigm of dynamical systems with dynamical structures. In brief, the form is represented at any time by a central data-structure that contains any topological, geometric, genetic and physiological information. The computational environment will provide in a user-friendly manner tools to up-load forms, to create them, to program their development, to analyze, visualize them and interact with them in 3D+time.

## 4 Application domains

Our application domains are developmental biology and plant science (see overall objectives, research program above).

## 5 Highlights of the year

- Olivier Ali defended his Habilitation, entitled “Stress-processing shapes” on October 31, 2025 in front of a jury composed on Alain Goriely (reviewer), Anja Geitmann (reviewer), Yoel Forterre (reviewer), Gwyneth Ingram and David Coeurjolly.
- A travelling-wave strategy for plant–fungal trade, Nature, 2025 [20]: The team has collaborated with the group of Dr. Tom Shimizu from the AMOLF lab and the group of Toby Kiers from the Vrije University of Amsterdam, in the Netherlands to analyze the development of mycorrhizal fungi and their partnership with plants. Here is a summary of the study:

For nearly 450 million years, mycorrhizal fungi have built trading networks that exchange nutrients with plant roots while relying on host-derived carbon, creating strong design trade-offs between construction costs, spatial coverage, and long-distance transport. To monitor how living networks resolve these constraints, the Netherland groups developed a custom robot for high-throughput time-lapse imaging that tracked more than 500,000 fungal nodes and enabled quantification of 100,000 cytoplasmic flow trajectories. Building on these unique, high spatiotemporal resolution data, we propose an initial analytical framework describing colony spread as self-regulating travelling waves. In this model, pulses of growing tips pull an expanding wave of nutrient-absorbing mycelium, whose density is regulated by hyphal fusion. The framework bridges microscopic hyphal behaviour and emergent macroscopic variables such as mycelial density and propagation speed. This design allows relatively modest carbon investments to drive range expansion beyond nutrient-depletion zones, supporting exploration for nutrients and new plant partners. Over time, networks maintain near-constant transport efficiency back to roots while adding loops that shorten paths to prospective trade partners. Transport is further enhanced by widening hyphae and accelerating flows along “trunk routes”. Altogether, the work reveals network-level control of structure and flows, and articulates design principles of symbiotic supply-chain networks shaped by natural selection.

## 6 Latest software developments, platforms, open data

Over the past year, following the integration of Manuel Petit in the coordination team of the Gnomon project, a coordinated development effort has been carried out across the software ecosystem underlying Gnomon, including notably several core libraries extensively used by Gnomon plugins, such as vt, vt-python, TimageTK, and bvpy. Regarding the Gnomon platform itself, a technological migration is currently in preparation, aimed at consolidating core components and ensuring a coherent evolution of algorithms, analysis tools, and simulation workflows. This migration is intended to support a new major release of the platform, to be made available following the publication of the Gnomon v1.0 scientific article, and to prepare the integration of new modeling, analysis, and simulation tools within the platform in the course of 2026.

### 6.1 Latest software developments

#### 6.1.1 bvpy

**Name:** bvpy

**Keywords:** Finite element modelling, Python, Partial differential equation

**Functional Description:** Bvpy is a python library, based on FEniCS, Gmsh & Meshio, to easily implement and study numerically Boundary Value Problems and Initial Boundary Value Problems through the Finite Element Method.

**Release Contributions:** Since v1.1.0 (March 2024), bvpy has introduced major new features for growing tissue simulations. v1.3.0 (January 2025) introduced a new hyperelasticity API based on potential energy models, making it easier to implement new material behaviors. This release also added morphoelasticity and growth support, with flexible growth laws (constant rate, time-dependent, strain-dependent, and heterogeneous patterns across subdomains). Domain handling was improved with direct .msh file loading, and boundary conditions now accept scalar, vector, and tensor values. v1.4.0

(November 2025) added tools to interact more easily with solver parameters and introduced tensor field visualization. v1.4.1–v1.4.3 (November–December 2025) improved visualization, expanded the documentation, and fixed critical issues related to meshes and growth computations.

A new v2.0 release is currently under development, its main change will be the migration from FEniCS to FEniCSx.

**News of the Year:** Since v1.1.0 (March 2024), `bvpy` has been extended with a unified framework for the morphoelastic modeling of growing tissues, enabling the explicit coupling of nonlinear elasticity and growth laws. In line with morphoelastic approaches, growth is treated as an intrinsic contribution to deformation, distinct from the elastic response, allowing for the emergence of residual stresses. The library now provides flexible growth laws—time-dependent, strain-dependent, or spatially heterogeneous—coherently integrated into energy-based hyperelastic material models.

**URL:** <https://gitlab.inria.fr/mosaic/bvpy>

**Contact:** Olivier Ali

**Participants:** Gonzalo Revilla Mut, Olivier Ali, Elsa Gascon, Manuel Petit

### 6.1.2 `dxtr`

**Name:** `dxtr`

**Keywords:** Discrete exterior calculus, Computational geometry

**Scientific Description:** At the core of the `dxtr` library lie two main data structures implementing respectively the concepts of simplicial complex and cochain. The library also encompasses a collection of operators (differential, geometrical, topological) that can be applied to these data structures to simulate differential geometry problems, formalized through exterior calculus.

**Functional Description:** A Python library implementing data structures and algorithms to handle simplicial complexes and perform discrete exterior calculus.

**Release Contributions:** It is the first official release of the library related to its acceptance for publication in JOSS and the corresponding repository on ZENODO.

**News of the Year:** This year we designed the major principles of the library: we implemented the core data structures and algorithms and we set the general architecture. We wrote unit tests and proper documentation in parallel of this development. We also started to write detailed tutorials based on basic use cases.

**Contact:** Olivier Ali

**Participants:** Olivier Ali, Chao Huang

### 6.1.3 `TimageTK`

**Name:** Tissue Image ToolKit

**Keywords:** 3D, Image segmentation, Fluorescence microscopy, Image registration, Image processing, Image filter

**Functional Description:** `TimageTK` (Tissue Image Toolkit) is a Python package dedicated to image processing of multicellular architectures such as plants or animals and is intended for biologists and modelers. It provides grayscale or labeled image filtering and mathematical morphology algorithms, as well as image registration and segmentation methods.

**Release Contributions:** **\*\*Automated pipelines (command-line)\*\*** Extension and consolidation of command-line pipelines covering lineage, segmentation, quantitative analysis via spatio-temporal graphs, multi-angle fusion, preprocessing, as well as data import and export to and from MorphoNet and dataset creation. These pipelines now support 3D+t temporal sequences with multi-channel and multi-angle data.

**\*\*Graphical interfaces (manual steps)\*\*** Development of dedicated graphical interfaces for steps requiring human interaction, including preprocessing, visualization, spatial and temporal 3D registration, dataset creation, and lineage inspection/correction, enabling interactive control and fine-grained validation of results.

**\*\*Algorithmic building blocks\*\*** Refactoring and improvement of core algorithmic components, including the restructuring of spatio-temporal graphs, enhanced multi-angle fusion, modernization of segmentation methods with bio-image/bioimageio interoperability, and enriched quantitative analysis of geometric and genetic cellular properties.

**\*\*Visualization and memory management\*\*** Integration of PyVista as the visualization backbone, also enabling fast extraction and generation of volumetric and surface tissue meshes. Upgrade related to the new memory management in vt/vt-python, relying on zero-copy mechanisms to improve performance.

**\*\*Software maintenance\*\*** Continuous strengthening of testing, continuous integration, and documentation.

**URL:** <https://mosaic.gitlabpages.inria.fr/timagetk/index.html>

**Contact:** Jonathan Legrand

**Participants:** Jonathan Legrand, Guillaume Cerutti, Manuel Petit

#### 6.1.4 vt

**Keywords:** Image analysis, Image processing, Image registration, Registration of 2D and 3D multimodal images, Image filter, Biomedical imaging, Medical imaging

**Functional Description:** 2D and 3D image processing library

**Release Contributions:** **\*\*API and memory semantics\*\*** Stabilization of the vtImageBridge through a unified memory model: non-owning inputs (View) and owning outputs (Move), ensuring safe zero-copy interoperability and reliable usage in downstream libraries (vt-python, timagetk)

**\*\*CI, tests, and documentation\*\*** Improvements to cross-platform CI, strengthened test coverage, and clearer documentation, with better control over dependencies and release processes.

**Contact:** Grégoire Malandain

**Participants:** Manuel Petit, Grégoire Malandain, Jonathan Legrand

#### 6.1.5 vt-python

**Keywords:** Image analysis, Image filter, Image registration, Registration of 2D and 3D multimodal images, Image processing, Biomedical imaging, Medical imaging

**Functional Description:** Python interface for some functionalities of the vt image processing library.

**Release Contributions:** **\*\*API, memory, and core semantics\*\*** Stabilized the vt-Python bridge by defining a clear ownership model for NumPy/Image conversions, separating view (borrow) and move (transfer) semantics. Enabled robust zero-copy interoperability based on vt >= 1.7.x, while preserving an explicit deep-copy option when required.

**\*\*Packaging, releases, and quality\*\*** Structured releases (1.3.x–1.4.1), migrated to a PEP 517 / pyproject.toml build system, refined dependency constraints, and hardened cross-platform conda CI with expanded tests focused on ownership semantics.

**Contact:** Grégoire Malandain

**Participants:** Manuel Petit, Jonathan Legrand

**Partner:** Inria

### 6.1.6 TimageTK\_geometry

**Name:** Tissue Image ToolKit - Geometry

**Keywords:** 3D, Computational geometry, Image analysis, Mesh generation

**Functional Description:** TimageTK - Geometry provides a suite of tools for the reconstruction and quantitative analysis of 3D multicellular tissues for which the common trait is to rely on meshes (essentially triangular meshes). The applications range from the estimation of tissue surface curvatures to the quantification of fluorescence microscopy image signal at the level of cell-cell interfaces, or the reconstruction of 3D simplicial complexes reflecting the topology of the tissue.

**Release Contributions:** The version 1.0 structures the contents of the library into 4 sub-packages: extraction of image surface meshes, reconstruction of tissue topological complexes, computation of cell and wall features and quantification of signal intensity.

It notably unifies the API for tissue complex reconstruction functionalities, harmonizing the high-level functions of each algorithm, and providing a consistent class API.

**News of the Year:** In addition to the DRACO and GRIFONE methods, the FENICE algorithm, that relies on iterative edge collapse operations, was added to the tissue complex reconstruction sub-package. It required more generic tools that operate a surface mesh of the tissue where vertices carry the cell label information, which were included in the image mesh sub-package.

A major effort has also been put on the documentation website, providing extensive in-code documentation of the library's components, but also detailed examples on how to use `timageTk_geometry` for specific tasks.

**URL:** [https://mosaic.gitlabpages.inria.fr/timageTk\\_geometry](https://mosaic.gitlabpages.inria.fr/timageTk_geometry)

**Contact:** Guillaume Cerutti

**Participant:** Guillaume Cerutti

### 6.1.7 cellcomplex

**Name:** cellcomplex

**Keywords:** Polyhedral meshes, 3D

**Functional Description:** The cellcomplex library is a Python library that allows manipulating 2D or 3D multicellular complexes, with the study of plant tissues as a main application. It is mostly structured around a data structure that is used to represent such complexes as incidence graphs of dimension 2 or 3, and provides several key functionalities:

- \* The creation of structures from more basic representation (polygons of points for instance), from some geometrical primitives (2D or 3D) and the generation of synthetic regular or irregular grids, allowing notably the simulation of tissues.
- \* The computation of topological and geometrical properties on the multicellular complex structures, including notably useful computations on triangle meshes, a specific case of complexes with simplicial faces (areas, normals, triangle eccentricity, curvature estimator).
- \* The edition of structures by local topological operations, notably in the case of triangle meshes (edge flip, subdivision, vertex insertion) and multi-criteria geometrical optimization processes and isotropic remeshing.

\* The import and export in various standard file formats for geometries (.obj, .ply, .msh) and notably in the standard format defined by the community of plant tissue modelling (PLY, Sainsbury Computational Workshop 2015).

**Contact:** Guillaume Cerutti

**Participant:** Guillaume Cerutti

### 6.1.8 tides

**Name:** TIDES - Transport-Induced Dynamics Equation Simulator

**Keywords:** Modelization and numerical simulations, Biological tissue, Transport model

**Functional Description:** TIDES allows to easily define cellular level ordinary differential equation (ODE) systems over the cells of a tissue represented as a cellular graph, to solve them numerically and to visualize the resulting dynamics. It notably makes it easy to include cell-to-cell exchanges in the models through a unified handling of cell and interface quantities, which makes it particularly suited to simulate transport-based processes.

**Release Contributions:** The definition of a model in TIDES relies on two main components: \* A representation of a tissue (graph) state with variables living either on the cells (graph nodes), cell interfaces (graph edges) or on either sides of a cell interface (graph oriented edges). This is provided by the 'state' module. \* A system of ODEs describing the temporal evolution of these variables as functions of all the state variables. This is provided by the 'rhs' module.

With this, it is possible to create a model, provided by the 'model' module, in which a solver relying on the 'scipy' library computes efficiently the dynamics of the variables, which are stored as trajectories to be visualized or analyzed.

