

UVED Resource

Plant Growth Architecture and Production Dynamics

GreenLab Course: Development

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Contents and Objectives

Presentation

GreenLab Structural aspects. This section presents GreenLab's development modelling principles.

GreenLab structural modelling aspects are greatly inspired from structural models built on botanical architectural concepts.

It focuses, however, on quantitative aspects, including stochastic aspects.

It also sets out to characterize plant structure without instantiating it, using formal equations to quantify the number of organs for each growth cycle.

On a single plant level, construction also takes advantage of structure duplications.

Lastly, it presents a novel way of building structures (if required), based on a limited number of sub-elements corresponding to axis topology, describing the plasticity that can be found at stand level.

Course Objectives

The purpose of this course is to enable students to:

- Revisit the botanical architectural concepts involved in plant structural models
- Learn about GreenLab's development simplification and assumptions
- Learn about the two aspects of development modelling: rules and, probabilities
- Understand the way structures are built
- Understand the principles of structure quantification formalism

Map

This section introduces the principles of GreenLab development modelling, highlighting the following aspects:

- Structural modelling is based on botanical architectural concepts
- Those concepts are implemented in a dual-scale automaton
- State transitions in the automaton can be quantitatively modelled using principles of the renewal theory.
- Factorization in the automaton application allows formal structural recursive equation definition
- Structure construction can then be implicit (equations only) or explicit up to 3D representation

Course content map

[Development Sub-Chapter](#)

[Sub-Chapter map](#)

[About modelling Plant development](#)

[Architectural Botany reminders](#)

[Modelling botanical concepts](#)

[Quantitative structural modelling](#)

[Structural equations](#)

[Structure construction](#)

[Supplementary resources](#)

About plant structural modelling

Background

The GreenLab model structural aspects are inspired from the AMAP's historical structural approach:

- structure construction results for a discrete growth process simulating the construction of leafy axes
- structure construction is defined according to various axis typologies, as defined in architectural botany
- structure construction authorizes the reiteration process
- construction is stochastic
- in structure simulation, topological aspects (the branching scheme) are separated from geometrical aspects

However, the model differs from the historical scheme:

- the basic component is the phytomer, not the internode
- the growth cycle is defined at low level (the phytomer), not at growth unit level (on rhythmic growth)
- axis typology is defined from the botanical notion of physiological age, and not from branching order
- stochastic modelling aspects are better defined
- the structure is not required to be explicit: the number of organs produced per growth cycle and their status is the only requirement of the model when 3D representation is not necessary
- as a consequence, the geometrical aspects are less developed when compared to AMAP's earlier models.

Stochastic structural modelling

Since the structure of a plant is established from discrete elements (phytomers), such modelling relies on statistical distribution modelling.

The proposed processes to be modelled concern:

- axis development: this means the probability of a new phytomer appearing (i.e. of repeating the current micro-state or of moving to the next one in terms of the automaton)
- axis mortality: this means the probability of a metamer dying
- axillary bud branching: this means the probability of a new axis developing

Such stochastic models can be derived from the classic Renewal theory.

Tree traversal

When generating a simulated tree structure, computational approaches do in fact generate a tree graph.

The way the process accesses the components of this tree graph (and construct it), known as tree traversal, plays a key role in the properties of the simulated structure.

Tree structure traversal

In most structural and functional-structural plant models, the plant structure is built from phytomer linkages according to a simulated growing process.

Phytomers are connected to each other (on the same axis or when branching), building an oriented graph, from the seed to the leaves.

Simulation of the growth process is thus a dynamic scheme integrating new (nodes) phytomers at the end of axis lists, or adding new pathways (new axes on axillaries) to existing nodes.

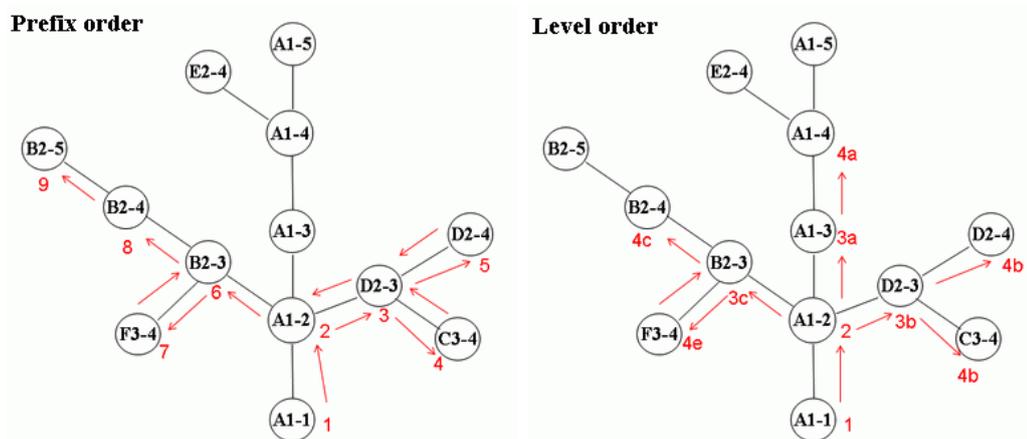
However, implementation of this growth process can be quite different from what happens in nature.

Two main strategies can be found in the literature:

1. Building the structure step by step, trying to mimic natural growth.
This approach is popular for FSPM, but is costly, especially for applications where periods of interest (harvest) will require use of the full structural plant history.
2. Building the structure at a given specific age, known from the outset.
This approach is popular in structural approaches, and is usually efficient (since intermediate stages are not explicitly considered).
Implementation in FSPM is, in this case, more difficult, since the history must be considered when building the structure.

Note that, when considering stochastic structures, for applications at stand level, both approaches require the building of a significant set of simulated structures, leading to significant computational and memory costs.

Another point is that, in both cases, construction of the structure, built by a mathematical tree transversal path, may not reflect growth dynamics, as illustrated below.



Various tree traversal construction methods (Drawings M. Jaeger, CIRAD)

Prefix order (left) is fast and of low spatial cost. Only the last step is faithful to living plant development. Hierarchical order is effective for visualization. Only the last step is faithful to real plant development. Level Order (right) is the closest to real plant development. Note, however, that phytomers appearing in the same cycle should be processed simultaneously.

In GreenLab model implementations, the preferred construction mode is a Prefix order transversal construction.

Botanical reminders

Architectural Botanical reminders

Summary

Plant structure establishment results from elementary components called phytomers, developed by terminal meristems.

They build leafy axes showing different levels of function and morphology. These levels define an axis and phytomer typology, which can be characterized by a physiological age.

Branching occurs at the leaf axis.

At the mature stage, the basic ramified structure strategy duplicates building reiterations.

Plant growth and development result from the meristem activity.

Structure establishment results from [primary growth](#), while branch thickness results from [secondary growth](#).

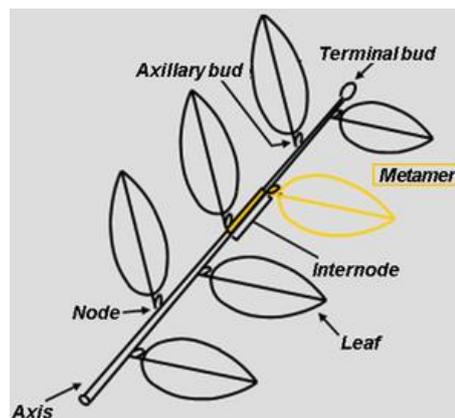
The Leafy Axis

The fundamental structural unit of the plant body is called a [phytomer or metamer](#).

A phytomer is formed by a node with its leaf (or leaves), its axillary bud(s) and the subtending node.

Successive phytomers formed from a terminal bud build an axis.

Axillary buds, at the axils of leaves, allow branching.



The leafy axis (Drawing D. Barthélémy, CIRAD)

*A leafy axis is built from successive phytomers formed from the apical (terminal) bud
A phytomer is defined by an internode and various organs branched on it, including leaves.*

Axillary buds, enabling branching, are located in the leaf axils.

In many species (for instance temperate) the edification of an axis is due to a rhythmic growth process. The axis is thus built from several [growth units](#).

Considering the growth unit is an important key for modelling, since some architectural patterns are defined at this level, such as the branching pattern.

Important facts to consider for modelling aspects

The leafy axis is a construction built from successive discrete elements: phytomers.

Continuous growth must be distinguished from the rhythmic case. In rhythmic growth, axis construction must occur on two scales: first the construction of the growth unit from successive phytomers, then the succession of growth units.

Branching potential must be considered at phytomer level.

A phytomer enables several types of branching (since several organs may arise from it)

Physiological age and reiteration (reminder)

Plant structure shows a different axis typology depending on the branching level or other anatomical criteria related to terminal bud differentiation.

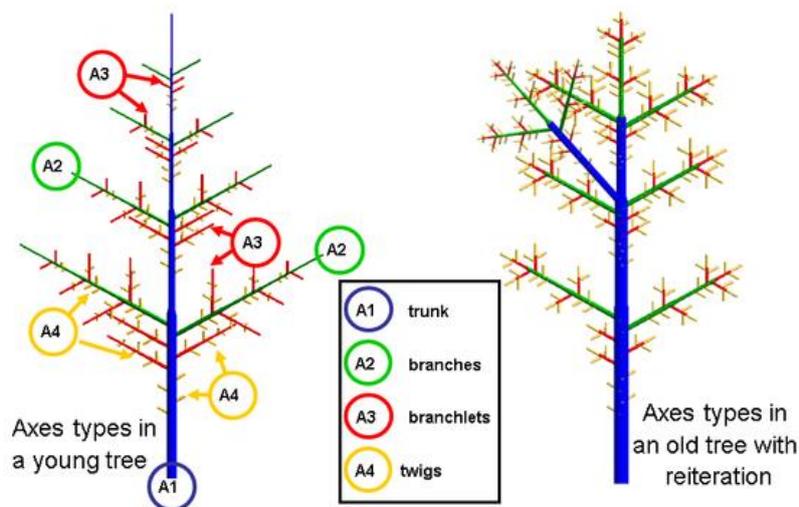
Physiological age

In architectural botany, the level of axis differentiation can be characterized by a **physiological age**. A given physiological age is associated with specific morphological and phenological traits, such as axis orientation, sexuality occurrence or not, specific branching patterns, etc.

Reiteration

As the plant develops, at mature stages the structure developing according to the architectural unit may duplicate.

This specific branching case is called **reiteration**.



Physiological age and reiteration (Images P. de Reffye, CIRAD)

In the above example, four physiological ages are used to define the axis typology.

- Physiological age 1, in blue, characterizes the vigorous axis (such as the trunk).

- Physiological age 2 in green stands for the branches
 - Physiological age 3 is coded in red for the branchlets
 - In yellow, physiological age 4 stands for the twigs.
- This colour code (with the colour magenta for physiological age 5) is used as a standard in GreenLab modelling representations.
- Left, the axes show physiological age transition (from blue to green, from green to red).
The structure also illustrates a reiteration (in blue).

