

# UVED Resource

## Plant Growth Architecture and Production Dynamics

### GreenLab Course: Application

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## Contents and Objectives

### *Presentation*

GreenLab model applications are numerous in agronomy and related plant and crop sciences. This section gives an overview of the procedures allowing parameter identification from field measurements. A case study is then presented.

This course introduces the procedure for fitting GreenLab model parameters. Structural and functional parameters to be fitted are seen first.

The fitting procedure is then presented:

- Structure must be fitted first, starting from development up to mortality and branching
- Functional parameters must be fitted after.

A case study is then presented.

Exercises are proposed in several sections, mobilizing inline and online tools.

## *Course Objectives*

The aim of this course is to enable students to:

- Identify parameters to be fitted from real measurements
- Learn about the fitting procedure, in particular the sequence of parameters to be fitted
- Familiarize themselves with the fitting tools
- Tackle a case study.

## *Map*

This section starts by identifying parameters related to field measurements in the GreenLab model equations.

The principles of parameter fitting are then presented, before giving keys for structural parameter and growth parameter fitting.

A case study carried out on Coffee is then presented.

## *Course content map*

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## Measurements

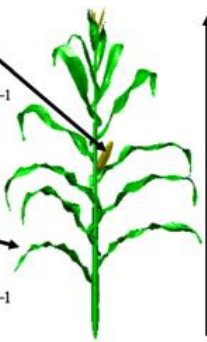
### Agronomic traits

The GreenLab model in practice

In the GreenLab approach, typical agronomic traits should be considered as model outcomes.

In the following example concerning maize, equations corresponding to the following traits are given:

- (i) individual organ weight or size,
- (ii) plant height,
- (iii) total biomass increase per growth cycle.



**Weight of cob**

$$w(n) = \sum_{i=t_{cob}}^n \frac{p_f \cdot f_f(i-t_{cob})}{D_i} \cdot Q_{i-1}$$

**Blade surface**

$$s_{t_l}(n) = \sum_{i=t_l}^n \frac{p_l \cdot f_l(i-t_l)}{e \cdot D_i} \cdot Q_{i-1}$$

**Height**

$$h(n) = \sum_{i=1}^n N_{n-i+1} \sqrt{b \left( \sum_{j=1}^i \frac{p_o \cdot f_o(j)}{D_{n-(i-j)}} \cdot Q_{n-(i-j)-1} \right)^{\frac{1-\alpha}{2}}}$$

**Growth rate**

$$Q(i) = \frac{E(i)Sp}{r} \left( 1 - \exp \left( -\frac{k}{Sp} \sum_{j=1}^i S(j) \right) \right)$$

Common agronomic traits of maize (Image Y. Guo and Y.T. Ma, CAU)

The cob weight at cycle  $n$ ,  $w(n)$  is cumulative biomass production defined by the supply  $Q_{i-1}$  to demand  $D_i$  ratio multiplied by the cob sink function  $\varphi_f(i-t_{cob})$ . This weight is a simple sum, starting from the appearance date  $t_{cob}$  up to the current cycle  $n$ .

The leaf area at a given stage is similar cumulative biomass production, divided by the leaf thickness  $e$ ; (the leaf appearance date is  $t_l$ ).

The height of the plant, at various cycles, is a classic measurable value.  $N_k$  defines the number of internodes in the trunk growth unit present at cycle  $k$ . While  $b$  and  $\alpha$  are allometric parameters.

Fresh plant weight increase is also a classic value of interest. The  $E$  function is related to climatic and resource conditions.  $(1/r_l)$  stands for plant Water Use efficiency.  $Sp$  is the plant's projected area,  $k$  is the Beer Law extinction coefficient.  $S(i)$  is the total functional leaf area at cycle  $i$ .

Note that these equations are expressed in their generic formulation:

On the studied variety, there was just one single cob per plant.  $w(N)$ , where  $N$  stands for the growth cycle stage at crop time, therefore gives the final production value for a given individual.

The organ sink functions  $\varphi_{organ}$  are expressed as a product of the sink function  $f_{organ}(l)$  with a conversion factor  $p_{organ}$ . The sink function is normalized, i.e.  $\sum_{j=t_s, te} \varphi_{organ}(j) = 1$ , where  $t_s$  and  $t_e$  define respectively organ appearance and the last functioning dates (expressed as growth cycles).

The height equation stands for any plant, considering  $N_k$  on the main axis. In the case of maize (or on any unbranched plant with continuous growth), each growth cycle defines a single internode, i.e.  $N_k$  equals 1, simplifying the expression of  $h(n)$ .

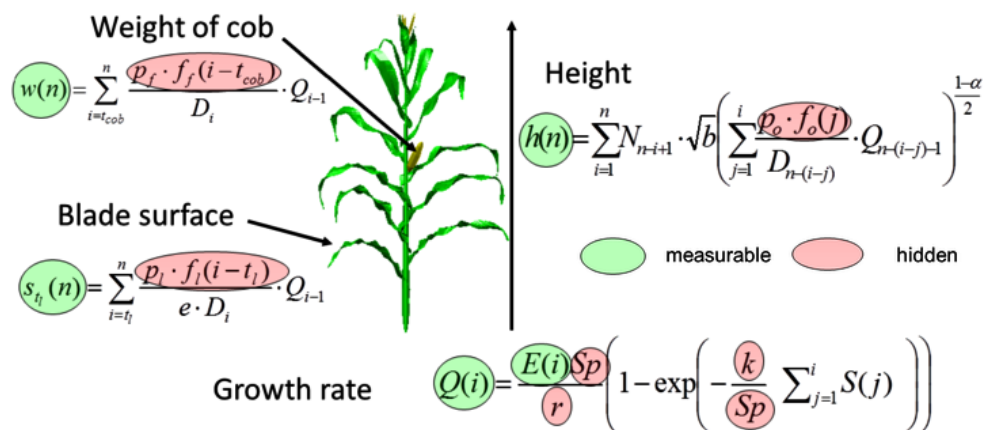
## Measurable and hidden parameters

The key step for model application is its validation on real plants, by estimating the specific parameters of a given plant variety from experimental data.