This initial version of the TIDES package relies essentially on the 'cellcomplex' library to represent and visualize the state of the tissue, but the core simulation machinery has been designed to be agnostic of the tissue representation, manipulating state variables as simple data arrays.

**News of the Year:** The generic functionalities from the code developed by L. Duguet in the course of his Ph.D have been gathered into a new Python package. While primarily used to simulate auxin transport by PIN exporter proteins, it is flexible enough to model a wide range of transport-induced processes.

**URL:** <https://mosaic.gitlabpages.inria.fr/tides>

**Contact:** Guillaume Cerutti

**Participants:** Landry Duguet, Guillaume Cerutti, Christophe Godin

### 6.1.9 Collects

**Name:** Collects

**Keywords:** Image processing, 2D, Spatio-temporal data, Computational biology

**Functional Description:** Collects is a Python-based biological image analysis software enabling automated segmentation, tracking, and extraction of morphological and dynamical descriptors from static 2D images and time-lapse sequences, without manual annotation.

**Release Contributions:** • Automated quantification of growth, motion, and morphology from 2D images and time-lapse sequences (2D + t). • Robust segmentation and tracking adapted to heterogeneous experimental conditions (variable contrast, complex morphologies, uncontrolled illumination). • Integrated extraction of a wide range of geometric, kinematic, and morphological descriptors without manual annotation. • Support for complex morphologies, including network-like structures through graph reconstruction and dedicated topological analysis. • Dual architecture combining an interactive graphical user interface with a Python API for exploratory analyses and automated processing. •

Standardized export of quantitative results, ensuring reproducibility and compatibility with conventional statistical analysis tools.

**News of the Year:** A first official stable release (v1.0.0) is scheduled for early 2026, marking a key milestone in the project's maturation. This release will be accompanied by a submission to the Journal of Open Source Software (JOSS).

**URL:** <https://aurele-b.github.io/Collects/>

**Contact:** Aurèle Boussard

**Participants:** Manuel Petit, Aurèle Boussard

**Partner:** CNRS

#### 6.1.10 Riemannian L-systems

**Name:** Riemannian L-systems: modeling form development in curved spaces

**Keywords:** Differential geometry, Fractal, Curved spaces, Declarative language

**Functional Description:** Classical L-systems are a computational formalism that makes it possible to construct a large variety of forms in a Euclidean space using a combination of (Euclidean) turtle geometry and rewriting rules. Riemannian L-systems can be seen as an extension of the concept of L-systems to curved spaces. With Riemannian L-systems, forms can be programmed as simply as in Euclidean space, but the instructions are automatically interpreted in specified curved spaces using built-in differential geometry operators.

**Release Contributions:** This version upgrades the computations of geodesics in the case of boundary value problems (BVPs).

**News of the Year:** In addition to the work on BVPs, there has been corrections of minor bugs, an upgrade of a large number of L-Py examples, and significant updates of the documentation.

**URL:** <https://gitlab.inria.fr/cgodin-dev/RiemannianGeometry/riemannien-l-systems>

**Publication:** [hal-04535182](https://hal.archives-ouvertes.fr/hal-04535182)

**Contact:** Christophe Godin

**Participants:** Christophe Godin, Frédéric Boudon

**Partner:** CIRAD

#### 6.1.11 Gnomon

**Name:** Gnomon

**Keywords:** 4D, Modelization and numerical simulations, Finite element modelling, Computational biology, Data visualization

**Scientific Description:** Gnomon is a user-friendly computer platform developed by the Mosaic team for seamless simulation of form development in silico. It is intended to be a major tool for the team members to develop, integrate and share their models, algorithms and tools. In Gnomon, a developing form is represented at any time by a central data-structure that contains topological, geometric, genetic and physiological information and that represents the state of the growing form. Flexible components (plugins) make it possible to up-load or to create such data-structures, to program their development, to analyze, visualize them and interact with them in 3D+time.

**Functional Description:** Gnomon is a plugin-based computational platform for the analysis and simulation of morphogenesis. It relies on a scalable software architecture based on the dtk kernel developed by the group of software engineers (SED) from the Sophia-Antipolis Inria Center. The development of Gnomon aims at answering four main challenges:

- \* Provide an easily accessible computational tool for the exploration of morphogenesis, by focusing on the ergonomics of the user interface, the deployability of the software and the availability of the documentation.
- \* Give access to powerful resources for manipulating dynamical forms, through the inclusion of algorithmic tools developed by the team (on image sequences of multicellular tissues or collections of branching forms) as plugins, and an interactive visualization framework allowing the exploration in space in time.
- \* Ensure the interoperability of computational libraries within the platform and its extensibility by a generalized plugin-based architecture (facilitated by the dtk framework) for algorithms, visualizations and data structures, enabling the members of the team and future users to feed the platform with their own C++ and Python libraries.
- \* Bridge the gap between experimental data and computational simulations by offering the possibility to go from one to the other in the same platform in a nearly transparent way, thanks to a common dynamical system framework integrated to the core of the platform.

Gnomon project organization:

- \* Project leader: Christophe Godin
- \* Software development coordinators: Manuel Petit, Guillaume Cerutti
- \* dtk coordinators: Julien Wintz, Thibaud Kloczko
- \* Plugin coordinators: Jonathan Legrand, Romain Azais, Olivier Ali, Frédéric Boudon
- \* Diffusion coordinator: Teva Vernoux

**Release Contributions:** This major version (v1.0) marks the release of a platform that can start to be used autonomously by non-computer scientists. The main new feature is the addition of a notion of project that gathers all the generated files (pipelines, plugins) in a shareable folder, while continuously saving the state of the user session so that no work is lost on shutdown. Other developments deriving from the alpha-testing phase include a more homogeneous behaviour of 2D and 3D views, a GUI component to replay pipelines on different input data, clearer and more abundant information in the interface, and a simplified command-line tool for installation and updates. Moreover, the documentation website was entirely redesigned to better guide the new users in their discovery of the platform.

**News of the Year:** During the past year, Gnomon has benefited from a coordinated consolidation effort involving several core libraries extensively used in the plugins of the platform, to stabilize and clarify the shared APIs and improve coherence and interoperability. In parallel, a significant effort was devoted to strengthening software quality, with major improvements to documentation and test coverage for both the core of the platform and key plugins, supported by reinforced continuous integration workflows. A software article presenting the v1.0 of the platform is currently in preparation and will be submitted for scientific publication in early 2026.

Following the integration of Manuel Petit in the coordination team, and while considering the technological migration of the platform, we have initiated a substantial revision of the software architecture, which will be the subject of a joint workshop with the SED of Lyon to determine the evolution strategy for the Gnomon platform for the next four years.

**URL:** <https://gnomon.gitlabpages.inria.fr/gnomon/>

**Contact:** Christophe Godin

**Participants:** Manuel Petit, Olivier Ali, Frédéric Boudon, Tristan Cabel, Guillaume Cerutti, Christophe Godin, Jonathan Legrand, Arthur Luciani, Grégoire Malandain, Karamoko Samassa

## 7 New results

### 7.1 Dynamical characterization of morphogenesis at cellular scale

**Participants:** Olivier Ali, Guillaume Cerutti, Elsa Gascon, Christophe Godin, Anamaria Kiss, Jonathan Legrand, Manuel Petit.

- Related Research Axes: RA1 (Representation of biological organisms and their forms in silico) & RA3 (Plasticity & robustness of forms)
- Related Key Modeling Challenges: KMC3 (Realistic integrated digital models)

Modelling morphogenesis demands an exploration of the intricate interconnections between the spatial and temporal scales that govern developing organisms. Central to this endeavor are fundamental questions: does the observed robustness of morphogenesis arise from highly conserved cellular properties, or does it emerge as a macroscopic phenomenon? Addressing these questions requires precise, quantitative analyses of complex, dynamic 3D structures.

At the cellular scale, this pursuit presents both technical challenges and theoretical inquiries:

- How can we characterize and track the evolving shapes of cells within tissues—or tissues within organs?
- How might these morphological changes couple with gene expression dynamics?
- How should we define and quantify cell-scale variability in morphogenesis, both within and across species?

This year, our team has advanced this field with several key contributions:

#### Impact of single-cell dynamics on moss phyllotaxis

In flowering plants like *Arabidopsis thaliana*, the Shoot Apical Meristem (SAM) is a multicellular structure where complex cellular dynamics regulate lateral organ initiation, ultimately establishing phyllotaxis. In contrast, the moss *Physcomitrium patens* employs a single Apical Cell (AC) to control leafy shoot development. The simplicity of this system (fewer cells and layers) offers a direct link between AC division orientation and the resulting phyllotactic arrangement.

To investigate this process, we analyze time-lapse images of young moss shoots, where cells are segmented, lineage-traced, and labeled by type. This cellular dataset allows us to explore how the geometry of the AC and surrounding primordia cells influences phyllotaxis. Specifically, we monitor cell shape descriptors (Guillaume Cerutti) and quantify 3D division angles over time (Jonathan Legrand).

Building on last year's findings and incorporating new data, we refined our quantification methodology to achieve greater stability in determining the main axis of the apical cell. The development of new visualization tools further enabled us to validate our approach, culminating in a comprehensive analysis of the entire database. This database comprises time-lapse acquisitions of growing *Physcomitrium patens* buds, captured at intervals of two or four hours, and generated by Laure Mancini (postdoctoral researcher).

This work is conducted in collaboration with Laure Mancini, Yoan Coudert, and Teva Vernoux from the Signal team at the RDP Lab.

#### Quantification and spatialization of cell wall signals in root cells

Cell walls play a central role in plant morphogenesis, serving as both structural and regulatory elements that mediate growth and development. Spatial variations in cell wall-related signals are particularly important to understand how plants coordinate morphogenesis at the cellular and tissue scale. To characterize precisely this spatialized information, we developed image processing pipelines using the *TimageTK* library [6.1.3](#) to enable the segmentation of cell walls and the quantification of fluorescent signals from high-resolution confocal microscopy images.

Focusing on *Arabidopsis* root cells, we are analyzing how cell wall signals vary depending on several factors. First, we investigated how the orientation of cell walls relatively to the root axis influences signal intensity, revealing potential anisotropies in their spatial distribution. Second, we analyzed how signals evolve with the age of a cell wall, relative to the timing of cell division, providing insights into the dynamic changes occurring in cell walls as they mature. Finally, we studied the distribution of signals at different distances from the cell wall, highlighting spatial patterns that may reflect local differences in wall composition or signaling activity.

This work is being conducted by Manuel Petit in collaboration with Antoine Chevallier, Ph.D. student, supervised by Charlotte Kirchhelle from the MechanoDevo team of RDP Lab. The tools developed during this work will be integrated into existing libraries to facilitate their use by other researchers. An article detailing these findings is currently being written for submission in 2026.

### **Constructing atlases of development at cellular scale: a practical usecase**

Developing digital atlases of organism or organ development is a complex challenge for tissues that do not present a stereotyped cellular layout, as it is the case for most plant organs. For instance, to generate a cell-based atlas representing the development of a floral meristem of *Arabidopsis thaliana*, we had to choose a single representative flower template, on which the spatio-temporal binary expression patterns of 27 genes were then introduced manually [9].

To proceed further, as the manual building of a cellular template remains a bottleneck of the method, we aim to automatize the construction of genetic atlases from several time-lapse image acquisitions displaying both cell interface markers and genetic reporters. This automation involves solving a series of key algorithmic challenges: (1) segmenting cells in 3D data, (2) tracking cells over time, and (3) integrating genetic information into the atlas. The integration of genetic data requires two essential substeps: (3.1) spatio-temporal alignment of time-lapse sequences from different individuals and (3.2) projection of genetic information onto a common template or between individuals.

Capitalizing on the Ph.D. work of Manuel Petit, where each of these algorithmic aspects has been methodically studied and addressed [43], we have been focusing on integrating the implementation of the developed methods into the *TimageTK* library 6.1.3. This library now centralizes the tools necessary to perform all the key algorithmic steps, hence enabling easier construction of complex pipelines. In the same spirit, the segmentation and tracking tools have also been made available as plugins in the *Gnomon* platform 6.1.11, to make these methods accessible to a broader audience.

A concrete application of these tools is currently being carried out in the context of a collaboration with Feng Zhao with the aim of constructing a genetic atlas of the *Arabidopsis thaliana* anther (tip of the stamen, the male reproductive organ). Starting from raw confocal time-lapse images, we are starting to combine the various integrated methods to build 3D+T cellularized templates with minimal recourse to hand-crafted, problem-specific code. The quality of the reconstructed templates could be conveniently assessed by collaborators through their upload on the MorphoNet web-based 4D browser [38] to provide feedback while developing the tools. By leveraging the automation brought by *TimageTK* and *Gnomon*, this collaboration demonstrates the practical benefits of these atlas construction methods for actual biological studies.

### **Reconstructing signal intensity profiles along the root axis**

For tissues with a less complex shape, and when the cellular resolution is not particularly relevant for the addressed biological question, it is possible to rely on simple geometric transformations to combine information coming from various individuals. For instance the root of *Arabidopsis thaliana* has a globally cylindrical shape (with varying radius) and exhibits symmetries that allow to consider tissue-level patterns as functions of the position along the main axis of the root and the radial distance in the orthogonal plane.