Comments for modelling

1. In the GreenLab modelling approach, the physiological age is not related to the axis but to the phytomer (and the growth unit).
As the axis develops, the terminal bud may change its physiological age. On a given axis, physiological age transitions are thus possible, but always in the same way of ageing, from the lower physiological age to the higher one.
2. To simplify, in the GreenLab approach, total reiteration is only allowed on physiological age 1. In other words, the physiological age of the branched axis is higher (classic branching) or equal (reiteration) to the phytomer bearer's physiological age.
3. Branching order. Note that the branching order (the rank given by the number of branchings from the current phytomer position to the seed) is not the physiological age. Defining structural simulations based on the branching order (such was the case of the first AMAP simulations in the 80s) does not allow easy implementation and modelling of morphological gradients and reiterations.

Bibliography

Barthélémy, D., Caraglio, Y., 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. *Annals of Botany*, 99 (3) : pp. 375-407 19 ([access to paper and pdf](#))

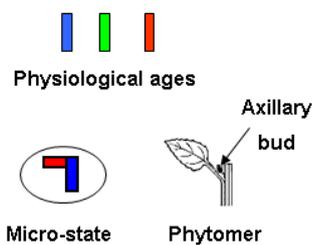
Modelling - Simulating plant organogenesis

The different levels of botanical plant structural elements (i.e. growth units, axis, architectural unit, and reiteration) can be generated using a [dual scale automaton](#) (Zhao, X. et al, 2001).

Micro-states

The phytomer (metamer), the fundamental structural unit of the plant body, is attached to a micro-state. In order to reflect the botanical typology, several micro-states usually need to be defined for a given physiological age.

A common usual framework leads to a micro-state $Mi_{i,a}$ being defined from both the physiological age of the internode (i) and the physiological age of its axillary bud (a).



Physiological ages, metamer and micro-state (Drawing X. Zhao, LIAMA, CASIA)

The physiological age of the micro-state's internode is 1, while the physiological age of its axillary bud is 3.

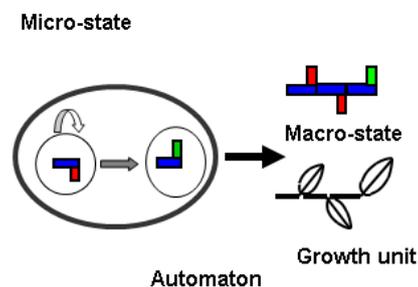
At a given physiological age, a simple automaton can generate a growth unit (or a full axis portion in the case of continuous growth) thanks to micro-state successions.

A growth unit is thus defined by a list of micro-states with their occurrences.

Macro-states

A micro-state sequence building a growth unit is called a macro-state

In the following example, this macro-state could be codified as $((Mi_{1,3}, 2), (Mi_{1,2}, 1))$, describing a growth unit of three metamers of physiological age 1, respectively bearing axillary buds of physiological ages 3, 3, and 2.



Micro-states, and a growth unit (Drawing X. Zhao, LIAMA, CASIA)

The automaton generates the sequence $((Mi_{1,3}, 2), (Mi_{1,2}, 1))$ and builds a macro-state, representing a growth unit.

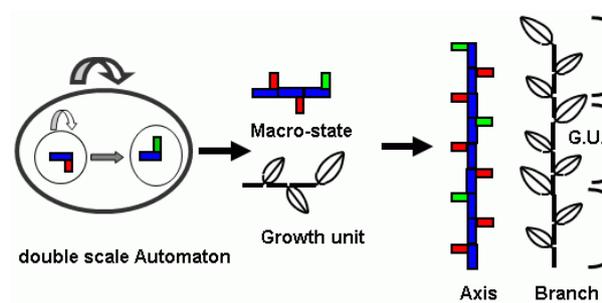
Bibliography

Zhao, X., De Reffye, P., Xiong, F. L., Hu, B. G., & Zhan, Z. G., 2001. Dual-scale automaton model for virtual plant development. The Chinese Journal of Computers, 24(60), pp. 608-617

From Micro/Macro-states to the whole plant

The different levels of botanical plant structural elements (i.e. growth units, axis, architectural unit, reiteration) can be generated using a dual scale automaton. The first scale relies on micro-states building macro-states. Macro-state transitions define the second scale.

We can build axes from a list of successive macro-states, representing the succession of growth units.



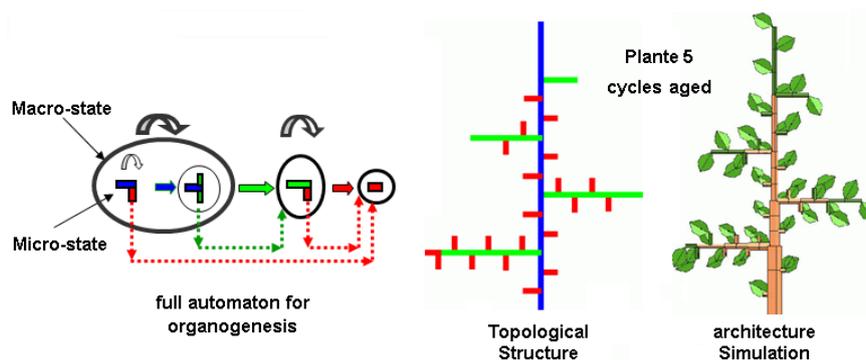
Micro-states, Macro-states and growth units (Drawing X. Zhao, LIAMA, CASIA)

This axis of three growth units repeats the same macro-state three times $((Mi_{1,3}, 2), (Mi_{1,2}, 1))$.

This construction remains similar to micro-states, except that the physiological age may vary, in order to model mutation.

The automaton is thus a double scale automaton, building, on the first scale, macro-scales from micro-state sequences, and then the whole structure from macro-state sequences and branching.

Note that micro-state and macro-state transitions are sufficient for building all levels of the plant architecture hierarchy: growth units, axis, architectural units and reiterations.



Building the whole structure (Drawing X. Zhao, LIAMA, CASIA, P. de Reffye, CIRAD)

Left: Three macro-states are involved in this construction structure.

Middle: This structure is obtained applying 5 cycles on the automaton. It characterizes the structure topology.

Right: A 3D graphical output is computed from the topology, adding geometrical traits to the metamers, such as length, diameters, angles and colour attributes.

Optimizing dual scale production

For a given cycle t , meristems of the same age and physiological age may produce the same pattern in a plant architecture. In other words, the dual scale automaton will produce similar productions arising from similar macro-states.

In the GreenLab model, the automaton productions are indexed, computed once, and instantiated if already computed, avoiding this redundancy.

Sub-structures

Similar patterns derived from organogenesis are called **Sub-structures**. In fact, all ramifications occurring at time ta from a set of identical micro-states share the same fate at a given date ts .

Therefore, by definition, a given substructure $S_{p,ta}(ts)$ is classically indexed by a physiological age p , and by two times corresponding respectively to the sub-structure appearance growth cycle ta (the date its first phytomer appears), and the current simulation time ts (the age of the tree expressed in growth cycles).

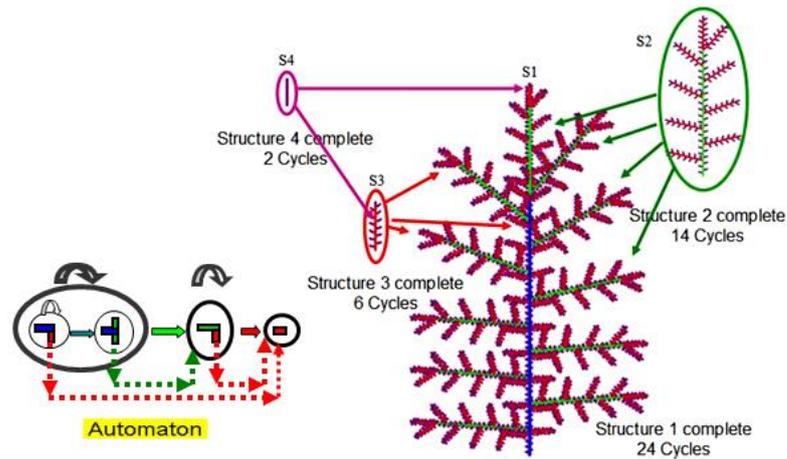
The value $ts - ta$ is thus the age of the substructure.

Computationally, substructures are defined recursively from the higher physiological stage (i.e. from the smaller pattern) to the lower (i.e. for the whole plant).

Since the number of physiological ages is limited, as well as the number of micro-state and macro-state transitions, the combinatory of sub-structures is also limited. It can be shown that their number is linear in time (proportional to ts).

Sub-structures make the GreenLab approach very efficient for computing plant architecture, since similar patterns are not computed again, or stored, a single representative is stored, and the others just refer to it.

However, plant 3D representations (required for instance for visualisation) still need to instance all sub-structures, exploring each substructure, the stored one and also each reference of it, with different geometrical positions and orientations.



Sub-structures on a simulated determinate plant aged 24 at the end of its growth (Drawing X. Zhao, M.G. Kang, LIAMA, CASIA, and P. de Reffye, CIRAD)

The dual scale automaton is on the left.

In this example, all axes show determinate growth.

In this case, all structures of a given physiological age are identical.

Sub-Structure S4, carries leaves of physiological age 3, and contains 2 phytomers.

Sub-Structure S3, carries 6 S4 sub-structures plus 12 phytomers.

Sub-Structure S2, carries 7 S3 sub-structures and two S4 sub-structures plus 18 phytomers.

Sub-Structure S1, carries 11 S2 sub-structures plus 22 phytomers.

The storage requirement is thus $2+(6+12)+(9+18)+(11+22)=81$ elements, instead of $11(9*(6*2+12)+18)+22=2596$ phytomers.*

Bibliography

Yan H.-P., Barczi J.-F. , de Reffye P., and Hu B.-G., 2002. Fast Algorithms of Plant Computation Based on Substructure Instances. International Conferences in Central Europe on Computer Graphics, Visualization and Computer Vision 3/10 (2002) pp. 145-153 ([pdf](#))

Stochastic development modelling

While some agronomic plants show a deterministic architecture (maize, wheat, etc.) which can be fully grasped by an automaton, most plants show significant variability in their structures, even considered at plant level, such as on two similar axes derived from the same phytomer: they may show a different number of phytomers.

Theoretical framework

Since plant structure is established from discrete elements (phytomers), such modelling relies on statistical distribution modelling.

The proposed process to be modelled concerns:

- axis development: this means the probability of a new phytomer appearing (i.e. of repeating the current micro-state or of moving to the next one in terms of the automaton)
- axis mortality: this means the probability of a metamer dying
- axillary bud branching: this means the probability of a new axis developing

The Renewal theory is the branch of probability theory that generalizes Poisson processes for arbitrary holding times. In probability theory, a Poisson process is a stochastic process that counts the number of events and the time points at which those events occur in a given time interval. Such stochastic models are derived from classic Renewal theory.