Some model parameters can be measured, while some cannot be directly assessed from experimental observations.

This concerns both development (when the rules of organogenetic grammars are too complex) and growth (such as the parameters of the sink and source functions).

These hidden parameters have to be estimated by model inversion.



Hidden and measurable data on maize (image Y. Guo and Y.T. Ma, CAU)

On maize, the organogenetic grammar is simple, without branching.

Growth cycles can be identified from leaf appearances.

Cob weight, total blade area, and plant height, at various cycles, define measurable parameters.

Fresh plant weight increases are also (destructive) measurable values.

The  $E$  function, related to climatic and resource conditions, is also found from measurable values.

Allometric parameters  $bb$  and  $\alpha$ , as well as leaf thickness  $e$ , can be retrieved simply from measurements taken on trunk internodes and leaves respectively.

Hidden parameters are:

the sink functions  $\varphi_{organ}$  (expressed here as a product of a conversion factor  $p_{organ}$  by a normalized sink function  $f_{organ}$ )

plant Water Use efficiency ( $1/r$ )

plant projected area:  $Sp$

the Beer Law extinction coefficient:  $k$

## Plant fitting procedure

### *Parameter fitting process*

The parameter identification process requires several steps possibly involving statistical analysis on the structure, building a target file, and finally fitting the functional hidden parameters.

#### Step 1. Retrieving structural parameters

This task can be simply deduced from plant architectural analysis when the structure is simple, especially when not branched, or when the structure is deterministic (palm trees, maize, beetroot, sunflower, etc.).

Otherwise structural parameters (more precisely rhythm ratio, pause, mortality and branching patterns) should be retrieved using the crown analysis approach, based on a statistical analysis.

#### Step 2. Simulating plant structure

This step helps to validate structural parameter identification.

In these simulations, organ sizes can be adjusted by the user, like simple constant values.

#### Step 3. Building a target file

This file retrieves output from simulations at different growth cycles, corresponding to different observation stages.

Hidden parameters are filled using default values.

However, at this stage, some measurable functional attributes can be set to their values, such as allometry parameters, expansion and function duration.

#### Step 4. Fitting the functional hidden parameters

In the target file, outcomes such as leaf areas, fruit weights, internode lengths, etc. must be replaced with the measured values.

The parameters to be identified are then fitted, usually in several steps.

Sink and source functions on internode, blades, petioles, flowers and fruits are classically evaluated first.

Secondary growth (rings) parameters are finally identified.

The overall fitting process may be reiterated, including on some structural aspects, especially when functional structural aspects are considered (fruit absorption for instance). Environmental condition changes can also be introduced in this loop.

#### Step 5. Applications

Once the parameters have been fitted, the calibrated model can be applied for various purposes, including for environmental pressure and density effect estimations.

## Plant structure fitting

### *Plant structure fitting principles*

Plant structure must be analysed in order to identify its parameters, following its development at a specific time or step by step.

The data sets required to fit structural parameters must be statistically significant for each axis typology.

They should be able to deliver distributions of phytomers for a given growth cycle range.

On a given species, such information is classically obtained through two types of experimental plots:

- from sets of individuals at different growth stages
- from a population of the same age.

It is understood that the fitting process is applied to each axis type.

In other words, fitting is carried out on the different physiological ages, independently.

More precisely, the parameters to be identified concern the development process, (i.e. the quantification of the production of the terminal buds building the phytomers of an axis), viability (expressed usually as the mortality of axes in relation to their age), and the branching process.

These processes are usually easier to quantify for continuous growth.

However, the approaches defined for the continuous case can usually be extended to rhythmic cases, applying the techniques on several levels, for instance within the growth unit, and from one growth unit to the next.

To sum up:

- structural parameters are fitted for each physiological age
- development parameters are to be considered first (assumed to result from a Bernoulli process)
- axis viability then has to be considered
- branching probabilities must be defined in a final step

Contents

- Fitting the axis development process.
  - Development is considered modelled as successive Bernoulli processes, leading to fit binomial or negative binomial laws.
  - Fitting of the development process parameters is first seen in a simple [continuous growth case](#).
  - Then, the case of [continuous damped growth](#) is considered.
  - The case of [rhythmic growth](#) is then considered.
- Fitting the axis [mortality](#) process.  
The mortality process is classically modelled by a mortality probability, applied to each phytomer appearance during development.
- Branching.  
[Branching fitting](#) can easily be related to a simple branched/(branch or unbranched) ratio, but can considerably increase in complexity if couplings have to be identified within growth units or from one phytomer to another.
- In the case of young populations, [crown analysis](#) is an efficient method for retrieving development parameters on the main axis and branches, analysing phytomer distributions from the top of the crown.

## Plant structure fitting - Development

In this section, fitting of the growth development process parameters for continuous growth is first described in its simplest case (constant growth)

### Fitting of the single Bernoulli process

Let us assume that, on an axis developing continuously, the appearance of a new phytomer follows a simple constant law.