We have been applying this idea in different biological contexts. We generally start by quantifying the cell-level intensities of nuclei-targeted reporters in 3D confocal images of roots, using tools now integrated in the *TimageTK* library 6.1.3. Then by approximating the main axis of the root, we can recover the axial and radial coordinates of each detected cell nucleus. Applying the same process on several individuals allows to superimpose, in a reference 2D space, cells that lie at the same relative position in the root, therefore enabling spatialized population statistics.

This framework has been developed by Jonathan Legrand, Guillaume Cerutti and Manuel Petit and applied either to quantify the differences in expression patterns of a muted promoter compared to its non-muted version [17] (in collaboration with Raquel Martin-Arevalillo and Teva Vernoux from the Signal team of the RDP Lab) or to evidence the efficiency of an inducible CRISPR system through its effect on affected and non-affected histone marks (in collaboration with Virginie Battu and Annick Dubois from the EpiChromDev team of the RDP Lab).

### Numerical reconstruction of cellular layers of plant seeds

During morphogenesis, plant organs acquire stereotyped shapes through complex biological processes including cellular growth, an irreversible expansion of the cell wall leading to tissue deformation. However, the importance of the cellular organization of multi-layered tissues for the mechanical control of growth directions, and thus the emergence of anisotropic shapes, is not fully understood. Taking as a model organ the seed of *Arabidopsis thaliana*, where various external layers are known to control the growth across development [4], we propose to study the contribution of the different cell layers to morphogenesis.

To investigate this question, we reconstruct numerically the full 3D layered structure of Arabidopsis seeds, through a pipeline going from confocal microscopy to FEM-ready meshes. Combining multi-angle acquisitions of seeds, we perform a 3D segmentation of the reconstructed image (using algorithms from the *TimageTK* library 6.1.3) from which we extract consecutive 2D simplicial complexes of cell adjacency (using tools from the *TimageTK-Geometry* library 6.1.6) to obtain a natural discretization of each layer of the tissue.

To represent tissue topology and geometry in 3D, we want to reconstruct a 3D simplicial complex consistent with the 2D triangulations of consecutive layers. This tetrahedral mesh is aimed for 3D mechanical simulations either in *BVPy* 6.1.1 or *Dxtr* 6.1.2, and its elements must therefore be sufficiently regular to ensure numerical stability in finite element method (FEM) and discrete exterior calculus (DEC). To achieve this, we developed an front-propagation algorithm that iteratively builds a complex taking into account both the cell connectivity and tetrahedra quality. We compare our results with meshes generated using state-of-the-art methods (TetGen) assessing both consistency with real cell adjacencies and element quality.

This work was carried out by Elsa Gascon, who defended her Ph.D. in december 2025 under the supervision of Olivier Ali in the context of the Inria AEx Discotik (see Section 9.1). Guillaume Cerutti was providing technical expertise and guidance on this project.

### Tracking seed growth dynamics under osmotic perturbations

The size and shape of the seed of *Arabidopsis thaliana* are largely determined by two inner cell layers (forming the outer integument of the seed coat) that develop distinct mechanical behaviors. These behaviors arise from differences in the composition and organization of their cell walls, and they are essential for locally regulating the growth of the organ. However, directly probing these mechanical properties is virtually unfeasible, especially for inner tissues. As a result, biologists infer them indirectly by analyzing cellular responses to controlled mechanical perturbations. For instance, they use changes in osmotic conditions, which differentially affects the turgor pressure (the main driver of seed growth) in the inner cell layers.

Relying on time-lapse 3D acquisitions of seeds exposed to hypo- or hyper-osmotic environments, the idea is to monitor the cell-level deformations over time and to interpret them in terms of mechanical properties. For that purpose, we used the *Gnomon* computational platform 6.1.11 and plugins based on *TimageTK* library 6.1.3 to develop a segmentation and tracking pipeline that follows each cell over time and measures its extension along the main axes of the seed. It relies on an approximation of the seed shape by a 3D ellipsoid to position a local reference frame within each cell. This approach provides a quantitative framework to characterize the mechanical properties of cells from inner layers during organ development.

This work is being conducted by Guillaume Cerutti in collaboration with Jeanne Braat and Benoît Landrein from the SeedDev team of the RDP Lab.

### Reconstruction of pollen tube trajectories on papilla surfaces

To fertilize the ovule during reproduction, the pollen grains of flowering plants first land on papillae, elongated cells located at the tip of the stigma, before "germinating" by forming a tube that will follow the surface of the papilla cell down to the ovule. Recent work mixing experimental and modelling approaches [21] showed

that the geometry of the papilla cell has a major influence on the guidance of the pollen tube, and therefore on the reproductive success.

We want to refine the mechanical models of pollen tube guidance, and quantify deviation of pollen tube trajectories from geodesic curves by using more realistic papilla geometries, hence we are working with 3D confocal images of *Arabidopsis* papilla cells fertilized with pollen grains. Relying on the *TimageTK* library 6.1.3 accessed through the Gnomon computational platform 6.1.11, we developed an image analysis pipeline that segments a papilla cell and extracts its surface as a 3D mesh.

We are now focusing on the extraction of the pollen tube trajectory on that surface, for which the microscopy images raise various problems (missing parts, self-contact when coiling). To address them, we are developing an optimization approach that aims to fit a Riemannian model of the trajectory on the curved surface to the pollen image information, based on the estimated landing point and initial direction of the pollen tube. This approach will rely on the library implementing Riemannian L-Systems 6.1.10 developed by Christophe Godin. The obtained trajectories will allow to quantitatively compare pollen tube trajectories predicted by mechanical models on realistic papilla geometries directly with the experimental data.

This work is carried out in collaboration with Florian Alonso (engineer, co-supervised by Guillaume Cerutti), Ingrid Revel and Isabelle Fobis-Loisy from the SiCE team of the RDP Lab.

## 7.2 Reconstruction of macroscopic forms from images and characterization of their variability

**Participants:** Julien Derr, Christophe Godin, Annamaria Kiss, Jonathan Legrand, Lucie Poupardin.

- Related Research Axes: RA1 (Representations of forms *in silico*) & RA3 (Plasticity & robustness of forms)
- Related Key Modeling Challenges: KMC3 (Realistic integrated digital models)

Studying the variability of macroscopic forms arising from organ or organism development necessitates the quantification of phenotypic traits across large populations. To achieve this, we propose the creation of digital organ models, which in turn requires the development of robust acquisition and reconstruction methods.

Acquisition methods are not universally accessible and often demand dedicated research and development to optimize data quality and streamline workflows. The design of custom acquisition methodologies is thus a critical step, as it directly influences the integrity and utility of data for subsequent digital reconstruction.

Digital reconstructions enable the precise identification of organs, quantification of macroscopic features, and analysis of their spatial—and potentially temporal—distribution. A central challenge lies in developing algorithms to analyze organismal structure and quantify phenotypic traits, as well as designing data frameworks that support future modeling efforts. Additionally, establishing metrics and statistical tools to define notions of morphological distance or averages is essential for comparing reconstructions and generated models.

Prior knowledge can significantly enhance this process. Realistic synthetic models of forms can guide reconstruction algorithms and serve as benchmarks for performance evaluation. Consequently, the automatic inference of computational representations of forms or organ traits from images emerges as a pivotal step.

These computational representations facilitate the analysis of morphological variation at multiple scales—within populations, across species, or between species—with applications ranging from species identification to the estimation of genetic or environmental robustness.

### Digital Reconstruction and Phenotypic Quantification in Plant Morphology.

The digital reconstruction of branching architectures and the quantification of phenotypic traits—such as internode lengths, organ angles, and leaf shapes—are essential for analyzing plant morphology at the population scale.

While the ROMI project concluded in 2022, ongoing efforts by members of the "Signals in Developmental Dynamics" and MOSAIC teams continue to advance 3D plant phenotyping. Their work focuses on refining

the 3D Plant Phenotyping Platform, which integrates the Plant Imager (a robotic scanner) and the Plant 3D Vision pipeline (for reconstruction and analysis). This research is now part of the 4D Plants project, funded by the ANR, with active participation from Jonathan Legrand, Fabrice Besnard and Arthur Luciani (Signals in Developmental Dynamics team).

In 2025, Arthur Luciani, an engineer specializing in computer vision and robotics, joined the team. His primary contributions include developing the third iteration of the Plant Imager, addressing key limitations of previous versions. His improvements span:

- A new tactile user interface controlling the Plant Imager robot,
- Enhanced communication between system components,
- Increased platform modularity, enabling multi-camera acquisition.

On the software side, the shift to a multi-camera system necessitated adjustments to our usage of the structure-from-motion algorithm, also led by Arthur Luciani. Additionally, Jonathan Legrand overhauled the database library, implementing role-based access control and data ownership management. The database now operates as a fully REST-compatible API, supported by dedicated server-client architecture for remote interaction. To streamline data acquisition, Jonathan Legrand developed a Dash-based WebUI, ensuring seamless integration and an improved user experience.

The people involved in this project aim to deploy all services—database, acquisition WebUI, and controller—with secure authentication and encryption, delivering a self-contained, open-source solution for biologists. However, this endeavor has proven more complex than anticipated, requiring further development.

### Characterization of 3D plant shape and texture at the organ scale

Complementary to the full 3D reconstruction of plant architecture (ROMI project), we have been developing a platform to characterize plants in 3D at the organ scale coordinated by Julien Derr (typically at leaf scale). We can have access to the geometry and the texture of the leaf with high spatial (millimetric) and temporal (seconds) resolution. This will make it possible to quantify in 3D the rich spatio-temporal growth patterns of leaves observed during unfolding [47, 46, 32, 22], where “fast” elastic phenomena (buckling) or ample (nutational) motions are occurring.

In collaboration with computer vision scientists from Université de Strasbourg (Franck Hetroy-Wheeler and collaborators), we built a multicamera set up [48]. The set up is installed at ENS de Lyon in the new M8 building dedicated to plant growth.

Lucie Poupardin started her PhD in October 2022. During her first year, Lucie set up and calibrated the platform. During her second year, Lucie used this platform to research the kinematics of leaf unfolding. She evidenced leaf growth synchronized to geometry changes in the leaf. In 2025, Lucie developed a phenomenological model recovering her experimental results and indicating that growth in leaves might be induced by mechanical stress. Lucie will defend her PhD in March 2026.

Additionally, we generated data (multi view time lapse photography) of leaf unfolding thanks to the set up. Steve de Rose started a PhD, in 2024, in computer science in Unistra, under the supervision of Franck Hetroy-Wheeler, and is still analysing these data.

### 3D morpho-space of sepal geometry

How robust 3D organ shape emerges during morphogenesis is a fundamental question in biology. Addressing this question requires a comprehensive quantification of organ geometry in 3D. To tackle these issues, we considered the sepal of *Arabidopsis* as a model. Using a unique pipeline, allowing to recover 3D sepal morphology, we analysed fifteen mutants affected in different pathways and reported the results in the publication [13].

The pipeline starts with automatic segmentation and extraction of geometrical parameters from confocal images of whole sepals, based on the *TimageTK* library 6.1.3 developed in the team. The results of a Principal Component Analysis of the extracted data reveal sepal curvature as an important parameter accounting for variations in sepal morphology within genotypes. Unexpectedly, despite genetic homogeneity of the wild-type plants and reproducible culture conditions, we found a significant level of variability in sepal

morphology. Our data also show that sepal shape from wild-type plants is more robust (less variable) than sepal size, hinting to a possible selective pressure on shape parameters.

This work was performed in tight collaboration with Françoise Monéger and Virginie Battu from the "Epigenetics, chromatin and development" team of the RDP lab.

### Learning to Infer Parameterized Representations of Plants from 3D Scans

Plants frequently contain numerous organs, organized in 3D branching systems defining the plant's architecture. Reconstructing the architecture of plants from unstructured observations is challenging because of self-occlusion and spatial proximity between organs, which are often thin structures. To achieve the challenging task, we propose an approach that allows to infer a parameterized representation of the plant's architecture from a given 3D scan of a plant. In addition to the plant's branching structure, this representation contains parametric information for each plant organ, and can therefore be used directly in a variety of tasks. In this data-driven approach, we train a recursive neural network with virtual plants generated using a procedural model. After training, the network allows to infer a parametric tree-like representation based on an input 3D point cloud. Our method is applicable to any plant that can be represented as binary axial tree. We quantitatively evaluate our approach on *Chenopodium Album* plants on reconstruction, segmentation and skeletonization, which are important problems in plant phenotyping. In addition to carrying out several tasks at once, our method achieves results on-par with strong baselines for each task. We apply our method, trained exclusively on synthetic data, to 3D scans and show that it generalizes well. This work has been submitted to the vision conference CVPR [25].

This work was performed in tight collaboration with Stéfanie Wuhrer from Inria Grenoble. Stéfanie and Christophe Godin co-supervise the PhD thesis of Samara Ghrer on plant phenotyping using deep learning methods.

### 7.3 Analysis and simulation of tree data

**Participants:** Romain Azaïs, Christophe Godin, Frédéric Boudon (*External Collaborator*).

- Related Research Axes: RW1 (Representations of forms in silico)
- Related Key Modeling Challenges: KMC1 (A new paradigm for modeling tree structures in biology)

Tree-structured data naturally appear at different scales and in various fields of biology where plants as well as blood vessels for example may be described by trees. In the team, we aim to investigate a new paradigm for modeling tree structures in biology in particular to solve complex problems related to the representation of biological organisms and their forms in silico.