According to Feller (1968), a renewal process is a stochastic model for events that occur randomly in time. The basic mathematical assumption is that the periods between successive arrivals, called renewal time, are independent and identically distributed.

Given the mean and variance of renewal time, the number of events during time T (whose distribution is known as the counting law), is asymptotically normally distributed.

In our discrete case, because of the convergence of the counting law towards a normal law, we can approximate this distribution by a binomial law, and the time T can then be replaced by a virtual discrete time N .

Axis development

Modelling axis development means modelling periodic and random rests in phytomer occurrences. In quantitative terms, we aim here to define the law characterizing the appearance of a new phytomer.

Such a process can be modelled by a Bernoulli process, characterized by a probability p of success (occurrence of a new phytomer) and thus a probability $q = 1 - p$ of failure (a rest).

Applying this process at successive time steps thus defines a list of Bernoulli trials, leading to a list of success (referred to here by the number "1") and failure (referred to by "0") sequences, where the number of successes ("1") stands for the number of phytomers.

With this encoding, the number of phytomers is simply given by the sum of the numbers referring to the status of each step.

In practice, the time step is chosen as an interval of thermal time, usually defined from the smallest time between the appearance of two phytomers on the plant's main axis (i.e. on an axis of physiological age 1). This time step is defined as the plant growth cycle.

In more detail, modelling the development of a given axis means characterizing two processes:

- The rhythm ratio w_φ of the axis (of physiological age φ) defined as the ratio of potential new phytomer occurrence on this axis of physiological age φ to the potential occurrence on an axis of physiological age 1, standing as a reference.
- Then on the axis, definition of the probability of a success, or more generally, definition of the number of phytomers n generated in a given period N .

In other words, the rhythm ratio involves periodic rests in phytomer production allowing different axis development rates in the plant structure, as opposed to random rests (failures) in phytomer occurrence.

Bibliography

Feller, W., 1968. An introduction to probability theory and its applications, vol. 1, 3rd edn. Wiley, New York

Stochastic axis development modelling

Rhythm ratio

The rhythm ratio w_φ of a given axis (of physiological age φ) is defined as the ratio of potential new phytomer occurrence to the potential occurrence on an axis of physiological age 1.

The rhythm ratio w of a given axis characterizes the relative alternating periodic rests and activity.

The rhythm ratio is modelled as a periodic rest.

In other words it defines a pattern of periodic sequences (1 and 0), in which pattern 1 stands for potential phytomer appearance (in fact a slot of a Bernoulli trial), and 0 for a rest (a phytomer will never appear on its corresponding growth cycle).

As an example, an axis with a rhythm ratio of 0.5 will develop twice as slowly as the main axis (assumed to be the reference with $w = 1$), and the rhythm ratio will be modelled by the following sequence 1010... 10...

This model is in fact the definition of a discrete linear stair function:

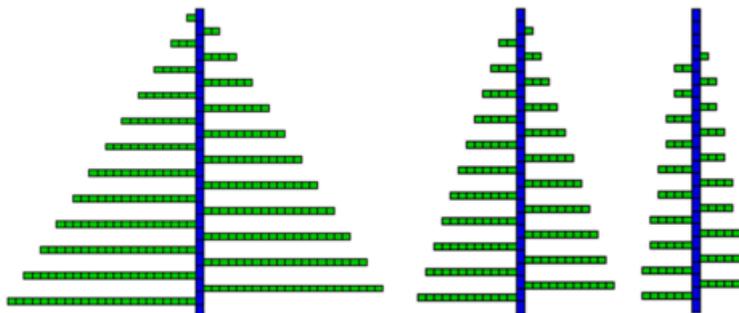
$$y_i = w \cdot x_i$$

where $x_i = 1, 2, 3, 4 \dots$ stands for the consecutive growth cycles, and y_i stands for the number of Bernoulli trials.

The slope increment is known to be expressed as a period of successes (1) and failures (0) where w is defined by the number of successes divided by the number of successes and failures.

Depending on the w value this period can be more or less long, leading to approximations if a short number of cycles is considered.

For instance, a rhythm ratio of 0.6 defines a 5 step period: 11010



Various rhythm ratios (Drawings P. de Reffye, CIRAD)

Left: both physiological ages 1 and 2 develop phytomers at the same rhythm; the rhythm ratio w_2 of the physiological age 2 axis is 1.

Middle: w_2 is set to 0.5

Right: w_2 is set to 0.25

Modelling the development of an axis

We consider now the non-periodic random aspect of phytomer occurrence.
We associated a Bernoulli process of probability b of a new phytomer appearing.

Case of a constant occurrence probability

If probability b is constant during axis life, after N growth cycles, the distribution of the number of phytomers follows a Binomial Law $B(N,b)$ (see preliminary Mathematical course). The expected value of $B(N,b)$, i.e. the average number of phytomers on the axis of N growth cycles is thus: $M = N \cdot b$ and the variance is $V = N \cdot b \cdot (1 - b) = (1 - b) \cdot M$

This simple model can thus be straightforwardly used on an axis showing continuous growth (cotton, coffee, etc.). It is interesting to note that the relation between the expected value M and variance V helps to define the b parameter from simple distribution measurements. It only requires the computation of M and V for a significant number of axes, at different stages N of growth.

This is still true if the relation between the expected value and variance is not linear; such is the case of damped growth.

The case of damped growth

Let us suppose that the probability decreases along the axis according to: $b(i) = b^i$ it can thus be shown that, for a given growth cycle K , the expected value X_N and the variance V_N are respectively:

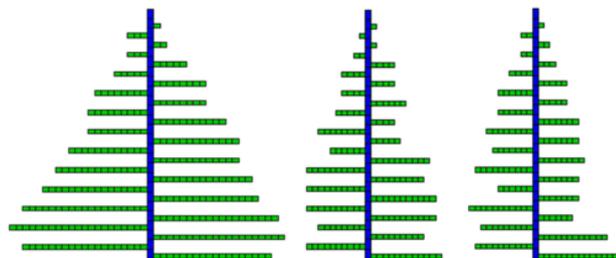
$$X_N = b \frac{1-b^N}{1-b} \quad V_N = \frac{1-b}{1+b} (X_N + X_N^2)$$

Once again, in this case, the definition of probability b can be derived from the relation between the expected value and variance, quadratic in this case.

This modelling approach is of great interest for practical use, since its full mean parameter (b) can be computed from statistics provided on phytomer distributions, resulting from actual plant internode counting.

This parameter fitting is described in the application chapter ([./App/GLapp_fitst_012.html](http://App/GLapp_fitst_012.html)).

Of course, the rhythm ratio and Bernoulli process convolve, as shown below.



Binomial phytomer law distribution and rhythm ratio. (Drawings P. de Reffye, CIRAD)

Left: Physiological age 2 axis appears by a probability $b = 0.8$

Middle: The rhythm ratio of these axis, in green, is now set to $w_2 = 0.5$

Right: Another stochastic realization with $b = 0.8$ and $w_2 = 0.5$

Stochastic axis viability modelling

Apical bud delays, corresponding to Bernoulli process trial failures in our modelling, slow down axis growth, but do not stop it. Terminal meristem death may appear at any cycle, stopping axis development irremediably. Introduction of the death process, called mortality, leads to dead axes being distinguished from living axes.

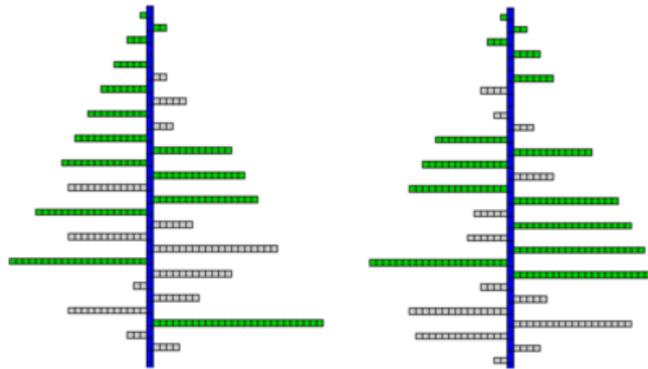
A simple mortality case

Mortality without development delays

Let us first suppose that axis development shows no delays (rhythm ratio set to 1, and probability of phytomer occurrence for each cycle also set to 1, i.e. $w = 1$; $b = 1$).

Let us then consider a distribution of living axes of K cycles, born from terminal buds whose survival probability - also called viability - is c .

Then, the probability of staying alive in the next cycle is: c^{K+1} , and thus the probability of becoming a dead branch is: $(1 - c) \cdot c^K$



Simulating terminal bud viability on a physiological age 2 axis. (Drawings P. de Reffye, CIRAD)
2 simulation examples with viability set to 0.95
Dead axes are shown in grey.
Living axes are drawn in green

The retrieval of viability c in this theoretical case can simply be assessed from the ratio of living and dead axes.

Mortality with development delays

Let us now consider the usual case with development delays where a new phytomer may appear according to a Bernoulli process with a probability b , and a viability c .

The probabilities of staying alive or die at cycle K are unchanged, c^{K+1} and $(1 - c) \cdot c^K$ respectively. This law is a truncated geometric distribution law, whose expected value M_N and variance V_N are respectively

$$M_N = \frac{1 - c^N}{1 - c} \quad V_N = \frac{c}{(1 - c)^2} (1 - c^N (2N + 1)(1 - c) - c^{2N+1}) \quad (\text{Eq. 1})$$

However, the number of phytomers in a given axis of N cycles becomes complex, since this law is a composition of this geometric law and the binomial $B(N, b)$ law.

The probability of an axis of N cycles having K phytomers is:

$$P(Y = K) = \sum_{i=K}^{N-1} (1-c)^i C_i^K b^K (1-b)^{i-K} + c^N C_N^K b^K (1-b)^{N-K}$$

The expected value and variance are then $M = M_N \cdot d$ and $V = b \cdot (1-b) \cdot M_N + b^2 \cdot V_N$ with M_N and V_N as defined in (Eq. 1) giving finally:

$$M_N^d = c \frac{1-c^N}{1-c} b$$

$$V_N^d = b(1-b) \cdot c \frac{1-c^N}{1-c} + b^2 \frac{c}{(1-c)^2} (1-c^N (2N+1)(1-c) - c^{2N+1})$$

A generic mortality law

We have seen that the death rate, or viability, when constant, can be retrieved from measurements on the living and dead axis statistics for given growth cycles.

However, in many cases this viability rate is not stable with the age of the axis, i.e. with the number of cycles.

In most cases, the mortality law is complex, following a sigmoid function shape.

It is thus interesting to fit cumulated dead populations to a classic sigmoid function, leading thus to expressing meristem viability along the axis as a function of the number of growth cycles, such that:

$$S(i) = 1 - \exp(-\alpha \cdot i^\beta)$$

Viability can then be expressed as:

$$c_i = \exp(-\alpha \cdot ((i-1)^\beta - (i-2)^\beta))$$

and the death rate at cycle i is given by:

$$P(i) = \exp(-\alpha \cdot (i-1)^\beta) - \exp(-\alpha \cdot i^\beta)$$

See fitting page ([./App/GLapp_fitst_016.html](http://App/GLapp_fitst_016.html)) as an example.