The shape of the phytomer number distribution produced over a given period is classically a bell shape.

Fitting this distribution by a binomial law  $B(N, b)$  makes it possible to retrieve the period of development  $N$  (expressed in growth cycles) and the Bernoulli parameter  $b$ .

We should, however, consider the stability of this parameter  $b$ , studying the expected value- variance relation, assumed to be linear, if the process follows a binomial distribution.

In such a case, parameter and age fitting is easily defined from the distribution expected value  $X$  and the variance  $V$ , since

$$b = 1 - V / X$$

and

$$N = X / b$$

Fitting can be performed at different stages of growth or at a specific time (for instance at the end of growth for annual crops).

### Example. Fitting of a cotton tree

The following example involves the main stems of 50 cotton trees. Two approaches are considered.

#### *Method 1: following expected values and variance relations at several growth stages*

If the development process is a Bernoulli process, the mean and variance are proportional to the Bernoulli parameter ( $V = (1 - b) \cdot X$ ).

The expected value increase is of course obvious when considering growth, thus several growth stages are necessary to build a significant data set.

In this example, 6 growth steps were studied on a population of 50 cotton trees.

Their respective expected values and variances are given below:

Expected value (X)	0,	4.15,	4.88,	7.30,	10.12,	17.70,	20.68
Variance (V)	0,	0.38,	1.05,	0.58,	1.12,	3.46,	3.49

A linear regression (see ["../P3\\_Tools/Tool\\_lreg\\_001.html"](http://../P3_Tools/Tool_lreg_001.html)) leads to :

$$V = 0.18 X (r=0.96) \text{ and thus gives } b = 0.82 (+/- 0.04)$$

*Method 2: analysing the distribution of the phytomer number at a given growth stage*

At the end of growth, the number of phytomers is recorded on each main plant axis.  
The expected value and variance are estimated to define the Bernoulli probability.

Number of internodes	16,	17,	18,	19,	20,	21,	22,	23,	24
Number of plants	1,	4,	2,	4,	6,	16,	12,	2,	3

The expected value is  $X = 20.68$  and variance  $V=3.42$

Leading to

$$b = 1 - (3.42 / 20.68) = 0.83$$

*Defining the number of growth cycles*

The number of growth cycles is simply derived from the definition of the expected value, thus giving:

$$N = X / b$$

At the crop stage ( $X=20.68$ ), methods 1 and 2 give the following results, respectively:

$$N = 20.68 / 0.82 = 25.22$$

$$\text{and } N = 20.68 / 0.83 = 24.86$$

The number of growth cycles is thus  $N = 25$ .



### Plant structure fitting - Damped growth

Let us fit the growth development process parameters for continuous growth in a more complex case, with damped growth on branches, also showing mortality.

Such is the case of the coffee tree. The architecture of the coffee tree is characterized by two different physiological ages, for the main axis and the branches, respectively.

The trunk and the branches show different development.

The main axis shows a classic continuous indeterminate Bernoulli development process ( $b=0.92$  on the species studied here).

On the other hand, branch growth is determinate, stopping gradually over time.

In order to retrieve the development process properties, only the distribution of living branches must be considered. On these, branches development slows down depending on the number of growth cycles.

Phytomer living branches distributions show a quadratic relation between the variance and the expected value. This property relates to damped growth, in which the Bernoulli parameter  $b$  changes according to the growth cycle as follows:

$$b(i) = b^i$$

Therefore, at a given growth cycle  $K$ , the expected value  $X_K$  and the variance  $V_K$  are respectively

$$X_K = b \frac{1-b^K}{1-b} \quad V_K = \frac{1-b}{1+b} (X_K + X_K^2)$$

The fitting of parameter  $b$  can thus be performed from a dataset of different growth stages.

#### Example. Coffee tree branches

Following expected values and variance relations at several growth stages

This example involves 1,416 coffee tree branches (*Coffea robusta*).

If the development process is a Bernoulli process, then the mean and variance are proportional to the Bernoulli parameter ( $V = (1 - b) \cdot X$ ).

The expected value increase is of course obvious when considering growth, and thus several growth stages are necessary to build a significant data set.

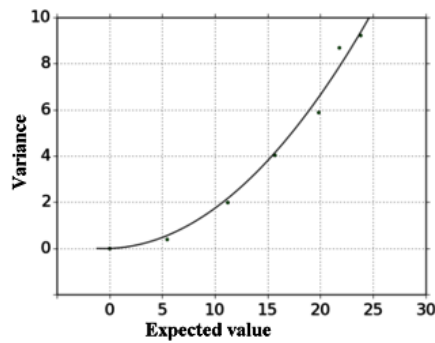
In this example, 6 growth steps were studied on population of 1,416 branches.

Their respective expected values and variances are given below:

Expected value (X)	0.0,	5.47,	11.25,	15.69,	19.84,	21.78,	23.81
Variance (V)	0.0,	0.38,	1.99,	4.02,	5.88,	8.69,	9.22

A least square regression (see <http://zunzun.com/>) leads to:

$V = 0.015826 \cdot (X^2 + X) = (1 - b^2) (X^2 + X)$  ( $r=0.9857$ )  
and thus gives  $b = 0.9688$



Variance and expected value relations (Graph P. de Reffye, CIRAD)

The points are the data observed at 6 growth stages.