In previous years, we investigated the following questions linked to the analysis of tree data. (i) How to control the complexity of the algorithms used to solve queries on tree structures? For example, computing the edit distance matrix of a dataset of large trees is numerically expensive. (ii) How to estimate the parameters within a stochastic model of trees? And finally, (iii) how to develop statistical learning algorithms adapted to tree data [2, 8]? In general, trees do not admit a Euclidean representation, while most of classification algorithms are only adapted to Euclidean data. Consequently, we need to study methods that are specific to tree data.

#### Statistical inference: the case of Galton-Watson models

In the team, the question of statistical inference of probabilistic tree models has been explored in the context of Galton-Watson models. Spinal-structured trees are two-type Galton-Watson models parameterized by a birth distribution  $\mu$  and a bias function  $f$ , generalizing the well-known Kesten's tree. These trees feature an infinite spine composed of special nodes, to which Galton-Watson trees of normal nodes (with birth distribution  $\mu$ ) are attached. The structure is defined by a biased offspring distribution for special nodes, derived from  $\mu$  through  $f$ . This model offers a flexible framework for studying branching processes conditioned to survive. We

investigate the statistical properties of spinal-structured trees, focusing on the problem of estimating  $\mu$ ,  $f$ , and the unobserved types of nodes from a single observation of the tree up to a fixed generation  $h$ . A maximum likelihood estimation framework is developed, enabling the estimation of  $\mu$  without type observations, while estimation of  $f$  requires partial type information. Theoretical results establish the convergence of these estimators under various growth regimes of the tree, highlighting the influence of tree structure and growth rate on parameter recoverability.

The motivation for this work is twofold: to contribute to the theoretical understanding of type estimation in multi-type Galton-Watson processes and to provide a statistical framework for testing whether population data have been conditioned to survive. By introducing the parameterization  $(\mu, f)$ , we generalize Kesten's tree and enable a rigorous comparison between survival-conditioned and unconditioned models. Our results demonstrate that spinal-structured trees are not only a powerful tool for analyzing survival-conditioned processes but also serve as a stepping stone toward solving broader challenges in multi-type Galton-Watson estimation with unobserved types. Through theoretical guarantees and practical algorithms, we hope that this study lays the groundwork for advancing the statistical analysis of complex branching processes. This work has been published this year in *Journal of Applied Probability* [12].

### **Hierarchical Timeline Warping (HTW): a generic method to design realistic plant architecture models**

Virtual models of plant architecture are needed for diverse applications in developmental biology, agronomy, botany or computer graphics. They can be used for hypothesis testing, data annotation and augmentation associated with deep-learning training or for producing photorealistic rendering of plants. To match the increasing needs of these applications in precision and realism, virtual plants with increasing realistic details are required. However, the design of such detailed models remains a complex task and new techniques are required to ease this process.

To address this complexity, we developed a timeline-based approach, where the hierarchy of plant parts is described by a corresponding hierarchy of developmental timelines. For each simple or composed organ, a reference (normalized) timeline is defined [36]. Different stages of development of the organ are associated with different time-points of this reference timeline between 0 and 1. These stages are characteristic morphological steps, which can be easily and reproducibly defined across different individuals, genotypes, or even species, but do not occur at identical time points.

We tested our HDTW strategy in order to reproduce realistic virtual architectures of the model plant *Arabidopsis thaliana*. For this, we grew real plants in standard indoor conditions and manually collected various quantitative information on the plant at different scales, focusing on the relative and absolute developmental dynamics of many plant parts and organs. Depending on the trait, hierarchical timelines were either calibrated by measuring the same plants over days, or from snapshot pictures, taking advantage of the repetition of the same developmental sequences along the plant axis. Models constructed with this strategy can reproduce precisely plant architectural dynamics at different scales.

This year, in collaboration with Fabrice Besnard, we refined our *Arabidopsis* model by improving the calibration of the growth dynamics with additional experimental data, with the aim to publish the corresponding paper in 2026

## **7.4 Mechanics of tissue morphogenesis**

**Participants:** Olivier Ali, Ibrahim Cheddadi, Andre-Claude Clapson, Ali Farnudi, Elsa Gascon, Christophe Godin, Annamaria Kiss, Guillaume Cerutti, Manuel Petit, Patrick Lemaire (*External Collaborator*).

- Related Research Works: RW2 (*Data-driven models*) & RW3 (*Plasticity & robustness of forms*)
- Related Key Modeling Challenges: KMC2 (*Efficient computational mechanical models of growing tissues*) & KMC3 (*Realistic integrated digital models*)

Deformations supporting morphogenesis require the production of mechanical work within tissues. Such mechanical stresses cannot yet be experimentally quantified in living tissues; the ability to simulate accurately

the mechanical behavior of growing multicellular structures is therefore a mere need in developmental biology and consequently a critical objective of the MOSAIC team.

From a macroscopic perspective, tissues mechanics can be formalized within the framework of continuum mechanics. However, the fact that tissues are composed, at the microscopic level, by mechano-sensitive elements out of equilibrium (namely cells) offers genuine modeling challenges and opportunities. Integrating cellular behaviors such as mechano-sensitivity and cell division into a macroscopic mechanical picture of plant tissue morphogenesis is the topic of this section.

### **Mechanical stresses guide the formation of tricellular junctions during cell division**

In most biological tissues, cells adhere through stable tricellular junctions (3WJs) [39]. In plants, the mechanisms underlying 3WJ formation during cell division remain poorly understood. Recent studies have shown that mechanical stresses influence the orientation of cell division [28, 40], suggesting that such cues might also govern 3WJ positioning, as observed in animals [29].

In collaboration with the SICE team, we investigated how tissue topology shapes mechanical patterns within cell walls that may trigger biochemical signaling involved in 3WJ formation. We identified a mechanism guiding the formation of new division sites near existing tricellular junctions. This process appears genetically regulated, as mutants defective in phospholipid metabolism exhibit malformed junctions.

Using FEM-based mechanical simulations on geometric templates of root cortex cells, we revealed local depletions of elastic energy around existing junctions, which may serve as cues preventing the cell plate from attaching at these locations. Finite element analyses derived from confocal image-based reconstructions confirmed these patterns, suggesting that subcellular elastic energy landscapes encode positional information of adjacent 3WJs. Moreover, perturbations of mechanical homeostasis, such as altered turgor pressure, partially disrupted the normal avoidance of four-way junctions, emphasizing the biomechanical role of 3WJs in orienting cell division.

This project, conducted jointly by the MOSAIC and SICE teams, was primarily carried out by Elsa Gascon, who defended her PhD in December 2025 under the supervision of Olivier Ali (MOSAIC) and with the strong support of Marie-Cécile Caillaud (SICE). The results were published in *Current Biology* [15] and generated notable interest within the plant biology community, as reflected by a commentary on our article [41] and the invitation of Elsa Gascon to present her work at the *Early Career Symposium* held by the Plant Science Center in Umeå, Sweden.

### **Investigating the role of mechanics in epidermal cell identity specification**

During morphogenesis of multicellular organs, cells acquire distinct identities that meet specific functional requirements. Epidermal identity is widely considered essential for plant morphogenesis due to the role of the epidermis in both restricting and promoting growth. In the preprint [26] we combine and present in silico and in vivo evidence that plants use mechanical cues to activate the expression of a sub-population of epidermal genes. To do so, we use root tips to explore the relationship between gene expression, cell mechanics, and growth control within epidermal cells. In this system the epidermis is partially covered by the root cap, a protective cell layer which undergoes programmed cell death, allowing the comparison between covered and uncovered epidermal cells.

For the in silico analysis we built 2D finite element models using the open source software FreeFem++ of lateral root cross-sections, with and without rootcap. Models with uniform cell wall properties and turgor across the whole root section are already known. However, in atomic force microscopy measurements, we observed that the root cap's apparent stiffness was 34 percent lower than the uncovered epidermis. Therefore we performed a more general analysis, where both cell wall Young modulus and turgor pressure were allowed to be different between layers and analyzed stress pattern differences in covered and uncovered epidermal cells in this more generic situation. In this context we show that cells at the root organ surface experience maximum tensile forces, necessitating mechanical reinforcement. Furthermore, the root cap can shield covered meristematic cells from maximum tension, but changes in root cap turgor pressure and/or mechanical stiffness can shift the tension maximum to the epidermal layer or maintain the two layers at a similar tension level. The simulation script is accessible at the repository .

This work is performed in tight collaboration with the "Mechanotransduction in development" team of the RDP lab, led by Charlotte Kirchhelle.

### **Investigating the role of buckling in plant morphogenesis**

Buckling plays also a fundamental role in plant morphogenesis by mediating how tissues respond to growth-induced compressive stresses. As plant cells divide and expand, certain layers, such as the epidermis, may grow faster than underlying tissues. This differential growth generates mechanical instability, leading to buckling when the stress surpasses a critical threshold. The resulting deformation produces characteristic structures like folds, ridges, or wavy surfaces—a phenomenon we investigated using the sepal of *Arabidopsis thaliana* as a model organ.

In a forthcoming paper, we propose an analytical mechanical model that demonstrates how differential growth between the inner and outer epidermal layers surrounding the mesophyll leads to compressive stresses. These stresses trigger buckling on the one hand and curve the sepal on the other hand. In parallel, a finite element model of the transverse section of a growing sepal is presented, implemented using Fenics and BVPy . From a technical perspective, this work contributed to advancements in BVPy, particularly in simulating nonlinear elastic models and growth processes in heterogeneous tissues. The release, incorporating these developments, is now on line.

The preprint further emphasizes the role of buckling in morphogenesis, highlighting that the deformation caused by buckling patterns the tissue, and that this patterning can regulate gene expression, creating feedback loops that reinforce specific growth patterns.

This work is made in collaboration with Arezki Boudaoud (Ecole Polytechnique, Paris, France) and Adrienne Roeder (Cornell University, Ithaca, USA).

### **Force inference**

In the context of the HYDROFIELD ANR project and the postdoctoral contract of André-Claude Clapson, we are developing a force inference method in the SAM that derives wall stresses and cell turgor pressures from the geometry of the cells. Plant cells are inflating thanks to their turgor pressure, but this quantity cannot easily be measured. We have suggested a new indirect method inspired by foam mechanics: combining Laplace law (that relates pressure, wall curvature and stress) and the Gauss-Bonnet theorem (that expresses a geometrical constraint on cell shape), we develop a methodology to estimate stresses and pressures from observations of cells shapes in confocal images. Force inference is an active field of studies with recent publications [37], but mostly on animal tissues. Preliminary results with our method indicate that it compares well with the state of the art in the literature, while being more robust and better adapted to plant tissues. Our results will be compared to direct pressure measurements by our collaborators in Singapour (Yuchen Long team). Two publications are in preparation and the corresponding code will be provided to the community.

### **Coupling wall mechanics and water fluxes**

We collaborate with biologists (Yuchen Long from National University of Singapour, and Weibing Yang from the Chinese academy of sciences, Shanghai) that explore the role of aquaporins (AQP) in the SAM, by comparing the growth dynamics of newly divided cells in WT and AQP mutant organisms; the interpretation of these data with the model [31] will allow to clarify the respective roles of wall synthesis and water transport in the regulation of plant growth.

### **Hydromechanical Field Theory of Plant Morphogenesis**

With Hadrien Oliveri (Max Plack Institute, Cologne), we have developed a new continuous formalism that couples water fluxes, wall mechanics and growth [19]. The model has the same phenomenology as the Lockhart model and its multicellular extension, in particular, the fact that pressure is not prescribed but results from the coupling between fluxes and mechanics. The model couples poroelasticity to describe fluxes through the network of cells and morphoelasticity to describe growth.

In a recent perspective paper [42], we propose that the coupling of water transport and wall mechanics is key to develop physically sound mechanistic models of plant growth, and provides a theoretical foundation for an active-matter theory of plant morphogenesis—a closed mathematical framework in which the growth phenomenon emerges as the product of multiple, coupled physical, chemical and mechanical fields acting more or less nonlocally.

### Modelling of cambial growth

The vascular cambium is the meristem producing two tissues essential to trees: the phloem (inner-bark) and the xylem (wood). Wood fulfils numerous functions ensuring the functioning of trees: mechanical support and postural control, water transport and storage of reserves. For human uses, wood is a high performance composite cellular material whose new assets are constantly being discovered. While the impact of environmental variations on wood growth and microstructure is largely studied, a mechanistic approach is still missing to link these variations to cell growth mechanisms. In trees, several studies have shown that mechanical perturbations (tree bending or tilting) strongly modulate the cambial functioning (cell division rate, expansion and differentiation). However, contrary to apical meristem, no study investigated the possible role of mechanical constraints that may be crucial in the functioning of the cambium.

We are part of the ANR project CEMACam coordinated by Eric Badel (INRAE Clermont-Ferrand, PIAF), that aims at unraveling fundamental aspects of wood formation with an interdisciplinary and integrated approach. In particular, we are developing a multicellular model of cambium based on a previously developed formalism [31].