Modelling development and viability in rhythmic growth

In the case of rhythmic growth, axis development and viability have to be considered as a dual scale process:

- at whole axis level, built from serial growth units, and
- at growth unit level, built from serial phytomers.

On both levels, the modelling approaches introduced for continuous growth can be used, with, of course, differentiated parameterization relative to each level of organisation.

Rhythmic Axis Development

The distribution of the number of phytomers in a growth unit always follows a unimodal or a bimodal curve shape.

The unimodal case (full pre-formation or full neo-formation)

The unimodal case is related to a single functioning process, either pre-formed or neo-formed. The difference lies in the fact that, in the pre-formed case, the phytomer expands building the full growth unit, while in the neo-formed case phytomers appear one after the other until a stop related to a season or to meristem death or flowering (sympodial growth). These unimodal shaped distributions can be fitted to binomial laws.

Growth unit construction is seen as a Bernoulli process with a probability b of each phytomer appearing, applied to a given number of growth cycles N .

The bimodal case (pre-formation followed by neo-formation)

The bimodal case is related to a mixed pre-formed / neo-formed growth unit building process. A first section of the growth unit is built from pre-formed phytomers, followed then by neo-formed phytomers.

This situation is common in many temperate species (poplar tree, wild cherry tree, etc.) but also in tropical species (e.g. cacao tree).

For a given physiological age, such bimodal distribution shapes can thus be fitted with two binomial laws and the probability p_n of having neo-formation.

p_n can be simply assessed by a ratio standing for the proportion of neo-formation occurrences.

However, the neo-formed section may show (-or not) significant dispersion for the number of cycles. This neo-formed section can thus be adjusted to a binomial or to a negative binomial law.

It is interesting to note that, on a single individual, the neo-formed part decreases with the physiological age. The neo-formed part can be systematically seen on the trunk, more or less established on the secondary axis, and not expressed at all on short axes.

On some species, binomial laws parameters are rather stable according to the physiological age, and the various distributions can be fitted by the variation in the proportion of neo-formation.

Stochastic axis branching modelling

At a given phytomer, the branching process is defined by three factors:

- its intensity, quantifying branching occurrence
- its delay, expressed in number of growth cycles, since branching can be immediate or delayed
- the branching pattern, not only as expressed in architectural botany, but also potentially showing couplings along the axis.

Branching intensity and delays

Branching intensity

Branching intensity, or in other words branching probability a_i at a given growth cycle N defines the probability of a new lateral axis occurring.

This value is in fact assigned to a physiological age couple (bearer physiological age and lateral axis physiological age) and classically retrieved from a simple ratio retrieved from distributions: branched phytomers out of total number of phytomers.

Branching delays

Branching may be immediate or delayed according to a specific delay law.

Note that $F(i)$ the axis proportion waking up at growth cycle i , then the occurrence probabilities a_i , are roots of the following system:

$F(0) = a_1$ (probability of immediate branching)

$F(1) = (1 - a_1) \cdot a_2$ (probability of branching in a second cycle, i.e. with a one cycle delay)

.....

$F(i) = (\prod_{k=1,i} (1 - a_k)) \cdot a_{i+1}$

$\sum_{k=0,i} F(i)$ is the total number of phytomers branched at cycle i .

F can classically be adjusted to a sigmoid function (see previous chapter on mortality modelling).

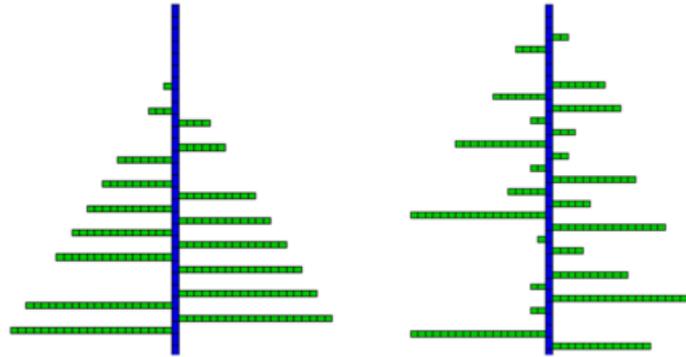
Reversing the model, the branching probabilities can be computed from:

$$1 - a_k = \frac{1 - \sum_{i=0}^{k-1} dF(i)}{1 - \sum_{i=0}^{k-2} dF(i)}$$

This formulation is generic:

Immediate branching is defined by $a_1 = a$, $a_i = 0$ for all $i > 1$

Delayed crowns, corresponding to a constant delay d value, is sometimes observed in bushes. It can be defined by $a_d = a$ and $a_i = 0$, for all $i \neq d$.



Simulating branching delays (Drawings P. de Reffye, CIRAD)
 Left: simulation of a constant branching delay of 7 growth cycles
 Right: the same simulation with stochastic delays

Branching arrangements

Branching arrangements concerns several aspects related to relative branching positioning along a given axis. According to botanical architectural branching patterns, branching may be continuous, diffuse or rhythmic.

Continuous or diffuse branching patterns can be simulated with the intensity model (with or without delays). Rhythmic patterns can be shown on rhythmic growth, as branching positional patterns in growth units (acrotony, mesotony, basitony), usually with morphological gradients within the growth unit. In such a case, one must first define the appropriate micro-states and micro-state sequences in order to mimic successive physiological age branching patterns (examples: growth units of poplar tree, pines, spruce, etc.).

However, branching rhythms on continuous growth, and within growth units, may also appear on phytomer sequences (simulated by the same micro-state). Such cases are classically studied using Markov Chains.

Remember that, in the GreenLab model, the fine geometrical position is not relevant, only the quantitative aspects for a given cycle and physiological age are; in practice a simple coupling model is efficient enough.

An example of branching coupling is given in the Application chapter (http://..App\GLapp_fitst_017.html).



Simulating branching with coupling (Drawings P. de Reffye, CIRAD)
 Left: stochastic simulation with a branching intensity $a = 0.5$
 Right: the same simulation with a coupling $r = 0.7$

Stochastic modelling implementation

Stochastic structural modelling can easily be implemented on the dual-scale automaton.
 A sub-structure strategy can be kept for efficient stochastic simulations.
 Structural factorization can thus also be kept, still allowing formal structure mathematical numbering.

Stochastic automaton

Principles

The dual-scale automaton can easily simulate stochastic transitions for both micro- and macro-scales. The principle is that each transition carries a probability of each process (development mortality, branching) occurring.

By proceeding in this way, implementation respects the modelling principles inspired from renewal theory.

Continuous growth

The Bernoulli process can be straightforwardly applied to micro-state (phytomer) transitions. And of course the rhythm ratio and the viability process too.

In practice, the rhythm ratio defines first whether or not a Bernoulli trial needs to be performed; then viability c is tested. If the terminal bud is still alive, development is finally tested (choosing a random number compared to the probability b).

Applying the process growth cycle by growth cycle, the simulated axis can be encoded by single "1" and "0" codes, respectively standing for phytomer occurrence and rest.

Rhythmic growth

In theory, the same approach could be implemented for both micro- and macro-scales in the case of rhythmic growth.

However, it is often more efficient to define the production of the axis for the whole growth unit (the macro-state), and then distribute it (proportionally among micro-states).

First, a random number K of phytomers is defined from the binomial law $B(N,b)$, where N stands for the number of effective growth cycles (after a potential rhythm ratio filter).

The corresponding macro-state thus holds K phytomers, with those mapped on the micro-state sequence defining the macro-state.

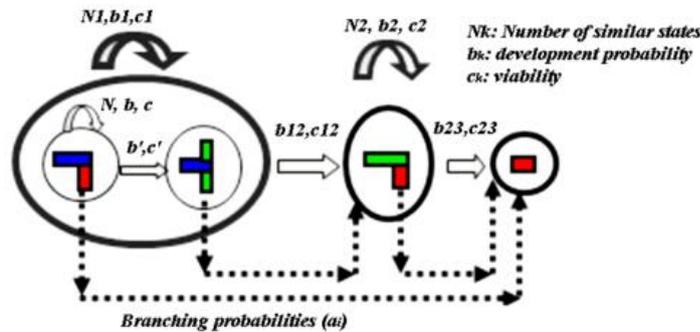
The same approach applies to polycyclism, with pre-formed and neo-formed parts. In this case the K definition from the binomial law $B(N,p)$ is replaced by $Kp + Kn$ where Kp stands for the number of phytomers in the pre-formed part (also derived from a binomial law) and Kn stands for the number of phytomers in the neo-formed part (derived from a binomial or a negative binomial law).

As a result, the construction process leads to a similar output. The simulated axis is encoded by single "1" and "0" codes, respectively standing for phytomer occurrence and rest describing the growth unit sequence. Usually, according to their botanical definition, simulated growth units are separated from each other by rest sequences (list of "0").

Branching

Each micro-state may carry several whorls of lateral buds of different physiological ages.

Each physiological age branching is tested, i.e. the delay expressed in the growth cycle is estimated. When coupling is modelled, branching simulation is potentially controlled by the branching results of the previous phytomer



Stochastic dual scale automaton. (Drawings X. Xhao, Liama-CASIA and P. de Reffye, CIRAD)

The dual scale automaton transitions are controlled by probabilities.

At micro-scale level, transitions are controlled by the development and the viability probabilities b and c applied to the first micro-state sequence,

while b' , and c' apply to the first micro-state to second micro-state sequence.

In the GreenLab model implementation those parameters are identical within macro-states ($b=b'$ and $c=c'$)

Branching probabilities (including delays) are processed by the lower transitions (dotted arrows).

Stochastic sub-structures

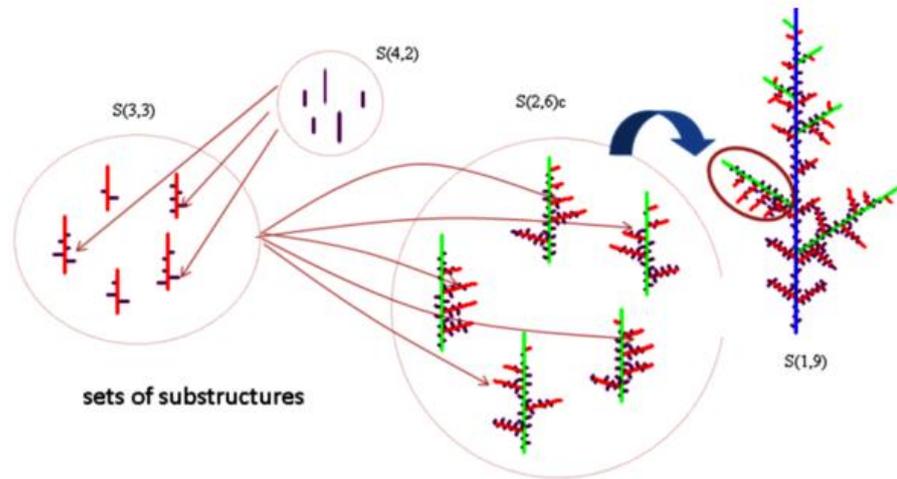
The use of sub-structures can also be extended to the stochastic case.