The curve stands for the fitted equation:  $V = 0.015826 (X^2 + X)$

The phytomer number distribution fitted satisfactorily to a binomial law, but resulted from a complex Bernoulli process, with a non-constant parameter.

The corresponding adjusted  $b$  parameter is an average value.

## *Plant structure fitting – Rhythmic development*

In the case of rhythmic growth, axis developments 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. In both cases, tools and methodologies (based on the Bernoulli process) introduced for continuous growth can be used, with, of course, differentiated parameterization relative to each level of organisation.

### Fitting of growth unit 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 occurs 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  $N$ .

Fitting  $N$  and  $b$  parameters can be performed using measurements taken on a significant number of growth units, analysing their distribution according to their respective number of phytomers. This fit can then be simply deduced from the distribution expected value and variance, as defined for continuous growth.

#### 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 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. the 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 negative binomial law.

Such fittings can be solved using, for instance, the least square approach, requiring implementation of the development model (and will not be detailed here). 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 a secondary axis, and not expressed at all on short axes.

On some species, binomial laws parameters are fairly stable depending on the physiological age, and the various distributions can be fitted by the variation of in the neo-formed section.

### Rhythmic development examples

The following examples concern pre-formed growth units on the beech tree and bimodal distributions on the poplar.

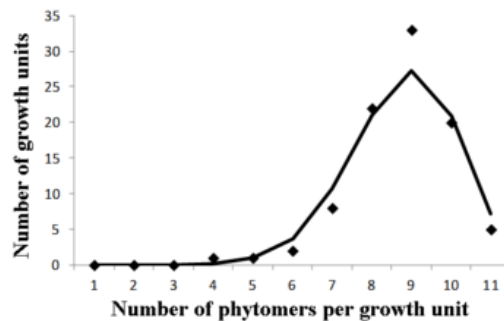
In this first example, 8 classes of growth unit size were considered.

Their respective number of phytomers and frequencies are given below:

Number of growth units	0	1	1	2	8	22	33	20	5
Number of phytomers	3	4	5	6	7	8	9	10	11

A single binomial fitting (see ["../P3\\_Tools/Tool\\_breg\\_001.html"](http://../P3_Tools/Tool_breg_001.html)) leads to :

$$N = 11 \text{ and } b = 0.79$$

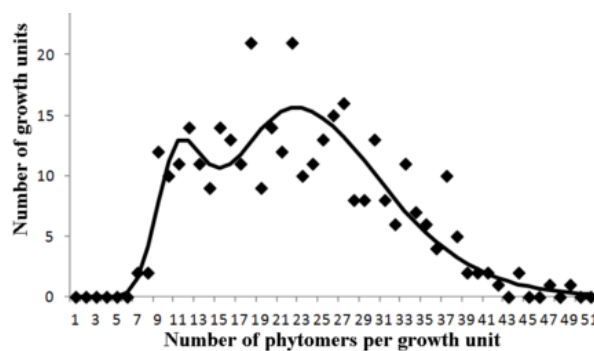


Pre-formed growth units on the beech tree (Graph P. de Reffye, CIRAD)

Ten classes of growth unit sizes are considered.

The curve stands for the fitted binomial law:  $N = 11$ ,  $b = 0.79$

The second example illustrates the growth unit size distribution on poplar tree branches (physiological age 2).



Growth units on the poplar tree (Graph P. de Reffye, CIRAD)

A classic bimodal distribution observed on poplar branches.

The curve stands for the following five parameters

- Binomial law parameters for the pre-formed part B (12, 0.68)
- Negative binomial law parameters for the neo-formed part Bn (5, 0.76)
- the proportion of neo-formation,  $p_n = 0.86$ .

## Mortality

### Retrieving mortality laws

Axis mortality, more precisely meristem viability, is a key point in structure development, and is usually easy to see in field measurements

Branched axis mortality increases gradually on the phytomers along the axis, until death occurs if the axis is long enough.

The number of branched dead axes (i.e. with a dead terminal bud) thus increases along the bearing axis from top (tip) to bottom.

This death rate is classically measured on a plant population by a percentage defined from the ratio of dead axes to the total number of axes. This rate increases with the age of the axis.

Remember that the age can be retrieved from the branching position (the rank) on the bearer.

For instance, on the coffee tree, one can define an average age  $i$  expressed in growth cycles for the phytomer located at rank  $K$  from the crown top defined as  $= K / b_1$ , with  $b_1$  standing for the Bernoulli parameter modelling stem development.

Death rates can be fitted to a classic sigmoid function, thus leading to expression of the meristem's viability along the axis as a function of the number of growth cycles.

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

the mortality probability is :

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

and the death rate at cycle  $i$  is given by:

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

### Example. Coffee tree branches

In axis fitting applications, mortality modelling must be performed after development, since its expression is a function of the bearing phytomer age.

In our *Coffea canephora* studies, the average number of cycles at rank  $K$  was  $N = K / b_1$  with  $b_1 = 0.92$ . Measurements were taken for 5 growth cycles on 600 axes for each cycle.