### Mechanics of tendrils

In the framework of the Dynavine project, we are investigating the force and torque generation of tendrils of climbing plants as a function of time and growth development. To do so, we have developed an experimental set up that we have been testing on synthetic rods.

This preliminary work have lead us to discover a new and exciting result about rod mechanics : One can completely change the chirality of a helical rod by unwinding it. Doing so, the rod goes through a transition state involving two helices with opposite chiralities spatially connected by a so-called “perversion”. In our work, we reported an experimental demonstration of this phenomenon. We monitored the axial torque and load upon such a transformation and revealed a phase transition like behaviour. We proposed a biphasic expansion of the elastic energy and reproduced the encountered behaviours. Our experiments also displayed hysteresis upon helical unwinding but numerical simulations seems to indicate that it is due to specific properties of our material. These results have been published previously in Physical Review Letters [34]

In 2025, we have pushed forward the analysis of the phase transition analogy. In particular we have looked with care at the behaviour of the perversion. These new results have been published in [14].

We have also used the set-up to monitor live plants. We have recorded universal signatures of force and torque evolution as a function of writhing. Based on our experimental results, we have developed a phenomenological model of tendrils writhing. We found two distinct results : 1. A simple bilayer model where the dorsal side of the tendril is growing is enough to recapitulate all the experimental data. 2. The growth law of the ventral side can be completely understood in the framework of the Lockhart model ; it advocates for the fact that elastic stresses could have a major contribution in plant’s autotropism. One paper has already been submitted [24] and a second one is in preparation.

### Analysis of early pollen tube growth

Pollen grains are transported from flowers to flowers by wind or animals. They can germinate if they land on specific elongated cells, called papillae located at the tip of the stigma, the female organ of the flower. When they germinate, a pollen tube starts to grow out downward the papillae, and keeping at the papillae surface [45]. Papillae have roughly a pin-like structure, but may vary in shape within or between species and present either convex or non-convex forms. Biologists try to understand the possible physical or chemical clues that guide the growth of the pollen-tube downwards. One of the hypothesis is that the precise geometry of the papillae may play an important role in the guidance of the tube and that the tube could follow geodesics of the papillae surface.

To study this hypothesis, a mechanical model was constructed to explore how pollen tube growth is guided on the stigma geometry. We found that in mutants stigmas, the WT tube tip moves freely on the curved papilla surface and follows geodesics, while the pollen tube growth deviates from geodesic trajectories on WT, suggesting an additional guidance mechanism. Based on a computational analysis of the magnitude of possible mechanical forces acting on the pollen tube during its growth, we show that these deflections can be explained by a mechanism based on the geometry of the papilla, cell wall elasticity and turgor pressure.

This work is made in collaboration with Isabelle Fobis-Loisy (RDP Lab, Lyon) Karin John, and Catherine Quillet (LIP, Grenoble) and Lucie Riglet (Sainsbury Lab, Cambridge, UK) and been published this year in PLoS Computational Biology ([21]).

## 7.5 Signaling and transport for tissue patterning and growth

**Participants:** Jeanne Abitbol Spangaro, Romain Azais, Guillaume Cerutti, Landry Duguet, Christophe Godin, Jonathan Legrand, John Thampi, Teva Vernoux (*External Collaborator*), Justina Stark, Aurèle Boussard, Corentin Bisot.

- Related Research Axes: RA1 (Representations of forms in silico) & RA2 (Data-driven models)
- Related Key Modeling Challenges: KMC3 (Realistic integrated digital models)

One central mechanism in the shaping of biological forms is the definition of regions with different genetic identities or physiological properties through bio-chemical processes operating at cellular level. Such patterning of the tissue is often controlled by the action of molecular signals for which active or passive transport mechanisms determine the spatial precision of the targeting.

The shoot apical meristem (SAM) of flowering plants is a remarkable example of such finely controlled system where the dynamic interplay between the hormone auxin and the polarization of efflux carriers PIN1 governs the rhythmic patterning of organs, and the consequent emergence of phyllotaxis. Using *Arabidopsis thaliana* as a model system, we develop an integrated view of the meristem as a self-organizing dynamical form by reconstructing the dynamics of physiological processes from living tissues, and by proposing computational models to study tissue patterning and robustness of biological shapes *in silico*.

We also consider other model systems, such as the moss *Physcomitrium patens* where different mechanisms need to be taken into account to understand the patterning of the organism.

### Analysis and modelling of auxin transport at cellular level in the SAM.

Macroscopic model of organ interactions in plants have been particularly successful in explaining phyllotaxis patterns at the SAM. However, the details of the molecular processes allowing the spatiotemporal coordination of the cells necessary to the maintenance of the regularity of the pattern is still a frontier question. Two main actors are thought to contribute to the emergence and maintenance of phyllotactic patterns. On the one hand, the plant hormone auxin accumulates at different sites of the SAM and triggers organ differentiation. On the other hand, polarized PIN1 proteins at the cell membranes directs auxin transport in the tissue. Recent experiments and methods developed in the team provided quantitative spatiotemporal data of auxin and PIN1 localization. These data have been analyzed at cell scale as discrete raw data, and at tissue scale as continuous data allowing to compare different individuals [5]. These observations question the mainly adopted interpretation of auxin transport in the SAM, mainly that PIN1 are polarized in the cell membranes according to the gradients of auxin in the tissue.

Our work builds on the mass of data collected in [5] to study alternative explanations of the auxin accumulation patterns. We analyzed the spatial organization of PIN1 polarities considering both their directions and intensities, and studied their effect on auxin transport using discrete and continuous modeling. This rigorous analysis shows that variations in PIN1 polarity intensities (largely overlooked in classical approaches) play a significant role in shaping auxin distributions. Rather than relying on localized directional convergence of PIN polarities, auxin accumulation would emerge from a dual inhibition–stimulation mechanism resulting from differential intensities of its advection field. This reinterpretation challenges purely lateral inhibition models of phyllotaxis and identifies regulation of PIN polarity intensities as a key driver of SAM patterning.

This work is part of a collaboration with Carlos Galvan-Ampudia and Teva Vernoux from the Signal team of the RDP, and was led by Landry Duguet supervised by Christophe Godin. It has been presented this year at the Shaping Life workshop [27], the discrete modeling framework gave rise to the TIDES library 6.1.8, and an article gathering the main results is being finalized.

### Single-cell analysis of temporal responses to auxin signaling for organ initiation

Morphogenetic signals such as auxin define spatial distributions that are thought to control tissue patterning, but it has been proposed in animals that they also carry temporal information in their dynamics. Recent work provided evidence that organ initiation in the SAM is indeed dependent on the temporal integration of the auxin signal [5]. The duration of cell exposition to auxin is used to differentiate temporally sites of organ initiation, and provide robustness to the rhythmic organ patterning.

We are now studying more precisely at the level of single cells how the history of exposure to auxin might affect the transcriptional behaviour of auxin-responsive genes. To do so, we use time-lapses of SAMs imaged with both an auxin signaling sensor and an auxin-responsive transcriptional reporter, over long ranges of time (36 hours, i.e. 3 organ initiations on average). Relying on the *Gnomon* computational platform 6.1.11, we have set up a new pipeline to reconstruct trajectories of individual nuclei with auxin signal and response information.

Using this quantitative information we investigate which form of temporal integration is being performed by the cells. To test integration models, we notably rely on the reiterative nature of the meristem to infer the auxin exposure history of the cells before the beginning of the time-lapse, and estimate the contrasted initial values of integrated auxin across the SAM. This analysis allows to evidence the parameters that may explain the delays observed between genes that respond to auxin at different stages of organ development.

This work is part of a collaboration with Hugo Caumon, who defended his Ph.D. thesis in december 2025, along with Carlos Galvan-Ampudia and Teva Vernoux from the Signal team of the RDP.

### Stochastic modelling of cellular auxin response in the SAM

Auxin accumulation is the primary determinant of new organ initiations in the Shoot Apical Meristem, and mathematical models of polar auxin transport by the PIN1 efflux carrier, whose distribution is also affected by auxin, have aided our understanding of this phenomenon. However, recent observations suggest that there is some stochasticity in auxin levels in individual cells and that cells integrate auxin information over time to initiate organs [5]. While the role of stochasticity in primordium initiation has been studied from an abstract perspective [44], it has not been linked to biological processes such as auxin sensing.

Hypothesising that a key mechanism explaining the temporal integration of auxin is the progressive decompaction of the chromatin of auxin-responsive genes, we implemented a simple, deterministic model of auxin-sensing in which we represent compacted and decompacted chromatin states as a Markov chain. Analysis of this model prompted us to further study the process using a stochastic model, which is currently being developed. We are also working on defining and quantifying temporal integration more formally using ideas from control theory.

This work is realized within the Ph.D. thesis of John Thampi, supervised by Christophe Godin in collaboration with Teva Vernoux from the Signal team of the RDP lab.

### Estimation of cell-to-cell conductivities in the SAM

Cell-to-cell transport processes play a key role in the patterning and organogenesis at the Shoot Apical Meristem (SAM), starting with water transport that is hypothesized to control organ outgrowth [1]. An essential contributor to these processes is symplasmic transport, which is mediated by the plasmodesmata, channels that connect the cytoplasm of adjacent cells. However, measuring to what extent these aperture-regulated channels locally allow the transport of water and other molecules between cells is a highly challenging task.

We aim to characterize differences in intercellular conductivity between biologically relevant areas of the SAM of *Arabidopsis thaliana* using multi-channel confocal acquisitions. We rely on existing tools from the *TimeTK* library 6.1.3 to segment the cells in 3D and obtain quantitative measures. Then, by modelling the diffusion process, we are developing a mathematical estimator to infer cell-level conductivities, which we try to validate on simulated data obtained through the *TIDES* library 6.1.8.

This work is carried out by Guillaume Cerutti and Jonathan Legrand, in collaboration with Géraldine Brunoud from the Signal team of the RDP, and is a continuation of the Hydrofield ANR project.

### Transport of auxin and branching patterns in mosses

Branching patterns are key determinants of plant morphology, and similar lateral branching modes have evolved separately in the leafy shoots of two major groups of land plants, the vascular plants (among which flowering plants) and the bryophytes (among which mosses), driving their independent architectural diversification. In both lineages, the inhibition of lateral branches by auxin is a shared key mechanism, and long-range polar auxin transport is known to play a central role in branching control in vascular plants. Yet in bryophytes, like the model moss species *Physcomitrium patens*, evidence suggests that auxin might only rely on diffusion through plasmodesmata (microscopic channels that link neighboring cells) to regulate branch distribution. However, whether this "symplasmic" auxin diffusion is a realistic biophysical mechanism, sufficient to explain the observed branch distribution patterns, still had to be assessed.

In collaboration with Yoan Coudert (RDP lab), we address this fundamental problem by developing a physics-based, 3D computational model of symplasmic auxin diffusion in the moss shoot, integrating molecular, cell and tissue scales. Each step of model design is guided by geometry measurements and biological experiments. Our integrative approach has demonstrated that branching control based solely on symplasmic diffusion for intercellular auxin movement can account for the observed branching patterns at the whole-shoot level. It also provides mechanistic interpretations of the changes in branch distribution caused by genetic perturbations affecting callose-dependent symplasmic permeability, as well as the unexpected increase in branch spacing robustness during shoot development. Altogether, our findings reveal that branching patterns arising from an auxin diffusion-based regulatory mechanism exhibit a specific developmental signature, not reported in vascular plants, but well exemplified in the moss *Physcomitrium*.

This work was carried out in the context of the Ph.D. thesis of Jeanne Abitbol-Spangaro, co-supervised by Christophe Godin, who defended in early 2025, and led to a publication in *Current Biology* [11].

### Development of *Physarum polycephalum*

Macroscopic organisms depend on specialized transport networks to acquire resources from their environment and to distribute these resources internally, thereby meeting spatially heterogeneous metabolic demands. The architecture of these networks must simultaneously optimize multiple functional objectives, including transport efficiency, construction and maintenance costs, and robustness to structural damage. Environmental fluctuations, such as changes in temperature or nutrient availability, impose additional constraints on network architectures.

Some networks, such as those in plant leaves, exhibit inherent architectural robustness that buffers against environmental perturbations. In contrast, other systems, such as animal vasculature and the networks formed by certain slime molds, display dynamic structural adaptation, continuously remodeling in response to changing external and internal conditions. The efficiency of adaptive remodeling, in turn, is influenced by architectural features of the network, including the presence of cycles and fractal branching patterns. However, the mechanical principles underlying this co-dependency between network architecture and adaptive capacity remain elusive.

To address these questions, in the context of the ANR project Fractals, we integrate discrete and continuous theoretical models based on graph theory and fluid mechanics to study dynamic network adaptation. The goal is to quantify how different functional objectives are balanced in various network architectures, and how these architectures govern adaptivity and resilience under changing environmental conditions. We validate our models using heat-stress experiments on the slime mold *Physarum polycephalum*, enabling direct comparison between theoretical predictions and observed adaptive responses.