Each deterministic sub-structure is replaced by a set of a limited number of sub-structures, as representative of the sub-structure distribution for the various phytomer typologies (in terms of expected value and variance).

In a first step, the different sub-structure sets are built, starting from the older physiological ages to the younger.

At each branching, or physiological mutation, the sub-structures are chosen from ones already created.

For practical reasons, the number of representatives is fixed at the same value, in order to minimize storage and construction costs.



Simulating stochastic sub-structures (Images H.P. Yan, LIAMA-CASIA)

In this example each sub-structure group has five stochastic representatives.

Each representative is built using the higher sub-structure groups

Each sub-structure group shows appropriate statistical properties (the sample's expected value and variance fit the theoretical values)

Factorisation

Factorisation basis

According to structural models, sets of similar organs are created for each growth cycle. However, simulation models usually handle each of them individually, which may lead to cumbersome computation in the case of tree growth simulations, as the number of organs may exceed several million.

However, it is not usually necessary to consider local environmental conditions at organ level.

Thus, we can assume that all organs of the same kind, created during the same growth cycle, behave identically.

From a modelling point of view, it leads to a powerful structural factorization of the plant, based on botanical instantiations derived from the concept of physiological age. Compact inductive equations of organogenesis can thus be deduced.

Arguments

About sink organ Geometry

Organ dimensions (internode lengths, diameter, leaf area, etc.) are assumed to be defined from functional modelling, resulting from the organ biomass increase.

The biomass allocated is a ratio of the common biomass pool, defined by the organ sink strength divided by plant demand (the sum of all sink strengths).

This sink strength is related to organ maturity, and does not depend on its position within the plant structure.

This applies for both structure geometry and structure topology.

About source organ geometry

In GreenLab, biomass production modelling is based on the Beer-Lambert law, thus light interception is evaluated by a simple global function.

It does not involve individual organs (leaf) or the orientation of groups of organs; the interception model considers the total leaf area for each growth cycle.

As a result, the geometrical and topological aspects of plant structure can thus be ignored.

Organ factorisation

In the GreenLab model, phytomers of the same physiological age and the same chronological age share the same fate.

GreenLab organ cohorts

Assumption

Metamers of the same physiological age and the same chronological age are considered as identical, whatever their positions in the plant structure.

The set defined by all metamers of the same physiological age p and the same chronological age t defines organ cohorts $C_o(p,t)$, where o stands for the various organs borne by the metamer.

Hence, in a given organ cohort, all organs are of the same type (leaf, internode, flower, etc.) and show the same properties and evolution.

The GreenLab model uses this assumption, evaluating biomass demand and biomass consumption from a single representative of each cohort, multiplied by the number of organs $N_o(p,t)$ in each cohort $C_o(p,t)$.

Compared to process-based models, GreenLab can thus be seen as an extension, defining several cohorts for each organ type instead of a single compartment.

The set of cohorts reflects the establishment of minimal architectural dynamics, restricted to the physiological age and the organ age.

In practice, the cohort chronological age has to be expressed from two dates: the cohort appearance date d_o and the current date d_c .

The appearance date must be expressed relatively to the full plant appearance date, while the current date can be expressed relatively to the appearance of the set of organs (i.e. the cohort age).

Notes

1. Two cohorts $C_o(p, d_o, d_c)$ and $C_o(p, d_o+i, d_c+i)$ of the same organ, with the same number of organs, the same physiological age, the same age, but two different appearance dates show different evolutions, since the biomass availability level is not stable during plant development and growth.
2. Theoretically, the cohort definition assumption fails if geometrical or positioning gradients are considered. However, this drawback can be overcome. In such a case, such as differentiation due to orientation or the cumulated reiteration order, the gradient should be considered as a new typological criterion that can be indexed by a new variable s ; cohorts will thus be indexed by three indexes $C_o(p, d_o, d_c, s)$.

Factorisation

Organic series

The evolutions of cohorts are called organic series, a term coined by R. Buis in 1983.

Ageing

The ageing evolution of a given cohort $C_o(p, d_o, d_{c+n})$, is simply the chronological evolution; the current date is incremented (by a number n of growing cycles).

In such a case, usually:

- the number of elements in the cohort is assumed to be constant
- the corresponding organ sizes (corresponding to the biomass allocated so far) increase
- the corresponding organ gets older, and may reach its term of functioning.

For the given Organ o , the organic series $C_o(p, d_o, d_{o+l})$, born on date d_o , built for the full organ life span l , defines the chronological organic series of o , born on date d_o , of physiological age p .

Position along an axis

Evolution can also be considered on the basis of structural elements.

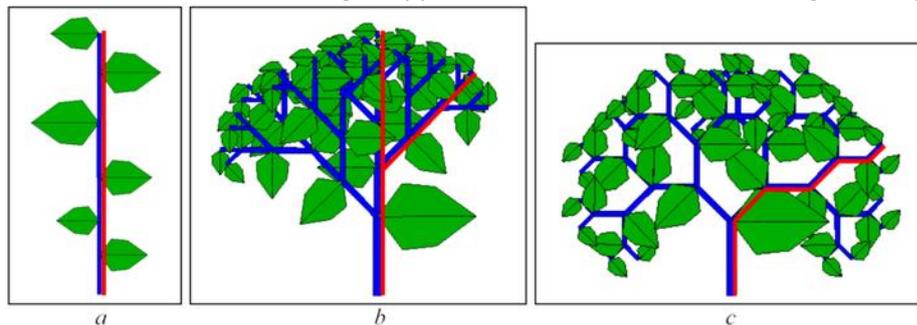
We will show further, that field observations carried out on series built from organs on the same axis, from tip to insertion, allow structural statistical properties to be expressed.

In this case, the series is built from representatives of cohorts on successive appearance dates, corresponding to successive ranks of organ insertion along the axis.

In fact, along the axis, the organic series can be considered from the list of cohorts related to the appearance dates $d_{oi} \rightarrow d_{of} (= d_c)$ of the organs.

From top to bottom, each organ position defines the rank in the cohort set.

These ranks will be consecutive if organ appearance was effective for each growth cycle (no rests).



Organ Series in plant structures (Drawings P. de Reffye, CIRAD)

These examples of series are shown in red, on three structures of the same unique physiological age and same chronological age.

a) A single axis with different phytomers. Two organic series respectively related to the leaves and the internodes describe the organ successions from upper tip to bottom.

b) A monopodial structure showing two similar organic series paths. From apex to seed, all organic series are identical; the successive organ ranks are related to the same cohorts.

c) A sympodial structure. Here also, from apex to seed, all organic series are identical. On this example, they are also identical to those of the monopodial structure, since cohorts from both monopodial and sympodial structures share the same number of organs and organ sizes.

GreenLab development equations

Retrieving the number of organs

Let $N_o(n)$ be the number of organs o functional at cycle n .

This number is to be defined by summing up the organs within the plant structure.

We can thus write:

$$N_o(n) = \sum_{p=1; p_{max}} \sum_{k=n-t_o+1; n} N_o(p, k)$$

where

p is a physiological age

p_{max} the older physiological age.

$N_o(p, k)$ is the number of organs o in all cohorts of physiological age p ,
born at cycle k ($k \leq n$)

t_o is the functional period of organ o

$N_o(p, k)$ can be retrieved when organogenesis is performed by the double scale automaton, using a simple counting programme.

It is possible to formalize recursively the computation of $N_o(k)$ using the sub-structure constructions.

Bibliography

Buis, R., Barthou, H., 1983. Relations Dimensionnelles dans une série organique en croissance chez une plante supérieure. IXème Congrès international de Biologie Mathématique, Paris, 8-10 septembre 1983. Bio-Mathematics revue, Les éditions européennes - France., pp. 1-19 ([pdf](#))

Substructure construction

Buds, Phytomers and Substructures

From the botanical description of the plant, we know that phytomers and buds are the elementary bricks of plant structure. They are derived from buds and build the axes.

Let P be the maximum number of physiological ages in the plant.
In practice, P is generally small ($P < 5$).

At growth cycle t , a metamer (i.e. a micro-state) is characterized by its physiological age p , and the physiological age of its axillary branches q , with $q \leq p$, and its chronological age n . It is denoted by $m_{p,q}^t(n)$.

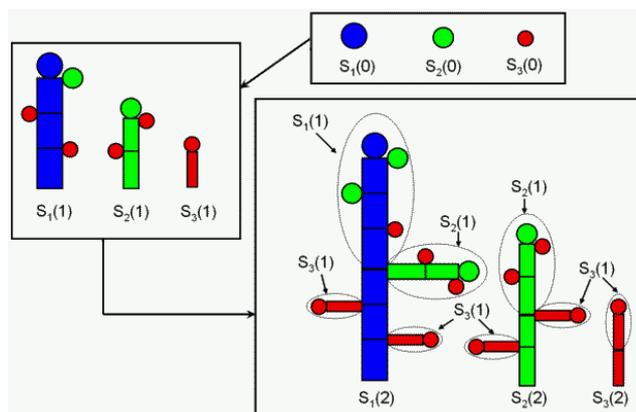
These three indices p , q , and n are sufficient to describe all the phytomers and their number grows linearly with t .

A bud is only characterized by its physiological age p and is denoted by s_p .

The terminal bud of a plant axis produces different kinds of metamers bearing axillary buds of various physiological ages. These buds themselves give birth to axillary branches and so on.

A sub-structure is the complete plant structure that is generated after one or more cycles by a bud. In the deterministic case, all the sub-structures with the same physiological and chronological ages are identical if they have developed at the same moment in the tree architecture.

At cycle t , a sub-structure is thus characterized by its physiological age p and its chronological age n . It is denoted by $S_p^t(n)$. Since the physiological age of the main trunk is 1, at growth cycle t , the sub-structure of physiological age 1 and of chronological age t , $S_1^t(t)$, represents the whole plant.



Substructures encoding (Drawings C. Loi, P.H. Cournède, ECOLE CENTRALE PARIS)

Factorizing plant development and its sub-structure inductive construction: example of a plant with three physiological ages.

Blue, green and red are respectively the colours corresponding to physiological age 1, 2 and 3.

Circles materialize the buds, while rectangles the phytomers.

$S_1(2)$, while $S_2(2)$ and $S_3(2)$ are substructures of age 2 at physiological ages 2 and 3, respectively. They may both appear in the tree at chronological age 3.

The total number of different sub-structures in a plant of chronological age t is very small, usually fewer than 30, even if the total number of organs is high. Sub-structures and phytomers are repeated many times in the tree architecture, but they need to be computed only once for each kind.