The data set table and the fitted sigmoid function are given below:

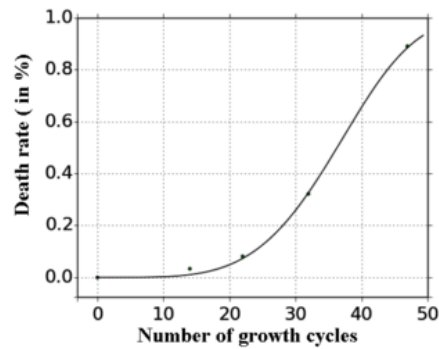
Rank (K)	0	10	15	20	30-35
Growth cycles (i)	0,	14,	22,	32,	47
Death rate (in %)	0.0,	0.032,	0.081,	0.321,	0.89

The least square regression (see <http://zunzun.com/>) gives:

$$S(i) = 1 - \exp(-8.9 \cdot 10^{-8} \cdot i^{4.42}) \quad (R=0.999)$$

The related viability at cycle  $i$  is :

$$1 - c_i = \exp(-8.9 \cdot 10^{-8} \cdot ((i-1)^{4.42} - (i-2)^{4.42}))$$



Death rate versus growth cycle (Graph P. de Reffye, CIRAD)

The points are data observed at 6 growth stages given in the above table.

The curve stands for the fitted equation:  $S(i) = 1 - \exp(-8.9 \cdot 10^{-8} \cdot i^{4.42})$  ( $R=0.999$ )

## Plant structure fitting – Branching

### *Retrieving branching laws*

Branching modelling and qualitative description is often a heavy task. On each phytomer, several axillary branches may appear, with immediate or delayed development.

This diversity can also be found on a given axis, even within the same growth unit, from one phytomer to another, as defined in the botanical arrangements of branching (acrotony for instance).

However, in the GreenLab approach, the model focuses on the number of phytomers of a given type (physiological age) appearing at a given growth cycle, without worrying about their positioning.

For each type of axis (i.e. each physiological age), the law of branching can thus be assessed from the ratio of the number of branched phytomers to the total number of phytomers.

Hence, this single ratio can be defined as a branching probability  $p_a$ . In practice, the definition of this ratio should be defined from a significant population, at a given rank, since this ratio may change along the axis.

Moreover, in some cases, the branching process is delayed. The retrieval of dormancy can be defined from an awakening probability in the branching process, for each growth cycle.

Finally, the branching process may show couplings on a local scale, in a whorl or from one phytomer to its predecessor.

### *Simple coupling in branching*

On a given phytomer, let us consider the case of couplings in a simple whorl that may have no, one (right or left) or two branches (right and left) per whorl.

The branching states can be described as follows:

- state (0,0): no branching on the phytomer
- state (1,0): one branch, either Left, or Right
- state (1,1): two branches on the phytomer, both Right and Left.

Let us now define  $n_{00}$ ,  $n_{10}$  and  $n_{11}$ , as the respective number of the different states measured on a given population.

The total number of phytomers is therefore  $n = n_{00} + n_{10} + n_{11}$

The number of potential branches is  $2.n$  since each phytomer may carry two branches.

The probability  $p_a$  of branching can then be estimated by the single ratio

$$p_a = (n_{10} + 2.n_{11}) / 2.n$$

$$(p_a = 0.5 (n_{10} + 2. n_{11}) / (n_{00} + n_{10} + n_{11}) )$$

The theoretical distribution among the three states can then be estimated without a coupling hypothesis.

the state (0,0) number should appear close to  $n * (1 - p_a) * (1 - p_a)$   
 the state (1,1) number should appear close to  $n * p_a * p_a$   
 the state (1,0) number should appear close to  $2 * n * (1 - p_a) * p_a$

If significant differences appear, the two potential branching processes on a single phytomer must not be considered as independent.

A simple coupling model can be tested in such a context.

Introducing a coupling  $r$  to the branching model, we can write the probability of branching depending on the 3 states as follows:

$$\begin{aligned} p(0,0) &= (1-p_a)(r+(1-r)(1-p_a)) \text{ (coupling of no branching)} \\ p(1,0) &= 2(1-r) p_a (1-p_a) \text{ (no coupling)} \\ p(1,1) &= p_a * (r + (1-r) * p_a) \text{ (coupling of branching)} \end{aligned}$$

The coupling coefficient  $r$  can then be retrieved using the real distribution of a state.

### Example. Coffee tree branches

Phytomers on the coffee tree main stem usually have two branches.

Three states (0,0): no branch, (1,0): a single branch, (1,1): two branches are thus possible.

For a given population, measurements led to this distribution:

Number of states (0,0) :  $n_{00} = 39$   
 Number of states (1,0) :  $n_{10} = 15$   
 Number of states (1,1) :  $n_{11} = 96$

The number of branches is thus:  $n_{10} + 2 n_{11} = 15 + 96*2 = 207$

And the number of phytomers is  $n = n_{00} + n_{10} + n_{11} = 39+15+96 = 150$ , thus giving 300 potential branches

The branching ratio (probability) is thus  $p_a = 207/300$ ;  $p_a = 0.69$

If no coupling is considered, the number of the different states should thus be:

for state (0,0) :  $(1-p_a)*(1-p_a)*150 = 14$  (14.415 to be compared with 39)  
 for state (0,1) :  $2 * p_a * (1-p_a) * 150 = 64$  (64.17 to be compared to 15)  
 for state (1,1) :  $p_a * p_a * 150 = 71$  (71.415 to be compared with 96)

This distribution is quite different from the measured one, showing higher distributions for the (0,0) and (1,1) states and less single branching. A phytomer thus shows a tendency to develop either two branches or none. The coupling model can be used in such a context. The theoretical number of unbranched phytomers is:

$$p(0,0) = (1-p_a)(r+(1-r)(1-p_a))$$

By identification we have:  $n_{00}/n = 0.31 * (0.69 r + 0.31)$  giving

$$r = 0.767$$



## Plant structure fitting – Crown analysis

### Principles

Plant structure can be straightforwardly analysed in order to identify its development parameters, without following its development step by step.