Partners:

- Sorbonne Université, Paris (Claire David, coordinator)
- Université Paul Sabatier, Toulouse (Audrey Dussutour)
- University of California, Riverside (Michel Lapidus)

### Branching structure development in mycorrhizal fungi

Mycorrhizal fungi build networks to exchange nutrients with plant roots. Relying on host carbon, they face trade-offs between construction costs, coverage, and long-distance nutrient transport. How they manage these

challenges is unclear. A custom robot for time-lapse imaging constructed in AMOLF Lab, made it possible to track over 500,000 fungal nodes and measured 100,000 cytoplasmic flow paths. We discovered fungi use ‘self-regulating’ waves: growing tips expand nutrient-absorbing mycelium, controlled by fusion. This strategy minimizes carbon costs while expanding beyond depleted zones to find new plants and nutrients. Networks maintain steady transport efficiency while adding loops for faster connections. Fungi also widen tubes and accelerate flows along main routes. These findings reveal how fungi optimize their networks for efficient nutrient trade, shaped by millions of years of evolution.

This work was carried out in the context of the Ph.D. thesis of Corentin Bisot, co-supervised by Christophe Godin, who defended in 2024. It results from a collaboration with the AMOLF Lab and the University of Amsterdam, and has been published in the journal Nature, [20].

## 7.6 Integration of processes for morphogenesis

**Participants:** Alexis de Angeli (*External Collaborator*), Corentin Bisot, Christophe Godin, Guillaume Metsdgah.

### Electro-chemico-mechanical model of stoma opening

Few models integrate at the various chemico-physical mechanisms that regulate cell shape change. In collaboration with the team of Alexis de Angeli in Montpellier, specialized in the biology of stomata, our main objective is to develop a multi-membrane, multiphysics model for the regulation of plant cell volume control and to illustrate this model on the process of opening and closing stomata cells. More precisely, we seek to integrate electro-chemical and hydro-mechanical processes in an explicit and mechanistic way, while keeping the model easy to interpret. For this, we unify the various physical processes by gathering their contributions into a common global energy function. This energy function naturally brings modularity to the model, as its components can be added or removed without impact on the other components of the system. In addition, it keeps generic features (e.g. implementation of the main physical processes) well separated from specific ones (e.g. choice of specific transporters, etc.). We exploit this approach to simulate ion transfer between the subcellular compartments of a guard cell during stoma opening. This results have been published this year, [18].

### Spatial dynamics of the Arbuscular Mycorrhizal Fungal network

The outcomes of arbuscular mycorrhizal (AM) symbiosis vary widely, influenced by plant and fungal species as well as soil conditions, making predictions difficult. During this symbiosis, plants provide photosynthetically fixed carbon to fungi, which use it to grow nutrient-absorbing networks in the soil. The nutrients fungi deliver to plants affect the plants’ future carbon investments in the fungi, influencing nutrient acquisition. Building on previous work, in collaboration with AMOLF lab in the Netherlands, we measured plant carbon investment in fungal networks and phosphorus uptake over time. We found a consistent proportional relationship between the plant’s carbon allocation to fungi and the phosphorus fungi transfer back, regardless of fungal strain differences. Incorporating this proportionality into a model reveals how fungal traits, plant control, and soil conditions interact to shape symbiosis outcomes. This insight helps reinterpret past data and develop testable hypotheses about AM symbiosis dynamics.

This work was carried out in the context of the Ph.D. thesis of Corentin Bisot, co-supervised by Christophe Godin, who defended in 2024, has recently been accepted in PNAS.

## 7.7 New computational approaches for morphogenesis

**Participants:** Olivier Ali, Frédéric Boudon (*External Collaborator*), Romain Azaïs, Christophe Godin, Henri Péchoux, Nino Salomon.

- Research Axes: RA1 (Representations of forms in silico) & RA2 (Data-driven models)

- Key Modelling Challenges: KMC2 (Efficient computational mechanical models of growing tissues) & KMC3 (Realistic integrated digital models)

### Theoretical and numerical investigations around Markov models

The cellular Potts model can be used to describe tissues and cellular complexes. It emerged in bioinformatics as a derivation of statistical physics models (in particular, Ising model and Potts model). The cellular complexes  $\sigma$  described by this model are distributed according to the Gibbs measure  $\mu(\sigma) \propto \exp(-\beta H(\sigma))$  where  $H$  denotes the energy function of the system.

To simulate this probability distribution, MCMC-type techniques are used, which tend to minimize the energy  $H$ . These techniques are difficult to analyze from both theoretical and numerical points of view. In particular, their convergence rate is complicated to obtain, and we know that the algorithm can be trapped in low-energy valleys that are not the global minimum.

As part of the ALAMO project, we are seeking to propose alternative algorithms to MCMC methods, and to better characterize existing methods so as to be able to precisely quantify the accuracy of the results obtained. During the start-up phase of the project, we have been working in three main areas: on small state spaces for which exact solutions are achievable by enumeration, we have carried out numerical analyses of several MCMC algorithms, enabling us to construct first numerical indicators of convergence. On the other hand, we have made significant progress on the proof of convergence of a cell division algorithm inspired by the Potts model. Finally, we have begun to explore new simulation techniques inspired by contour models.

During the development of the simulation algorithms, we identified the need to rapidly estimate the invariant distribution of Markov chains with a known transition kernel. We explored several approaches to address this problem and identified a new algorithm to perform this task. The theoretical and numerical analysis of this algorithm accounted for a substantial part of this year's work. A paper is currently being prepared and will be submitted early next year.

We also took a slight detour to investigate the estimation of the division rate in growth-fragmentation models. Specifically, we conducted a rigorous theoretical and numerical comparison of state-of-the-art nonparametric methods. This analysis revealed that none of the currently available methods uniformly outperforms the others, even within the same model. Achieving this result required detailed studies of the convergence properties of Markov chains and vector-valued martingales. These findings underscore the importance of exploring the aggregation of state-of-the-art methods to enhance estimation performance. A paper [23] has been submitted and is currently under revision.

### Developing a python DEC-library for plant morphodynamics

Modeling morphogenesis of living organisms requires to numerically solve systems of ODEs and PDEs on cellularized domains. Currently, state-of-the-art approaches rely on classic *Finite Element Methods (FEM)* and require a precise triangulation<sup>3</sup> of the domains at stake [30]. This is a tedious task, for the natural cellularization of these domains must be preserved, even when cells are expanding and dividing. To alleviate this difficulty, we got inspired by recent advances in the field of computer graphics, where a new method to solve differential systems has been developed: *Discrete Exterior Calculus (DEC)* [33].

Over the past years, in the context of the *Action Exploratoire Discotik 9.1*, we have been developing a python library, named *dxttr* (6.1.2), to adapt the tools of *DEC* within the context of plant morphodynamics. Our objective with this library is to provide the community with efficient tools (data structures and algorithms) to estimate differential systems on simplicial complexes, inspired by developmental biology. In 2025, the first version of the *Dxttr* library has been submitted to publication in an Open Source Software journal and is currently under review.

### Riemannian L-systems.

We are used to think of the development of forms in biology as a process that takes place in our 3-dimensional Euclidean space. However, various forms, patterns or processes in biology take naturally place in a non-euclidean space. The vein networks of leaves for instance grow within the leaf blade, which is in general a growing curved (non-euclidean) surface. Likewise, molecular signals are transported actively or passively

<sup>3</sup>or tetrahedrization in 3D

within tissue layers (epithelia) that are in general curved 2-D or 3-D domains. Modeling the growth or dynamics of these systems thus requires that we account for the curved nature of the underlying medium and involves the use of advanced geometric concepts (geodesics, curvature, parallel transport, etc.) coming from differential geometry and connected mathematical fields such as differential topology, algebraic topology ...

To address this issue, in collaboration with Frédéric Boudon from CIRAD, we developed over the last years a new major extension of L-systems, called Riemannian L-systems, that makes it possible to simulate the growth of patterns or the movement of molecules within curved 2-D domains. The framework provides a declarative language (as an extension of the L-Py language for modeling L-systems) high level primitives to develop models and simulations within curved spaces. In these models, growing structures follow in general geodesics. Deviation from these geodesic lines can be used or interpreted as resulting from extra forces due to various physical or chemical origins. A paper describing this new paradigm and its associated language has been published in the journal *Quantitative Plant Biology*, [16].

## 7.8 Preparation of a new team: TRABOULE

**Participants:** Romain Azais, Adrien Marion, Henri Pechoux.

Romain Azais, originally from the MOSAIC team, recently decided to construct a new research team at the Inria Lyon center: TRABOULE, with a new and completely different objective. The ambition of TRABOULE is to address problems in geography using applied mathematics approaches, through deterministic or stochastic models. In this context, some work was carried out this year on topics different from those of MOSAIC, in particular on issues related to urban mobility.

In particular, the new team focusses on pedestrian mobility in urban environments. they analyze pedestrian mobility using automatic counters data focusing on disaggregating sub-populations based on their travel objectives (e.g. home-to-work, shopping, leisure). For each group, they propose a deterministic model informed by expert data (e.g. spatial distribution of workplaces, distribution of shopping hours), which are used to build transport equations with source terms of the form

$$\partial_t v_k(t, x) + v \partial_x v_k(t, x) = \frac{v_k(t, x)}{F_0(x)} f_0(x) - F_0(x) f_e(t, x).$$

While this deterministic approach does not give a means to directly disaggregate the different travel objectives, it does provide mobility patterns for each sub-population throughout the day and within an area of interest. They use them to develop a statistical model enabling us to estimate the sub-population sizes at each time and each location from the counters data. We especially implement an Expectation-Maximisation (EM) algorithm to infer the most likely distribution of the observed pedestrians into the different sub-populations.

A project on the modeling of mobility in public transportation systems was also in its start-up phase in 2025. The objective is to understand the relationships between the spatio-temporal use of public transport and local socio-geographical determinants within cities.

This spin-off of Mosaic will most probably become a full-fledged project-team at the Inria Lyon centre in 2026.

## 8 Bilateral contracts and grants with industry

### 8.1 CIFRE PhD thesis with ACOREL

**Participants:** Romain Azais.

As part of the construction of the new Inria project team TRABOULE, a collaboration was initiated with the company ACOREL, which notably equips public transport vehicles with passenger boarding and alighting sensors. These passenger count data make it possible to assess public transport usage. A CIFRE

PhD project was set up in collaboration with this company and the Institut Camille Jordan in Lyon, with the objective of modeling bus and tramway ridership in the Lyon metropolitan area as a function of network characteristics and usage patterns, as well as climatic variables and local socio-economic determinants.

## 9 Partnerships and cooperations

### 9.1 National initiatives

#### CNRS 80 prime fellowship : DYNATROP (2025-2027)

**Participants:** Julien Derr, Dražen Zanchi (*External Collaborator*).

This project explores the unique mechanical behaviors of plant tendrils—flexible, helical structures found in climbing plants like vines, cucumbers, and peas. These tendrils attach to supports through thigmotropism and can undergo rapid, snapping-like movements. Our research focuses on understanding the physical instabilities in elastic rods that lead to these critical snapping events, both in living tendrils and synthetic models.

By analyzing these mechanisms, we aim to develop a groundbreaking “tendrill motor”: a bionic device that mimics the natural snapping action of tendrils. Unlike traditional motors, this device will operate without frictional articulations, using differential growth and mechanical instabilities to generate rapid, controlled movement. The project bridges the fields of biomechanics and bioinspired engineering, offering new possibilities for sustainable, plant-based technologies.

A new PhD student Amziane Dalache will be funded by this fellowship, and will join the Mosaic team in January 2026. He will focus on investigating the tendrill structure both microscopically (light sheet imaging) and macroscopically (3D shape evolution).

Partners:

- Université Paris Cité, France.

#### Inria-INRAE PhD funding (2025-2028)

**Participants:** Romain Azais, Raphael Forien (*External Collaborator*), Adrien Marion, Florian Patout (*External Collaborator*).

In the context of preparing the new Inria team TRABOULE, this Inria-INRAE PhD funding aims to investigate spatial epidemic models from both deterministic and stochastic perspectives.

More specifically, the project seeks to develop an innovative mathematical framework to model the spread of epidemics in highly heterogeneous territories, using the 2013-2016 Ebola outbreak as a primary case study. It is structured around three main stages: (i) the construction of a deterministic model accounting for spatial heterogeneity in the population, (ii) the retrospective inference of the infection tree at the individual level, and (iii) the correction of this tree using deep learning methods that incorporate realistic geographical constraints.

The final goal is to achieve a refined understanding of the spatial dynamics of epidemic spread in territories characterized by strong demographic heterogeneity.

#### Inria ADT - Mechaverse (2024-2026)

**Participants:** Olivier Ali, Julien Derr, Manuel Petit, Gonzalo Rivella.

The BVPy library [6.1.1](#) is a python library aimed at implementing Boundary Value Problems (*BVP*) and Initial Boundary Value Problems (*IBVP*) in the Finite Element Method paradigm. Such problems are

ubiquitous in the study of morphogenesis and the BVPy library provides tools to address them, not only to the researchers and engineers of the team but also to external collaborators. Since its first release [35], the users of the library have raised a number of limitations (*e.g.* impossibility to consider dynamical meshes, absence of tools to design 3D cellularized domain, compatibility of the library with the newest versions of its main dependence - FEniCS-X). Solving these limitations have become critical for two PhD students of the team are relying on the library to develop their scientific projects.