The sub-structure construction equation

The concatenation operator to describe the organization of plant phytomers and sub-structures and deduce their construction at growth cycle t by induction is as follows:

1. Sub-structures of chronological age zero are buds:

$$S_p^t(0) = s_p$$

2. If all substructures of chronological age $n - 1$ are built, we deduce the sub-structures of chronological age n as:

$$S_p^t(n) = [\prod_{p \leq q \leq P} (m_{p,q}^t(n))^{u_{p,q}^{(t+1-n)}} (S_q^t(n-1))^{b_{p,q}^{(t+1-n)}}] S_p^t(n-1) \quad (\text{equation 6})$$

for all (p,q) such as $p \leq P$ and $(p \leq q \leq P)$

where

$u_{p,q}$ corresponds to the number of metamers $m_{p,q}(t)$ in growth units of physiological age p appearing at growth cycle t

$b_{p,q}$ corresponds to the number of axillary sub-structures of physiological age q in growth units of physiological age p that appeared at growth cycle t

These sequences can be deterministic or stochastic.

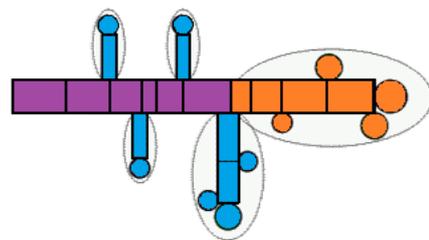
This construction equation is used to count the metamers of each sub-structure.

Formula interpretation

$\prod_{p \leq q \leq P} (m_{p,q}^t(n))^{u_{p,q}^{(t+1-n)}}$ stands for the existing old phytomers on the sub-structure main axis (the base growth unit)

$\prod_{p \leq q \leq P} (S_q^t(n-1))^{b_{p,q}^{(t+1-n)}}$ stands for the lateral sub-structures borne by the base growth unit (they are one cycle younger)

$S_p^t(n-1)$ stands for the sub-structure grown from the apical bud of the base growth unit (also one cycle younger).



(Drawing M. Jaeger, CIRAD)

Note

\prod is the product operator, used in mathematics to represent the product of a bunch of terms.

$$\prod_{k=2,5}(k) = 2 \times 3 \times 4 \times 5 = 120$$

Bibliography

Yan H.-P., Barczi J.-F. , de Reffye P., and Hu B.-G., 2002. Fast Algorithms of Plant Computation Based on Substructure Instances. International Conferences in Central Europe on Computer Graphics, Visualization and Computer Vision 3/10 (2002) pp. 145-153 ([pdf](#))

Stochastic equations

Organ numbering using the sub-structure approach can be extended to the stochastic case.

This topic is beyond the scope of this course.

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Kang, M.G., Cournède, P.H., de Reffye, P., Auclair, D and Hu, B.-G., 2008. Analytical study of a stochastic plant growth model: Application to the GreenLab model. *Math. Comput. Simul.* 78, 1 (June 2008), pp. 57-75

Structure construction

Reminders: The GreenLab model structural principles are:

- structure construction results for a discrete growth process simulating the construction of a leafy axis by phytomers
- in the structure simulation, topological aspects (the branching scheme) are separated from the geometrical aspects
- axis typology is defined from the notion of physiological age, and not from branching order
- the construction can be stochastic
- the structure topology and geometry are not required: the number of organs produced per growth cycle and their status are the only requirement of the model when 3D is not necessary.

Structure construction modes

Implicit and explicit structures

In the GreenLab model, structure construction can be

- fully implicit:

without geometrical construction
without topological construction
the description is limited to the definition of the number of organs per cohort
This mode is called the **matrix construction mode**.

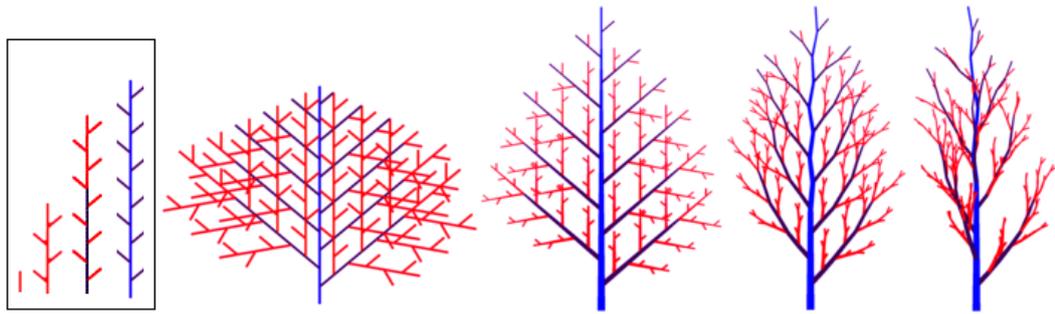
- topological only

without geometrical information
simple flat representation possible
the construction defines what is branched to what, building a topological graph.
This mode is called the **list construction mode**.

- fully explicit

with a geometrical construction
allowing 3D representations
this construction is built on the list mode, applying organ dimensions to the structural components, and introducing angles at branching.

In the GreenLab approaches, in most implementations, the geometry is post-processed.



From structural simulation to 3D representations (Images M. Jaeger, CIRAD)

From left to right:

Four axis representations (internode cohorts) at the final growth cycle.

The structure construction showing its topology (geometry is flat)

The fully explicit structure with organ sizes

The fully explicit structure with organ sizes, branching angles and deviations

The fully explicit structure with organ sizes, branching angles, deviations and phyllotaxy (3D).

Structure construction basis

The phytomer builds the elementary unit that the structure is built with.

We have however seen that organogenesis and stochastic modelling apply to a given number of growth cycles, thus considering the axis level.

Axis of Development notion

In structural and functional structural plant models, plant structure construction is performed individually, plant by plant.

In the GreenLab model, since an explicit structure is not required to simulate plant development and growth (only the number of organs per cohort needs to be known), structure construction is only partially done.

More precisely, only simple sequences of structure are computed and stored, one for each physiological age. In the case of stochastic simulations, a limited number of stochastic realisations are computed for each physiological age.

These sequences are in fact defined by the Bernoulli trials applied to each physiological age (and stochastic realization).

They define the plant's **axes of development**.

Axes of development

The axis of development Axd_{φ} of physiological age φ defines the successive results of the Bernoulli trials applied to the terminal meristem of physiological age φ from the seed stage to plant age.

Axd_{φ} is thus a state list for instance $\{0,0,0,1,1,1,0,1,0,1,1,\dots\}$

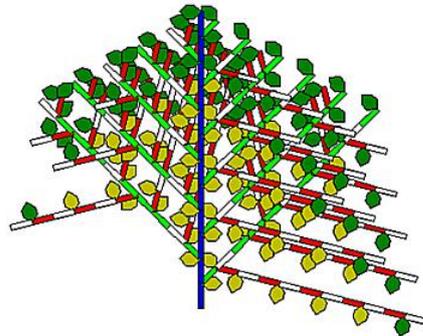
where

- $Axd_{\varphi}(i) = "1"$ (a Bernoulli trial success) defines therefore a phytomer of physiological age φ , whose ontological age is i .
This phytomer is thus explicit, and its properties are explicitly defined; in particular, its bearing organs, defined from the dual scale automaton.
An efficient way of encoding is to encode the physiological age of its axillary bud instead of "1" (see figure below).
- $Axd_{\varphi}(i) = "0"$ (a Bernoulli trial failure) defines therefore a rest occurring at cycle i .

Axd_{φ} defines any axis paths of physiological age φ in the plant.

A simple example

2	2	2	2	2	2	2	2	2	2	2	2	2	2	W=1	
3	0	3	3	3	0	3	3	3	0	3	3	3	3	W=0.75	
4	0	4	0	4	0	4	0	4	0	4	0	4	0	4	W=0.5



An example of continuous axes of development (Image P. de Reffye, CIRAD)

This continuous growth example shows three physiological ages

Top, the 3 axes of development are shown on 13 growth cycles.

Physiological age 1 axis has a development ratio of 1, has no rest, and each phytomer bears a physiological age 2 axis.

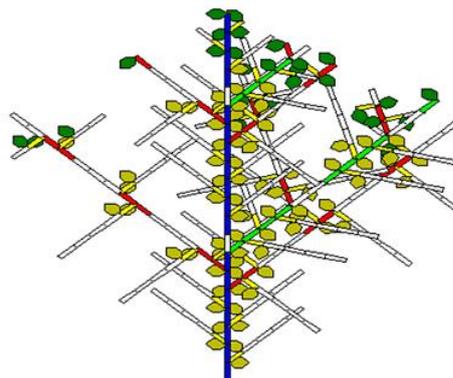
Physiological age 2 axis has a development ratio of 0.75, has no rest, and each phytomer bears a physiological age 3 axis.

Physiological age 3 Axis has a development ratio of 1, has no rest, and each phytomer bears a physiological age 4 axis, but does not branch.

The corresponding reconstructed structure is shown below. Internodes in grey are virtual ones and indicate rests.

Another example with rhythmic growth

4	4	4	4	3	3	2	0	4	4	4	4	3	3	2	0	4	4	4	4
4	4	4	3	0	0	4	4	4	3	0	0	4	4	4	3	0	0	4	4
4	4	0	0	0	4	4	0	0	0	4	4	0	0	0	4	4	0	0	0
5	0	0	0	0	5	0	0	0	0	5	0	0	0	0	5	0	0	0	0



An example of a rhythmic axis of development (Image P. de Reffye, CIRAD)

This rhythmic growth example shows four physiological ages

The 4 axes of development are shown on 20 growth cycles.

All axes show acrotony

Rest periods on rhythms of the 4 physiological ages are not synchronized.

The corresponding reconstructed structure is shown below. Internodes in grey are virtual ones and indicate rests.

Axes of development lists define the basis of structure construction in the GreenLab model.

Axis of Development representation

The axis of development state list can be easily represented as a part of an axis, with a simplified geometry. Attributes can be reported for each awakened state.

So far, we have encoded the physiological age of the axillary in the previous examples.

But other characters are worth encoding such as:

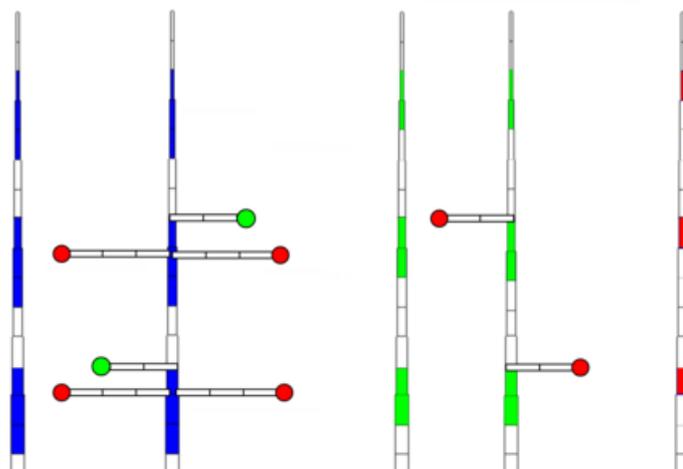
- branching delay
- other organs (leaves, sexuality), etc.