In fact, development parameters describe the functioning of buds as they build the pathways of the plant structure.

#### Crown definition for analysis

Let us define a crown as a structure composed of its main stem, bearing branched axes sharing the same physiological age.

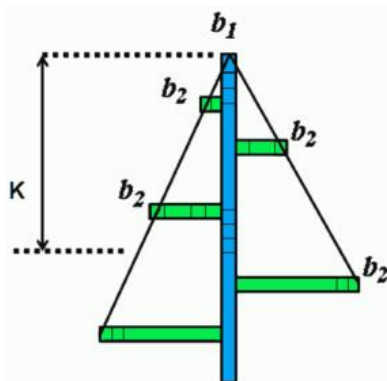
On the main axis, considering the pathway from top to bottom, one can see that the chronological age of the branches increases. Hence, for a given axis typology, several development stages can be observed. However, development is usually stochastic.

Each crown results from a randomized model defined from three parameters:  $w$ ,  $b_1$  and  $b_2$ .

Parameter  $w$  stands for the rhythm ratio (it is understood that the main axis rhythm ratio is the reference, i.e. set to 1).

Parameter  $b_1$  stands for the Bernoulli process related to phytomer appearance on the main axis, while  $b_2$  stands for those related to branches.

At rank  $K$  from the tip, the phytomer's chronological age follows a negative binomial law  $Bn(K, b_1)$  on the main axis. Remember that the negative binomial law characterizes the number of trials leading to a given number of successes. The rank,  $K$ , thus stands for the number of successes ( $K$  here, i.e.  $K$  formed phytomers from the tip); while pauses, which are hidden, increase the chronological age of the phytomer likely to appear at rank  $K$ .



*Crown definition (Image P. de Reffye, CIRAD)*

*At rank  $K$ , on the main axis, in blue, there are  $K$  phytomers from the crown top.*

*The chronological age of the phytomer at rank  $K$  follows a negative binomial Law  $B(K, b_1)$  of parameter  $K$  and  $b_1$ .*

*The branches derived from the main axis, in green, share the same physiological age.*

*Their age of development is derived from a negative binomial law  $B(w, T, b_2)$ , where  $w$  is the rhythm ratio and  $T$  is the chronological age of the phytomer bearing the branch.*

Let us now suppose that, on the main axis, the chronological age is  $T$  (derived from a negative binomial law  $Bn(K, b_1)$ ). This age also defines the age of the branch arising from the phytomer at rank  $K$ . According to the rhythm ratio  $w$ , the number of development cycles on the branch arising from rank  $K$  will be  $w \cdot T$ . On this branch, the number of phytomers also follows a negative binomial law of parameter  $b_2$ .

As a result, the phytomer distribution on the branch is a composed law, derived from negative binomials laws of parameters  $K, b_1$  and  $b_2$ .

### Crown analysis equations

In this section all the main axis phytomers are assumed to branch, and branches are living (no mortality occurs).

In addition to the theoretical conceptual framework, it is also assumed that statistical data are available on the full sets of studied crowns. In more detail, on each crown, those data express the phytomer distribution at rank  $K$  from the tip, defined by its expected value and variance. Those statistics relate to their underlying stochastic processes, and we aim to determine their relationships with the crown development parameters.

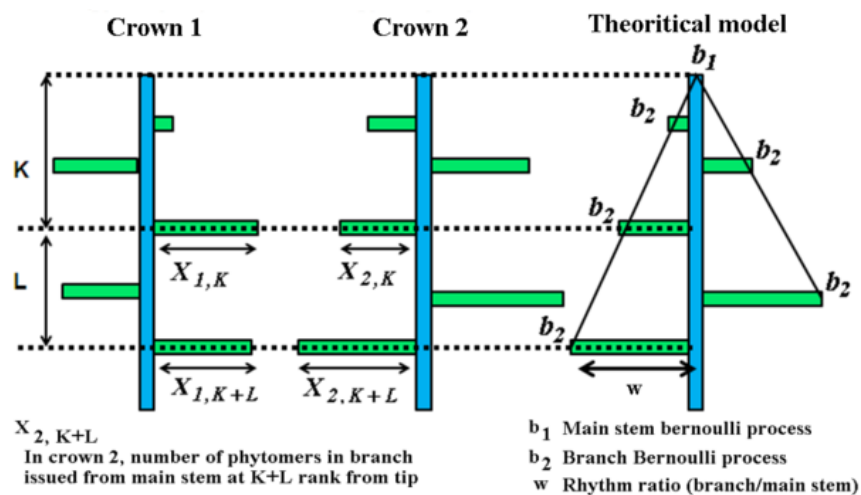
Let  $X_{i,K}$  be the number of phytomers of the axis at rank  $K$  in crown  $i$ .

Three parameters,  $w, b_1$  and  $b_2$  have to be estimated, requiring three statistical values on all the crown data sets.

\* Considering rank  $K$  first, we can retrieve the expected value and the standard deviation (among the various crowns).

\* Then, considering couples of branches at respective ranks  $K$  and  $K+L$ , the expectation of couple variances in all the crowns specifies intra-crown variance.

These statistical values are expressed here from datasets measured on  $N$  crowns, at rank  $K$ .  $X_k$  stands for the expected value and  $V_k$  for the variance at rank  $K$ , expressed according to the  $w, b_1$  and  $b_2$  parameters, whose theoretical values are noted  $X_k'$  and  $V_k'$ , respectively



Crown analysis data (Image P. de Reffye, CIRAD)

Left and middle. Two crowns on which statistics are computed.