The goal of the project is to address these limitations. To that end, Gonzalo Rivella has been recruited in October 2024 to develop the needed new features and to roll-out an updated version of BVPy.

### **Inria AEx Discotik (2021 - 2025)**

**Participants:** Olivier Ali, Elsa Gascon.

Computational morphomechanics is the study of living tissue morphogenesis through the scope of physics-based computational modeling. It has become a forefront tool to study organogenesis, where mechanical stresses play a paramount regulating role. At macroscopic scale, smooth living tissues can be described as Riemannian manifolds, subject to continuous mechanics. Concomitantly, at the cellular scale, they appear as networks of discrete effectors, where mechanics should be expressed in a combinatorial manner. Current state-of-the-art models, based on “classic” Finite Element Methods, struggle to efficiently integrate this cellular (discrete) / tissular (continuous) dichotomy. The Discotik project aims to alleviate this difficulty through the use Discrete Exterior Calculus to express the laws of mechanics. While classic FEM rely solely on simplicial meshing of manifolds, “DEC” also exploits their dual structure, composed of cellular complexes. Strikingly, such cellular structures appear naturally in living tissues. Our goal is to assess this modeling approach on a specific, circumscribed problem: The morphomechanics of plant seed. We expect the “DEC” framework not only to enable faster computations but also to expose the deep connection between mechanical stress, tissue geometry and the corresponding cellular network topology.

Partners:

- Benoît Landrein, SEED team RDP, Lyon.

### **Inria AEx ALAMO (2023 - 2027)**

**Participants:** Romain Azaïs, Henri Péchoux.

Stochastic lattice models are of constant interest to the scientific community, both for their fundamental properties and the wide variety of applications they offer, notably in statistical physics, computational biology and population ecology. Their numerical simulation often requires the use of MCMC (Markov chain Monte Carlo) techniques. The ALAMO project aims at proposing alternative algorithms for the simulation of these models by studying and estimating the law of the contours formed by the nodes of the lattice having common characteristics. By controlling the error to the target distribution, these new simulation techniques will allow to fine-tune the MCMC algorithms or even to overcome some of their limitations and could therefore offer a credible alternative.

Partners:

- Benoît Henry, Institut Mines Télécom Nord Europe à Lille.
- Philippe Andrey, INRAE Versailles.

### **ANR Netflux (2022 - 2026)**

**Participants:** Christophe Godin, Ibrahim Cheddadi (*External Collaborator*), Guillaume Cerutti.

The identification during the last decades of the molecular actors involved in guard cells signaling and ion transport highlights the fact that stomata opening or closure relies on the balanced control of ion fluxes across both plasma and vacuole membranes (PM and VM). However, how ion fluxes are coordinated between PM and VM membranes remains almost unknown. In this proposal, we hypothesize that the coupling between the ion transport at the PM and the VM is a major factor controlling stomatal aperture. Therefore, the main objective of the NetFlux project is to understand how cellular membranes are finely and tightly coordinated during cellular responses. For this purpose, we will use the guard cells from *Arabidopsis thaliana* as our cellular and biophysical model. To reach our goals the Netflux project will:

- characterize the ion flux across the PM and VM combining original genetic resources and highly resolutive techniques in living cells (refers to WP1 and WP2)
- develop mathematical and computational models of intracellular ion fluxes in GCs to quantitatively understand the coupling between ion transport across the PM and VM to control stomatal movements (refers to WP3)
- identify new regulators of ion transport in GCs using an original genetic screen based on a genetically encoded biosensor (refers to WP4).

Partners:

- BPMP Unit, Montpellier
- SAVE BIAM CEA, Cadarache

#### ANR Hydrofield (2021 - 2025)

**Participants:** Arezki Boudaoud (*External Collaborator*), Christophe Godin, Ibrahim Cheddadi (*External Collaborator*), Guillaume Cerutti, Yuchen Long (*External Collaborator*).

Plant architecture continuously develop throughout their lifetime through the activity of the apical meristems located at the tip of growing axes. The genetic regulation of the shoot apical meristems (SAMs), which produces all plant aerial organs, has extensively been studied, various key molecular actors have been identified and their function in patterning the SAM has been mapped in space and time. In addition, recent work has established that these molecular actors not only regulate cell identities but also likely induce the physical deformation of tissues by modifying cell wall mechanical properties, in turn inducing leaf or flower primordia outgrowth. From these works progressively emerges a new mechanistic insight on the link connecting gene regulation, tissue deformation and organ growth in plants. However, despite these recent progresses, the contribution of turgor pressure and water fluxes regulation, that decisively contribute to tissue morphogenesis, is still elusive.

Partners:

- SIGNAL Team RDP, Lyon, (Teva Vernoux)
- Ecole Polytechnique, Saclay (Arezki Boudaoud)
- University of Singapour (Yuchen Long)
- University of Helsinky (Juan Alonso-Serra)

**ANR Fractals (2024 - 2028)**

**Participants:** Christophe Godin, Justina Stark, Aurèle Boussard.

Understanding the different strategies of how organisms adapt to external changes, such as temperature increase, is of critical importance. Robustness to environmental variation is often related to phenotypic plasticity. Strikingly, some organisms are even able to adapt by drastically modifying their shape (plants or filamentous structures such as slime molds). In the latter case, the organism adapts by modifying its complex fractal structure, deeply redefining its growth and transport processes. The project aims to understand this adaptive fractal remodeling process. Slime-molds display two levels of fractality (intracellular cytoskeleton and plasma membrane). Temperature is one of the main factors affecting motion. To date, no work has been focused on network morphogenesis and topology, nor on the evolution of the membrane to explain motion response to temperature change. We will develop and test the idea that plasticity and resilience toward temperature change could be connected with the ability of the organism to dispatch its fractality between either level.

On the mathematical and computational side, based on recent work of partners, we will model these living forms with the aim of obtaining specific (discrete) differential operators on fractal structures, in order to express the evolution equations associated with the morpho-biological phenomena. To date, the exploration of the likely interactions between the mathematical theory and the biological phenomena which occur in fractal-shaped living forms remain an unexplored field.

The project FRACTALS aims at developing and applying a new mathematical framework to model the dynamics of a fractal cytoskeleton network, along with its fractal membrane, in response to external stresses, in particular, heat stresses, its adaptation and its resilience.

Partners:

- Sorbonne Université, Paris (Claire David, coordinator)
- Université Paul Sabatier, Toulouse (Audrey Dussutour)
- University of California, Riverside (Michel Lapidus)

## 10 Dissemination

### 10.1 Promoting scientific activities

#### 10.1.1 Journal

##### Editorial boards

- Romain Azais is an Associate Editor for Communications in Statistics.
- Christophe Godin is an associate editor for *PLOS Computational Biology*, **Academic Editor**; *PCI in Mathematical & Computational Modeling* (**Recommender**), *PCI in Plant Science* (**Recommender**).
- Christophe Godin is a guest Editor for **collection of papers on Phyllotaxis** in the journal Quantitative Plant Biology (2025-2026).

##### Reviewing activities

- Olivier Ali reviewed papers for Journal of Mathematical Biology and PLoS Computational Biology.
- Romain Azais reviewed papers for International Journal of Biostatistics and Methodology and Computing in Applied Probability.
- Julien Derr reviewed papers for New Phytologist.

- Christophe Godin reviewed papers for PLoS Computational Biology, Quantitative Plant Biology, Royal Society Open Science and a Book for Springer Mathematics
- Annamaria Kiss reviewed a paper for Protoplasma.

### 10.1.2 Invited talks

- Olivier Ali has been invited to give presentations at the *LiPhy* laboratory in Grenoble (january), at the *9th Plant Computational Biology Workshop* in Cambridge (september) and to the *1ere Journées de Biologie Théoriques*, held in Grenoble (november).
- Guillaume Cerutti was invited to give a presentation at the CGAL Developer Meeting held at the Centre Inria d'Université Côte d'Azur in Sophia-Antipolis (april).
- Julien Derr was invited to give a talk at the "statistical physics and low dimensional conference" in may, in Pont à Mousson, France, and to give a seminar at IUSTI (Aix-Marseille Université) in september.
- Elsa Gascon has been invited to give a presentation at the Invited Seminar of the LIRIS Lab in Lyon (january) and at the *Early Career Symposium* held by the Umeå Plant Science Center in Umeå, Sweden.
- Christophe Godin has been invited to give talks at:
  - the Workshop on Modeling Plant Stem Cells Evolution, Development and Regeneration, 18-21 May 2025, FanHam Hall, Hertfordshire, UK,
  - the Joint Meeting of Asian Conference for Mathematical Biology and Annual Meeting of Japanese Society for Mathematical Biology (ACMB-JSMB2025), 7-11 July 2025.
  - Kyushu University, Department of mathematics, Fukuoka, Japan, 17 July 2025, Kyoto.
  - the monthly seminar of the Société Française de Biologie du Développement (SFBD), 13 Nov 2025

### 10.1.3 Leadership within the scientific community

- Olivier Ali is an elected member (since 2023) of the Inria Commission d'Évaluation.
- Romain Azais is an elected member and the president of the mathematical statistics group of the French Statistical Society.
- Christophe Godin is the Coordinator of the ANR project Hydrofield (2021-2025) and the head of the Inria project-team MOSAIC.

### 10.1.4 Scientific expertise

- Olivier Ali, as a member of the CE, participated to the IFSP assessment committee and the RIPEC C3 committee of Inria for 2025 and the instruction committee of one new Inria Project Team this year.
- Julien Derr was scientific expert for HCERES for the evaluation of the UMR PIAF.
- Christophe Godin is a member of the national scientific committee *Explorae*.

### 10.1.5 Research administration

- Olivier Ali participated to the organisation of the *Journées au vert* of the Lyon Inria center (july). As a CE member, also coordinated the evaluation of 4 Inria Project Teams in 2025.
- Christophe Godin is
  - a member of the Comité d'Orientation Stratégique du centre Inria de Lyon
  - a member of the Lyon Inria comité des équipes-projets
  - a member of the Direction Committee of UMR RDP
  - a member of the Inria National commission for Information et Edition Scientifique (IES) for the Lyon Center.

## 10.2 Teaching - Supervision - Juries - Educational and pedagogical outreach

### 10.2.1 Supervision

- Olivier Ali has been the PhD advisor of Elsa Gascon (defended in december 2025), is the supervisor of Gonzalo Revilla Mut (research engineer) and the co-supervisor of Gauthier Weissbart (Post-doc, in collaboration with Marie-Cécile Caillaud, SICE Team, RDP).
- Romain Azais is the PhD thesis advisor of Henri Pechoux (with Benoît Henry, IMT Nord Europe), Adrien Marion (with Raphaël Forien and Florian Patout, INRAE Avignon), and of Hicham Belafquih (with Cécile Mercadier, Institut Camille Jordan in Lyon).
- Romain Azais was the supervisor (with Florian Patout, INRAE Avignon) of the internship of Adrien Marion at the Master 2 level in mathematics (Spring-Summer 2025).
- Julien Derr is the PhD advisor of Lucie Poupardin (with Mohammed Bendahmane, RDP, ENS Lyon).
- Julien Derr was the supervisor of the internship of Ritish Verma at the Master 2 level in Physics (Spring 2025)
- Christophe Godin was:
  - PhD co-supervisor of Jeanne Abitbol-Spangaro (PhD Defended in June)
  - co-supervisor of John Thampi's PhD thesis
  - co-supervisor of Samara Ghreer's PhD thesis
  - Post-doc advisor of Justina Stark
  - Post-doc co-advisor of Aurèle Boussard
  - Post-doc advisor of Guillaume Mestdagh

### 10.2.2 Juries

- Olivier Ali has served as jury member (CE activity) for two Inria CRCN/IFSP concours (Paris, Saclay) and also for the Inria CRHC and CRHC-8 examination.
- Julien Derr was president of the Jury for the PhD defense of Marianne Lang (Spring, 2025)
- Christophe Godin has been
  - Reviewer of Alexandre Durrmeyer's PhD thesis, U. Paris-Saclay,
  - Reviewer of L. Collet's PhD thesis, U. Montreal,
  - Referent and Jury member of O. Ali's Habilitation (Oct. 2025)

### 10.2.3 Educational and pedagogical outreach

- Olivier Ali conducted practicals (TD) on dynamical systems, Master 1 Biosciences, ENS Lyon (8h) in coordination with Julien Derr (in charge of the lectures).
- Romain Azais taught supervised classification at the Master 2 level in mathematics at Université Lyon 1 and ENS de Lyon, and Fourier analysis at the Master 1 level in biology at ENS de Lyon.
- Guillaume Cerutti taught Fourier analysis (8h) at the Master 1 level in biology at ENS de Lyon.
- Julien Derr taught statistics, introduction to modelization, models for developmental biology, advanced concept in modelization, scientific communication at the L3 level in biology at ENS de Lyon. He taught Dynamical systems and developmental biology at the Master 1 in biology at ENS de Lyon. He taught practicals in bio-modeling and scientific communication at the Master 2 level in biology at ENS de Lyon. He taught physics of living system at the CPES program (third year) at ENS de Lyon.