In our representation examples, the underlying geometry is simple.

For instance, in our examples, all states are represented by a rectangular cell, with a unit length and a width reversely proportional to the ontogenetic age.

Axillaries are shown with an insertion angle of 90 degrees, and 60 degrees for leaves.

Cell colours reflect the status: grey if virtual (no phytomer, corresponding to a rest), blue if phytomer physiological age is 1, green for 2, red for 3, red for 4, etc.



An example of axis of development representation (Drawing M. Jaeger, CIRAD)

This rhythmic growth example shows three physiological ages for a temperate species.

From left to right:

Physiological age 1 axis of development. Cells in blue stand for phytomers, while grey stand for a rest cycle.

Physiological age 1 with its axillaries. Note the branching delays, allowing synchronisation for the next growth cycle.

Physiological age 2 axis of development. Cells in green stand for phytomers.

Physiological age 2 with its axillaries.

Physiological age 3 axis of development. Cells in red stand for phytomers.

The set of axes of development allows implicit and explicit structure reconstruction.

Axis development

The successive states describing a specific axis in the plant structure can be retrieved from its corresponding axis of development (same physiological age). It is in fact a simple copy, with an offset corresponding to the ontogenetic age.

This copy ends at the shorter term derived from:

- plant age,
- a transition to a higher physiological age,
- a termination specified in the axis of development (determinate growth, or death)

Axis branching

The branching process is a similar operation, except that the corresponding axis of development is defined by the physiological age of the axillary (and not the bearer's age)

Reconstruction representation

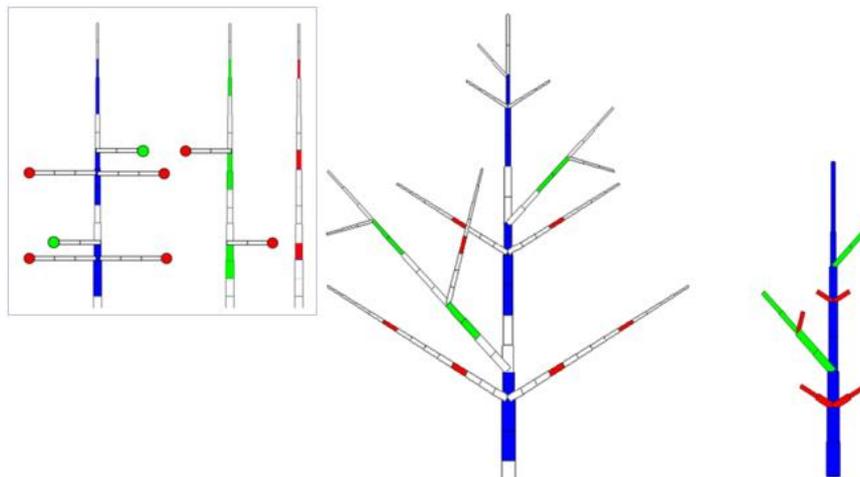
Using the simple axis of development representation framework, it is easy to build flat (2D) structure schemes.

In our representations, branching angles are set at 60 or 45 degrees for better visibility.

The rest periods (in grey) are interesting to visualize, defining the chrono mode view, showing the structure framework from a chronological point of view.

While skipping the grey cells, i.e. skipping the rests, offers a more realistic view, representing only the phytomers, underlying the structure's "real" topology, defining the topo mode view.

These modes are illustrated below.



An example of structure reconstruction (Drawings M. Jaeger, CIRAD)

This example is a reconstruction derived from the axes presented above.

Left: the 3 axes of development.

Middle: representation of the structure reconstruction in chrono mode.

Right: representation of the structure reconstruction in topo mode, skipping the rests.

Note that in this example, the structure is explicitly reconstructed.

The three axes of development are partially copied to define the overall structure.

Stochastic axis of development

Axes of development lists define the basis of structure construction in the GreenLab model. In stochastic simulations, a limited number of axes allows numerous structure reconstructions.

Stochastic reconstruction

In the stochastic case, structure reconstruction using the axis of development remains similar to the deterministic case.

Generation of stochastic axes of development

Principles: for each physiological age, $Nrep_{\varphi}$ stochastic axes of development are created, on the basis of stochastic modelling:

- random generators are initialized for each axis (defining a new seed for random sequences)
- in the development simulation, the Bernoulli trial tests each phytomer occurrence
- viability is estimated at each growth cycle; if mortality occurs, the axis is filled to the dead state ("-1") until the end
- on awakened phytomers, branching occurrence and delay are estimated then stored with the phytomer attributes
- a random number is attributed for each axillary, defining the appropriate "random" axis of development to be considered in structure reconstruction.

In practice, $Nrep_{\varphi}$ is set at 10 to 20 simulations per physiological age.

At high physiological ages, some stochastic axes of development creations may be identical (such is also the case when event probabilities are high).

Structure construction remains virtually the same as the deterministic case.

Axis development

The successive states describing a specific axis in the plant structure can be retrieved from one of its corresponding axes of development (same physiological age). Defining a seed number, the axis description is still a simple copy, with an offset corresponding to the ontogenetic age.

This copy ends at the shorter term derived from:

- plant age,
- a transition to a higher physiological age,
- a termination specified in the selected axis of development (determinate growth, or death)

Axis branching

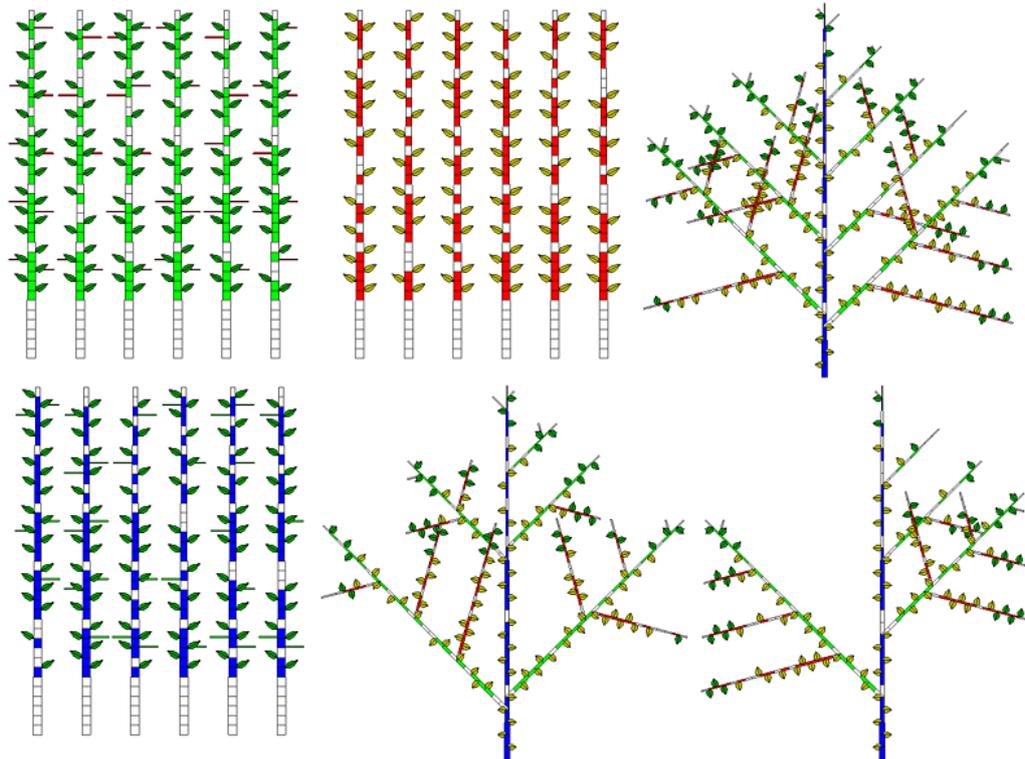
The branching process is a similar operation, except that the corresponding axis of development is defined by the physiological age of the axillary and the seed number computed during axis construction.

Using this procedure, the number of potential structure reconstructions increases considerably.

At each branching, there are $Nrep_{\phi}$ possibilities of using a different axis of development.
 That is to say that, on a simple plant with 2 physiological ages branching at each phytomer, with a stochastic axis on physiological age 2, the number of combinations at N growth cycles is $Nrep_2^{N-1}$.

Example

In the following example, $Nrep$ is set to 25 for all physiological ages.
 Leaf insertions are also presented



Stochastic axes of development (Drawings M. Jaeger, CIRAD)
Simulations of stochastic axes of development ($Nrep = 25$, three physiological ages)
Left and top left: Six axes of development out of the 25 for each physiological age are shown
Right and bottom right: Three stochastic reconstructions derived from the 75 stochastic axes.

Implicit and Explicit Structure construction

In computation terms, structure construction is a costly operation, since it requires multiple axes of development copies and instantiations.

If plant 3D structure representation is not required, these rewritings can be skipped, storing the number of organs in tables (matrices). This fast construction is called the **matrix mode**.

If not, axis of development state lists are effectively copied. By building a tree graph those nodes stand for a state. This construction is called the **list mode**.

Structure Matrix mode

Axes of developments state lists define the patterns on which the structure is built. Building a tree structure thus means defining paths in these axes from state to state within the same axis (axis development) or jumping to another axis (branching).

In a word, the structure matrix mode stores the number of visits of a given state.

The structure matrix mode encodes the plant structure as a multidimensional table, indexed by:

1. The organ nature o
Leaves, roots, internodes, female, male fruits, etc.
However, since the number of organ types is limited and the typology quite constant, separate tables may be used.
In the following, index o is omitted
2. The physiological age φ
as defined from architectural botany, the physiological age φ (in practice limited to 5) is the most representative index
3. The ontological age a
from the bud age, relative to the axis appearance date (set to 1), expressed in growth cycles
4. A random identifier r
specifying an identifier $r = 1, Nrep_{\varphi}$ when stochastic modelling and simulation are chosen.

Each matrix cell thus stands for an organ cohort and encodes the number of organs of the cohort.

Given such tables, organ cohort series can easily be retrieved from single additions. The complexity of the encoding is linear in growth cycles, making it really efficient.

Building the structure in matrix mode

Building the structure means updating the matrix for consecutive growth cycles. After a new growth cycle, the functional model requires structural changes to be defined:

- the number of functional source organs at their different ages (the number of functional leaves),
- the number of functional sink organs at their different ages (in order to evaluate the plant demand).

We assume that the current growth cycle is i .

Let us consider organs / phytomers / axes of physiological age φ borne at cycle a living at cycle i and

write their number $M(\varphi, a, i)$ (assumed to be known at cycle i)

At cycle $i+1$ all cells are initialized to 0: ($M(*, *, i+1) = 0$)

Let us evaluate the new number of organs / phytomers / axes at the next cycle $i+1$ in the determinate case (not stochastic).