Right. Theoretical model to be assessed.

The following relations can be demonstrated:

For inter-crown expected values at rank  $K$ :

$$X_K = \frac{\sum_{i=1}^N X_{i,K}}{N} \quad X_K' = W \frac{K}{b_1} b_2$$

For inter-crown standard deviations at rank  $K$ :

$$V_K = \sum_{i=1}^N \frac{(X_{i,K} - \bar{X}_K)^2}{N-1} \quad V_K' = W \frac{K}{b_1} b_2 (1-b_2) + (W b_2)^2 \frac{K(1-b_1)}{b_1^2}$$

The third relation required to estimate the three parameters is given by the intra-crown variance  $v_K$  defined from couples of branches distant  $L$  ranks from  $K$ .

$$v_K = \frac{\sum_{i=1}^N (X_{i,K} - X_{i,K+L})^2}{2N} \quad v_K' = W b_2 (1-b_2) \frac{K+L}{b_1} + (W b_2)^2 \frac{2L(1-b_1)}{2b_1^2} + (W b_1)^2 \frac{L^2}{2b_2^2}$$

We have thus three equations, identifying numerical solutions for the  $w$ ,  $b_1$  and  $b_2$  values at rank  $K$ .

$$1-b_2 = \frac{1}{X_K} \left( v_K - \frac{L}{2} \left( \frac{V_K}{K} + L \left( \frac{X_K}{K} \right)^2 \right) \right)$$

$$1-b_1 = \frac{1}{X_K^2} \left( K \left( V_K - v_K + \frac{1}{2} \left( \frac{L X_K}{K} \right)^2 \right) + \frac{L V_K}{2} \right)$$

$$w = \frac{b_1}{b_2} \cdot \frac{X_K}{K}$$

In practice, small values for  $L$  are better for minimizing variances.

$L=0$  is chosen for plants showing multiple axillaries per node (such as *Coffea* with an opposite decussate phyllotaxy), and  $L=1$  for plants bearing a single axillary per node (such as cotton trees with alternate phyllotaxy).

## Crown analysis example

### A simple first example

Fitting cotton tree crowns: a case of continuous growth.

50 cotton tree crowns were analysed. The following table summarizes the number of phytomers found at rank 10 and 11 from the top, respectively.

Plant	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Rank 10	3	3	4	3	3	3	3	2	3	4	3	3	4	3	3	3	3	2	3	3	2	3	4	4	4
Rank 11	4	4	3	4	3	4	4	4	4	4	3	3	4	3	4	3	3	4	1	3	3	3	4	4	4

Plant	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Rank 10	3	3	3	3	3	3	4	3	3	3	3	3	4	2	2	4	4	3	3	3	3	4	3	5	4
Rank 11	4	3	3	4	2	3	4	4	3	3	4	3	5	3	3	4	4	4	3	4	3	4	4	5	4

*Table 1. 50 cotton tree crowns. Rank 10 and Rank 11 give the number of phytomers found on branches at position 10 and position 11 from crown top, respectively.*

Statistics were then computed on the 50 crowns at position  $K = 10$ .

The expected value and variance were  $X_{10} = 3.2$  and  $V_{10} = 0.4$ , respectively.

The development parameters were: (one significant digit)

$$b_1 = 0.9 \quad b_2 = 0.9 \quad w = 0.3$$

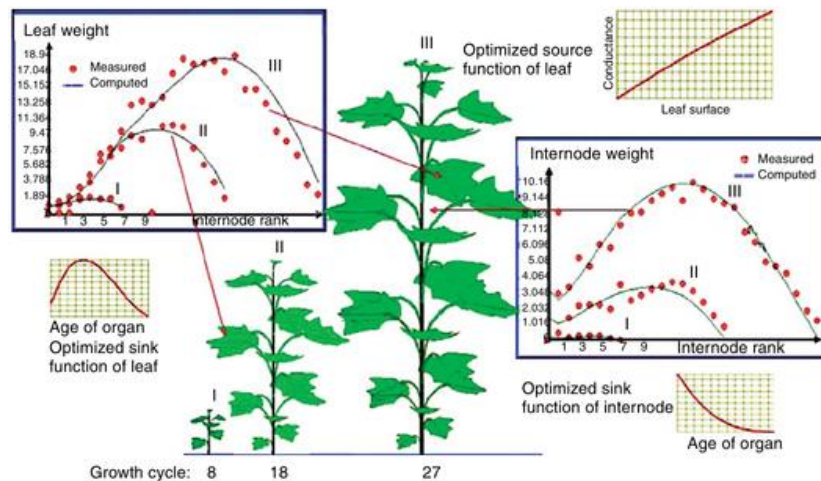
## Fitting functional parameters

### Overview

Since plant growth can be modelled in the form of a dynamic system, classic methods of parameter estimation can be used, based on maximum likelihood criteria and Newtonian methods of optimization.

The model outputs from which this identification can be achieved are the organ masses, as they can be easily measured on real plants and as they result from plant functioning and thus keep track of the whole history of source-sink balances.

If we consider a mono-species population, several plants at different ages can be used simultaneously to form the observation vector.