- Elsa Gascon taught at the ENS Lyon Biology department: 57 hours in Licence 1 and CPES levels (introduction to cell biology, Biological systems modelization, Practicals in plant biology) and also 9 hours in the Chemistry department at the Licence 1 level (Physics and Chemistry of biological systems).
- Christophe Godin taught a 4h class for CPES students (third year) on Physics of Living systems program coordinated by Julien Derr, and a 25h Introductory class on computational morphogenesis to the same CPES level. He also contributed to a 2h class on phyllotaxis to non-plant specialist students at ENS, at master level.
- Henri Pechoux taught at Université Lyon 1 in mathematics: 36 hours of algebra tutorials at the Licence 1 level; 12 hours of analysis practical sessions at the Licence 1 level, and 16 hours of oral examinations: 12 hours in analysis/algebra at the Licence 2 level and 4 hours in analysis/algebra at the Licence 1 level.
- Manuel Petit taught statistics (16h) and python programming (18h) at the L3 level in biology at ENS de Lyon.
- Lucie Poupardin taught hydrodynamics in chemistry at ENS de Lyon.

#### 10.2.4 Participation in Live events

- Christophe Godin and Jeanne Abitbol-Spangaro organized a **stand on flowers and flower development modeling** at the PopScience Festival en Beaujolais, open to participants of all ages.
- Christophe Godin together with Fabrice Besnard contributed a one day training session on phyllotaxis at the **Camp BioMaths**, a one-week training for high-school pupils on applications of maths in biology.
- Christophe Godin organized a presentation on "What is Research at the Interface between Biology and Digital Sciences?" to high-school pupils (Lycée Lumière, Lyon).
- Jonathan Legrand, in collaboration with Fabrice Besnard, co-organized the regional edition (RDP) of the "Visites Insolites du CNRS"—an immersive public outreach initiative designed to bridge the gap between scientific research and society. During this event, participants explored laboratory environments in small groups, gaining firsthand insight into the daily workings of research teams and the innovative projects driving modern science.

A highlight of the program was the 3D plant phenotyping project, where attendees engaged directly with the scientific process. Through a hands-on experiment, they measured plant traits themselves, experiencing the technical challenges and broader implications of phenotyping in agricultural and environmental research. This interactive approach not only demystified the research process but also underscored its significance in addressing real-world challenges, from crop improvement to climate resilience.

## 11 Scientific production

### 11.1 Major publications

- [1] J. Alonso-Serra, I. Cheddadi, A. Kiss, G. Cerutti, M. Lang, S. Dieudonné, C. Lionnet, C. Godin and O. Hamant. 'Water fluxes pattern growth and identity in shoot meristems'. In: *Nature Communications* 15.1 (2024), p. 6944. DOI: [10.1038/s41467-024-51099-x](https://doi.org/10.1038/s41467-024-51099-x). URL: <https://cnrs.hal.science/hal-04680262> (cit. on pp. 7, 27).
- [2] R. Azais and F. Ingels. 'The Weight Function in the Subtree Kernel is Decisive'. In: *Journal of Machine Learning Research* 21 (Apr. 2020), pp. 1–36. URL: <https://hal.archives-ouvertes.fr/hal-02097593> (cit. on pp. 7, 21).

- [3] E. Azpeitia, G. Tichtinsky, M. Le Masson, A. Serrano-Mislata, J. Lucas, V. Gregis, C. Gimenez, N. Prunet, E. Farcot, M. Kater, D. Bradley, F. Madueño, C. Godin and F. Parcy. ‘Cauliflower fractal forms arise from perturbations of floral gene networks’. In: *Science* 373.6551 (2021), pp. 192–197. doi: [10.1126/science.abg5999](https://doi.org/10.1126/science.abg5999). URL: <https://hal.archives-ouvertes.fr/hal-03291136> (cit. on p. 7).
- [4] A. Creff, O. Ali, C. Bied, V. Bayle, G. Ingram and B. Landrein. ‘Evidence that endosperm turgor pressure both promotes and restricts seed growth and size’. In: *Nature Communications* 14.1 (2023), p. 67. doi: [10.1038/s41467-022-35542-5](https://doi.org/10.1038/s41467-022-35542-5). URL: <https://hal.science/hal-03927054> (cit. on pp. 7, 18).
- [5] C. Galvan-Ampudia, G. Cerutti, J. Legrand, G. Brunoud, R. Martin Arevalillo, R. Azaïs, V. Bayle, S. Moussu, C. Wenzl, Y. Jaillais, J. U. Lohmann, C. Godin and T. Vernoux. ‘Temporal integration of auxin information for the regulation of patterning’. In: *eLife* 9 (7th May 2020). doi: [10.7554/eLife.55832](https://doi.org/10.7554/eLife.55832). URL: <https://hal.archives-ouvertes.fr/hal-02368529> (cit. on pp. 7, 26, 27).
- [6] C. Godin, C. Golé and S. Douady. ‘Phyllotaxis as geometric canalization during plant development’. In: *Development (Cambridge, England)* 147.19 (12th Oct. 2020), pp. 1–45. doi: [10.1242/dev.165878](https://doi.org/10.1242/dev.165878). URL: <https://hal.archives-ouvertes.fr/hal-03014239> (cit. on p. 7).
- [7] L. Guignard, U.-M. Fiuza, B. Leggio, J. Laussu, E. Faure, G. Michelin, K. Biasuz, L. Hufnagel, G. Malandain, C. Godin and P. Lemaire. ‘Contact area-dependent cell communication and the morphological invariance of ascidian embryogenesis’. In: *Science* (10th July 2020). doi: [10.1126/science.aar5663](https://doi.org/10.1126/science.aar5663). URL: <https://hal.inria.fr/hal-02903409> (cit. on p. 7).
- [8] F. Ingels and R. Azaïs. ‘Enumeration of Irredundant Forests’. In: *Theoretical Computer Science* 922 (27th Apr. 2022), pp. 312–334. doi: [10.1016/j.tcs.2022.04.033](https://doi.org/10.1016/j.tcs.2022.04.033). URL: <https://hal.science/hal-02511901> (cit. on pp. 7, 21).
- [9] Y. Refahi, A. Zardilis, G. Michelin, R. Wightman, B. Leggio, J. Legrand, E. Faure, L. Vachez, A. Armezzani, A.-E. Risson, F. Zhao, P. Das, N. Prunet, E. Meyerowitz, C. Godin, G. Malandain, H. Jönsson and J. Traas. ‘A multiscale analysis of early flower development in Arabidopsis provides an integrated view of molecular regulation and growth control’. In: *Developmental Cell* 56.4 (Feb. 2021), 540–556.e8. doi: [10.1016/j.devcel.2021.01.019](https://doi.org/10.1016/j.devcel.2021.01.019). URL: <https://hal.inrae.fr/hal-03299500> (cit. on pp. 7, 17).
- [10] F. Zhao, F. Du, H. Oliveri, L. Zhou, O. Ali, W. Chen, S. Feng, Q. Wang, S. Lü, M. Long, R. Schneider, A. Sampathkumar, C. Godin, J. Traas and Y. Jiao. ‘Microtubule-Mediated Wall Anisotropy Contributes to Leaf Blade Flattening’. In: *Current Biology - CB* 30.20 (2020), p. 3972. doi: [10.1016/j.cub.2020.07.076](https://doi.org/10.1016/j.cub.2020.07.076). URL: <https://hal.archives-ouvertes.fr/hal-02370615> (cit. on p. 7).

## 11.2 Publications of the year

### International journals

- [11] J. Abitbol-Spangaro, G. Cloarec, A. Muller, S. Hallet, C. Boulogne, C. Gillet, V. Schmidt, P. Dobrev, R. Skokan, V. Couvreur, J. de Keijzer, C. Godin and Y. Coudert. ‘Robust branch patterning in moss shoots via symplasmic auxin diffusion’. In: *Current Biology* (Oct. 2025). doi: [10.1016/j.cub.2025.09.031](https://doi.org/10.1016/j.cub.2025.09.031). URL: <https://hal.science/hal-05306843>. In press (cit. on p. 28).
- [12] R. Azaïs and B. Henry. ‘Maximum likelihood estimation for spinal-structured trees’. In: *Journal of Applied Probability* 62.1 (2025). URL: <https://hal.science/hal-03109867> (cit. on p. 22).
- [13] V. Battu, A. Kiss, A. Delgado-Vaquera, F. Sénéchal, C. Mollier, D. Hartasánchez, A. Boudaoud and F. Monéger. ‘A 3D morpho-space of sepal geometry reveals the importance of organ curvature’. In: *Quantitative Plant Biology* 6 (27th Mar. 2025), e9. doi: [10.1017/qpb.2025.5](https://doi.org/10.1017/qpb.2025.5). URL: <https://hal.science/hal-05011833> (cit. on p. 20).
- [14] É. Dilly, S. Neukirch, J. Derr and D. Zanchi. ‘Mechanical instabilities and snapping phenomena in helical rods with perversion’. In: *Journal of the Mechanics and Physics of Solids* 207 (2026), p. 106402. doi: [10.1016/j.jmps.2025.106402](https://doi.org/10.1016/j.jmps.2025.106402). URL: <https://hal.science/hal-04838602> (cit. on p. 25).

- [15] E. Gascon, C. Goldy, A. Lebecq, S. Moulin, G. Cerutti, V. Bayle, F. Gacon, A. Bauer, A. Fangain, R. Azaïs, O. Ali and M.-C. Caillaud. ‘Conserved mechanical hallmark guides four-way junction avoidance during plant cytokinesis’. In: *Current Biology* 35.12 (May 2025), 2789–2801.e6. DOI: [10.1016/j.cub.2025.04.046](https://doi.org/10.1016/j.cub.2025.04.046). URL: <https://hal.science/hal-05084380> (cit. on p. 23).
- [16] C. Godin and F. Boudon. ‘Riemannian L-systems: Modeling growing forms in curved spaces’. In: *Quantitative Plant Biology* (2025). DOI: [10.1017/qpb.2025.10014](https://doi.org/10.1017/qpb.2025.10014). URL: <https://inria.hal.science/hal-04535182>. In press (cit. on p. 31).
- [17] R. Martin-Arevalillo, B. Guillotin, J. Schön, A. Hugues, M.-F. Gerentes, J. Lucas, E. Thevenon, G. Vissers, M. Mohammed Ateequr, C. Galvan-Ampudia, G. Cerutti, J. Legrand, C. Cancé, A. Dubois, F. Parcy, K. D. Birnbaum, M. D. Zurbriggen, R. Dumas, F. Roudier and T. Vernoux. ‘Synthetic deconvolution of an auxin-dependent transcriptional code’. In: *Cell* 188.11 (15th Apr. 2025). DOI: [10.1016/j.cell.2025.03.028](https://doi.org/10.1016/j.cell.2025.03.028). URL: <https://hal.science/hal-05005515> (cit. on p. 18).
- [18] G. Mestdagh, A. de Angeli and C. Godin. ‘Multi-physics modeling for ion homeostasis in multi-compartment plant cells using an energy function’. In: *PLoS Computational Biology* 21.11 (20th Nov. 2025), e1013474. DOI: [10.1371/journal.pcbi.1013474](https://doi.org/10.1371/journal.pcbi.1013474). URL: <https://hal.inrae.fr/hal-04901993> (cit. on p. 29).
- [19] H. Oliveri and I. Cheddadi. ‘Hydromechanical field theory of plant morphogenesis’. In: *Journal of the Mechanics and Physics of Solids* 196 (2025), p. 106035. DOI: [10.48550/arXiv.2409.02775](https://doi.org/10.48550/arXiv.2409.02775). URL: <https://inria.hal.science/hal-04867942> (cit. on p. 24).
- [20] L. Oyarte Galvez, C. Bisot, P. Bourriane, R. Cargill, M. Klein, M. van Son, J. van Krugten, V. Caldas, T. Clerc, K.-K. Lin, F. Kahane, S. van Staalduine, J. Stewart, V. Terry, B. Turcu, S. van Otterdijk, A. Babu, M. Kamp, M. Seynen, B. Steenbeek, J. Zomerdijk, E. Tutucci, M. Sheldrake, C. Godin, V. Kokkoris, H. Stone, E. T. Kiers and T. Shimizu. ‘A travelling-wave strategy for plant–fungal trade’. In: *Nature* 639.8053 (26th Feb. 2025), pp. 172–180. DOI: [10.1038/s41586-025-08614-x](https://doi.org/10.1038/s41586-025-08614-x). URL: <https://hal.science/hal-04996172> (cit. on pp. 9, 29).
- [21] L. Riglet, C. Quilliet, C. Godin, K. John and I. Fobis-Loisy. ‘Geometric and mechanical guidance: Role of stigmatic epidermis in early pollen tube pathfinding in arabidopsis’. In: *PLoS Computational Biology* 21.5 (27th May 2025), e1013077. DOI: [10.1371/journal.pcbi.1013077](https://doi.org/10.1371/journal.pcbi.1013077). URL: <https://hal.science/hal-05087781> (cit. on pp. 18, 26).
- [22] M. Rivière, A. Peaucelle, J. Derr and S. Douady. ‘Plant nutation relies on steady propagation of spatially asymmetric growth pattern’. In: *Quantitative Plant Biology* (2025). DOI: [10.1017/qpb.2025.10013](https://doi.org/10.1017/qpb.2025.10013). URL: <https://hal.science/hal-05235631>. In press (cit. on p. 20).

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