We have seen that structure development occurs from the apical bud (leading to new phytomer occurrences on the current axis) and from axillaries (branching process).

Axis development

A new phytomer appears on the axis if $Axd_{\phi}(i+1) > 0$.

Such will be the case of all axes borne at ontological case a and of physiological age φ

We then have:

$$M(\varphi, a, i+1) = M(\varphi, a, i+1) + M(\varphi, a, i) \quad (M(\varphi, a, i+1) \text{ was initially set to } 0)$$

Branching

Let us now consider the case of a branching (or a transition), with m axillary buds of physiological age φ_2

Note that:

- with our list encoding φ_2 is given by $Axd(\varphi, i)$
- we may have partial or total reiteration with $\varphi = \varphi_2$.

In the branching process a new axis appears, borne at age $i+1$.

We thus have:

$$M(\varphi_2, i+1, i+1) = M(\varphi_2, i+1, i+1) + m \cdot M(\varphi, a, i)$$

At this point, a loop must be performed on all ontogenetic ages, since development and branching may occur for each of them.

This recursive definition is in fact one implementation of the recursive sub-structure construction, as defined previously (see [here](#)).

The stochastic case is derived straightforwardly from the deterministic case, using the stochastic axes of development for each random identifier.

In more detail, matrix mode cell filling must be filtered by the corresponding organ properties:

- the appropriate number of organs per phytomer
- filter organ occurrence in respect of a minimal ontogenetic age if required
- filter organ occurrence according to its lifespan(*)
- limit reiteration development if the maximal order is reached

(*) Self pruning is not always a good idea to be implemented at this stage:

it is better to check if the organ is still a biomass producer/consumer when estimating production. By doing so, the encoding allows the matrix to be revisited at past growing stage cycles.

Explicit Structure construction

Axes of development state lists define the patterns on which the structure is built.

Building a tree structure thus means defining paths in these axes from state to state within the same axis (axis development) or jumping to another axis (branching).

The structure matrix mode stores the number of visits of a given state.
While the structure list mode stores the state paths.

List mode

Building the structure in list mode

Building the structure means updating the list structure for consecutive growth cycles.

In our implementations, we chose to define the list structure at the final simulation stage, using a prefix tree transversal construction. The structure list is therefore never updated on past states; it only adds states along the tree transversal at the final stage.

Topological information (what is borne by what) is not necessary in our application but helps for geometrical feature integration (mechanics) and visualisation.

Given an empty list $lst \leftarrow 0$, a final age N expressed in growth cycles, and the axis of development $Axd_{\varphi()}$, the construction scheme introduces a stack S and can be described as follows:

Step 1:

```
lst ← 0 ; // the list is empty
i = 1 ; // the current growth cycle, initialized to 1
φ = 1 ; // the current physiological age, initialized to 1
```

Step 2:

```
S ← Axdφ=1(i=1) ; // stack the first phytomer
```

Step 3:

```
if (S is living, awake and i < N)
  // check if the phytomer is awake and if its age has not reached the tree age
  lst ← S ; // store the top of the Stack (the current phytomer of axis φ and cycle i)
  for (each axillary of S not processed yet)
    S ← axillary(S);
    // Stack the axillary with i=i+1 and φ set to the axillary physio age
    goto step 3 ; // process the branched substructure
    S ← Axd(&phy;,i+1);
    //Stack the next phytomer on the axis with i=i+1 and same φ
    goto Step 3; //Process the axis
  end for
else // all branches in the current stack are explored
  Unstack S; //go back to the bearer axis
  if (S is empty)
    goto Step 4 ; // the stack is empty, all branches are explored
  else
    goto Step 3; // the bearer axis must be explored
```

Step 4:

```
end; // all states are written in lst
```

Optimizing reconstruction

The proposed algorithm constructs an exhaustive list of all states.

It can be optimized, if the list item allows instantiation indexes instead of exhaustive contents:

- either $lst(n)$ contains a state with its attributes (a phytomer with its bearing organs)
- or $lst(n)$ contains a reference to another list item and the length of its description

This implements the sub-structure approach: on the first call to Stack S with (φ, i) arguments the axes of development are explored and the list is updated, while on the next call to the Stack with the same arguments the existing position in the list is retrieved, and the exploration is skipped and a simple reference item is added to the list.

Once more, the stochastic case is derived straightforwardly from the deterministic case, using the stochastic axes of developments for each random identifier in Stack S . Each stochastic plant structure realization will be attributed a different list lst .

In more detail, as for the matrix mode the list state should be filtered by its attributes:

- the appropriate number of organs per phytomer
- filter organ occurrence in respect of a minimal ontogenetic age if required
- filter organ occurrence according to its lifespan
- limit reiteration development if the maximal order is reached.

3D Structure construction

Computing plant 3D geometry

Once the topological structure has been built, 3D geometrical construction can be performed.

This construction is defined in two steps

- computing axis position and orientation, i.e. computing the first internode orientation
- computing axis shape, adding the sequence of internodes building the axis one by one.

Axis position and orientation

The first phytomer defines the branch position and orientation.

The position of the branch is defined by its origin, set to the top of the internode bearing the axis. The orientation is computed relatively to the bearer orientation introducing relative angle deviations due to:

- the branching itself (the new axillary shows a branching angle with the bearer)
- the phyllotaxis angle
- where applicable the whorl angle, if the considered phytomer rank in the whorl is not one.

The way these angles are computed also depends on the geometrical arrangement of the axis (orthotropic or plagiotropic).

The same approach is used to define the orientation and position of other organs (leaves, fruits, etc.)

Axis shape

The total length of the axis is first evaluated (as the sum of its internode lengths).

A global deformation angle is then computed in order to simulate or mimic mechanical bending. Then, starting from the first internode orientation, the axis is constructed internode by internode, applying local deformations, part of the global deformation and, where applicable, twists and torsions.

Note

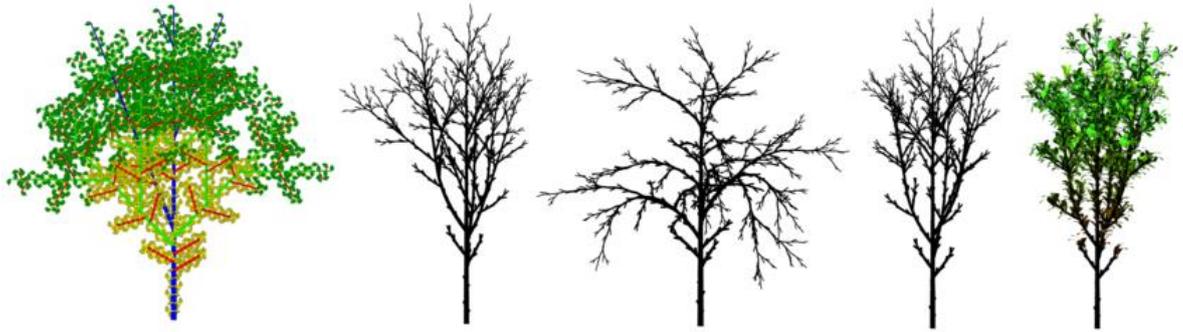
Most of structural and FSP model implementations integrate 3D geometrical computation at early simulation stages.

In the GreenLab approach, since structure is not required to be explicit, 3D geometrical computation is a post-process.

In some implementations, this computation is not even integrated:

- plant topology is exported and geometry is generated by large range tools
- the user parametrizes geometrical parameters interactively (angles, mechanics, etc.)
- the self pruning process can be added and past sequences can be reconstructed
- advanced graphics can be generated.

The following figure illustrates such an example.



From structural explicit simulation to 3D representations (Images M. Jaeger, CIRAD)

From left to right:

The explicit 2D structure construction topology with its organs.

Three geometrical 3D structure reconstructions with various branching angles, bending and twists

The last reconstruction shows leaves.

The four 3D reconstructions were generated by the [Xplo](#) tool.

Geometrical construction (branching angles, phyllotaxis, deviations, mechanical like shapes), and 3D graphics are not detailed in this course.

See references below (Jaeger et al 1992 and 2010) for more information.

Bibliography

Jaeger M., de Reffye P., 1992. Basic concepts of computer simulation of plant growth. Journal of Biosciences, 17, 3, pp. 275-291. ([pdf](#))

Jaeger M., Sun R., Jia J.-Y, le Chevalier V., 2010. Efficient virtual plant data structure for visualization and animation. In: Proceedings of IADIS International Conferences Computer Graphics, Visualization, Computer Vision and Image Processing 2010, MCCSIS 2010 Freiburg, Germany, July 27-29, ISBN 978-972-8939-22-9, 2010 IADIS, pp. 65-75 ([pdf](#))

Xplo: an open source software for plant architecture eXploration: <http://amapstudio.cirad.fr/soft/xplo/start>

Supplementary resources

Development supplementary resources

Recommended on-line resources

Architectural Botanical concepts (English)
../P1_Prelim/Bota/Bota_intro.html

Introduction to Models (English)
../P1_Prelim/Model/Model_intro.html

GreenLab Model implementations (English)
../P3_Tools/Tool_simul_001.html

More detailed GreenLab structural papers (pdf files)

GreenLab: a new methodology towards Plant Functional-Structural Model.
Structural aspect ([pdf](#))

Fast Algorithms of Plant computation Based on Substructure Instances ([pdf](#))

Stochastic modelling of tree annual shoot dynamics ([pdf](#))

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Barthélémy, D., Caraglio, Y. 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive Approach to Plant Form, Structure and Ontogeny. *Annals of Botany*, 99 (3) : pp. 375-407 19 ([access to paper and pdf](#))

Feller, W. 1968. An introduction to probability theory and its applications, vol. 1, 3rd edn. Wiley, New York

Hu B.-G, de Reffye P., Zhao X., Yan H.-P. and Kang M.-G, 2003. GreenLab: A new methodology towards plant functional-structural model. Structural aspect. In: Hu, B.G., Jaeger, M. (Eds.), *Plant Growth Modeling and Applications: Proceedings - PMA03*, Tsinghua University Press and Springer, Beijing. pp. 21-35. ([pdf](#))

De Reffye P., Kang M.-Z., Hua J., and Auclair D., 2012. Stochastic modelling of tree annual shoot dynamics. *Annals of Forest Science*, 69(2), 2012. ([pdf](#))

Yan H.-P., Barczy J.-F. , de Reffye P., and Hu B.-G., 2002. Fast Algorithms of Plant Computation Based on Substructure Instances. *International Conferences in Central Europe on Computer Graphics, Visualization and Computer Vision 3/10 (2002)* pp. 145-153 ([pdf](#))

Web sites

[Digiplante project \(Ecole Centrale Paris\) Web site: http://digiplante.mas.ecp.fr/](http://digiplante.mas.ecp.fr/)

[GreenLab project Web site: http://GreenLab.cirad.fr/](http://GreenLab.cirad.fr/)

[Une histoire de la modélisation des plantes \(French\)](#)