*Fitting parameters from several growth stages (Zhang Zhiguan, LIAMA/CAU 2008)*

*Several growth stages of the same plant are fitted simultaneously at organ biomass level with an optimized common set of parameters that ensure biomass production and biomass partitioning. The organs of different types are fitted together because they share the same plant demand and production.*

*Plant growth dynamics may be controlled by a small set of constant parameters.*

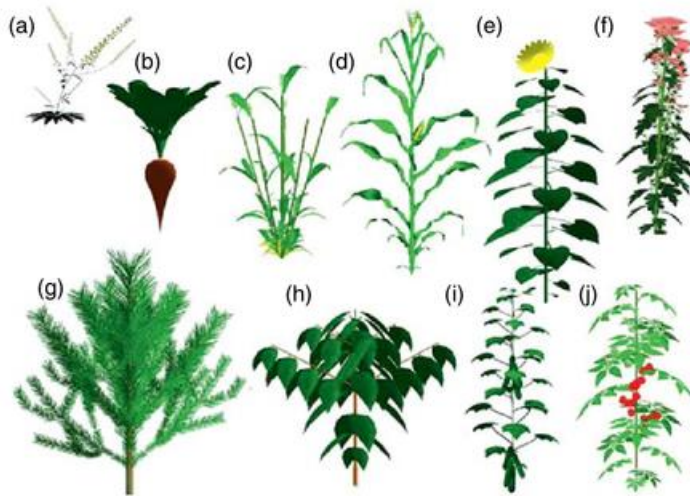
Complications can be induced if the population has strong intraspecific genetic variability and environmental variability.

The amount of data collected is a compromise between the statistical accuracy of estimation and the heaviness of the measurements.

In most cases, the simplifications used in the physiological model are justified by the comparison of the model with real plants, since a very small number of model parameters are sufficient to predict a large number of data.

Even though all the complex phenomena underlying plant growth and development are not accounted for, the prediction ability of such models remains quite good.

The reason is that the simple theoretical plant given by the model is such that its architectural trajectory is very close to that of the real complex plant.



*Simulations of 3-D plant architectures including growth and development  
(using versions of the GreenLab model: developed at INRIA, ECP, LIAMA, CIRAD)*

- (a) Arabidopsis plant, LEPSE (DigiPlante software: ECP)*
- (b) Beetroot plant, Institut Technique de la Betterave (DigiPlante software)*
- (c) Wheat plant, Wageningen University (GreenScilab software: LIAMA)*
- (d) Maize plant, Chinese Agricultural University (software CAU)*
- (e) Sunflower plant: INRA/LEPSE (DigiPlante software)*
- (f) Chrysanthemum plant, Wageningen University (GreenScilab software)*
- (g) Pine tree, Chinese Academy of Forestry (DigiPlante software)*
- (h) Coffee tree, CIRAD (DigiPlante software)*
- (i) Cucumber plant, CAU (DigiPlante software)*
- (j) Tomato plant, CAU (CornerFit software: LIAMA)*

Compared to structural simulations, the representations of the above simulations are more accurate, because the sizes of organs depend on biomass production and on biomass partitioning and do not directly result from empirical data sets.

## *Fitting functional parameters Procedure*

### Functional parameter fitting Workflow

Reminder.

As shown earlier, the parameter identification process requires several steps, starting with the structural parameters.

Functional parameter fitting is performed with measured data corresponding to precise development observation stages.

The collected data are usually classic [agronomic traits](#) as defined previously. They are usually collected on a plant population, at the various observation stages. Follow-up is often impossible since some traits are often easier to collect by destructive collection (such as organ weights and dimensions).

The hidden functional parameter procedure classically follows this workflow:

1. The plant structure is simulated at the various observation stages.  
This simulation (stochastic in general) helps to define a target file showing, for each observation date (i.e. for each observation growth cycle):
  - hopefully the number of organs (distribution of) per cohort
  - organ default properties (for instance their volume set as a constant value in the structural simulation).
2. Functional parameters related to organ phenology and allometry are analysed and modelled.  
These parameters are mainly related to the definition of the functioning durations of the growth cycle.
  - The appearance date. For instance, flowering may appear at a given growth stage only)
  - The expansion duration: the number of cycles the organ takes to reach its mature stage and end of development
  - The functioning duration (specifically for leaves). This duration is greater than the expansion time.
  - Allometry parameters are deduced from the collected organ dimensions. (This means collecting organic series, as defined earlier).

These parameters are usually considered as constant and are classically estimated from simple statistics.
3. Building the target file  
This file retrieves output from simulations at different growth cycles, corresponding to different observation stages.  
The default agronomic traits generated by the simulation are corrected, and replaced by the data measured at the various observation stages.
4. Fitting the functional hidden parameters  
The parameters to be identified are then fitted, usually in several steps, starting from the production equation.
  - The first level estimated is usually the  $Sp$  and  $r$  values, with the Beer Law extinction factor  $k$  set to 1.
  - Organ sinks are then estimated as a single ratio

- Beta laws are then defined for biomass partitioning (the  $a$  parameter first, then the  $b$  parameter)
- Lastly, secondary growth is estimated (if required)

At each step, the parameter to be estimated is given a default value (assumed to be close to its final value).

The fitting iterates on the target file, updating the hidden parameter values until the distance between the simulated traits and the measured ones stays constant (and significantly weak).

The underlying fitting process is, in our implementations, the generalized least square method or renewal annealing.

Once a parameter is fitted, the others are added according to the sequence given thereby.



## Supplementary resources

On-line resources and tools

[Parameter identification](#)

[Parameter estimation](#)

[Linear regression](#)

[Binomial Law fitting](#)

[Crown analysis tool](#)

On-line tools

Zunzun.com, a Web fitting interface tool. Url: <http://zunzun.com/>

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