

# UVED Resource

## Plant Growth Architecture and Production Dynamics

### GreenLab Course: Production

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### Contents and Objectives

#### *Presentation*

GreenLab function modelling aspects are greatly inspired from process-based approaches.

However, GreenLab function modelling differs in terms of organ compartment definition, making use of structural temporal positions.

It also differs in the definition of organ sink strength.

It adapts crop biomass production modelling formalism to the single plant scale.

This section presents GreenLab's functional modelling principles.

- The growth cycle is the unit thermal time period for which biomass production and allocation are evaluated
- Biomass production follows the classic PbM Beer Lambert law, applied to the individual plant
- Biomass is allocated to cohorts of organs defined by their appearance date and physiological age
- Organs compete for a common biomass pool according their sink strength function, characterizing their phenology
- The expression of biomass production, biomass allocation and plant and organ scales are mathematically explicit, leading to a set of equations describing the plant as a dynamic system.

### *Course Objectives*

The aim of this course is to enable students to:

- Revisit the eco-physiological concepts involved in plant crop models
- Learn about GreenLab's functional simplification and assumptions
- Learn about the biomass production and biomass partitioning approach
- Understand the model's equations with its meaningful parameters

### **Contents and Map**

The section introduces the principles of GreenLab functional modelling, highlighting the following aspects:

- Eco-physiological reminders
- Principles and assumptions
- Biomass allocation to organs
- Biomass production
- Model equations

### *Course content map*

[Overview Sub-Chapter](#)

[Sub-Chapter map](#)

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[About modelling plant growth](#)

[Biomass partitioning](#)

[Plant biomass production](#)

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## Eco-physiology reminders

### *Relevant physiological concepts*

A reminder is given of the following concepts, introduced in the [Physiology preliminary course](#):

#### **Thermal Time normalization**

Thermal time normalization makes it possible to compare plant growth for both organogenesis (organ numbering) and development (organ size) aspects.

#### **Light interception: PAR, LAI and the Beer-Lambert Law**

Only part of light energy is used in plant crops. A limited fraction of the light spectrum is absorbed by the leaves; this part is restricted to the upper leaf area and decreases in the canopy.

#### **Photosynthesis: Light Use Efficiency**

The photosynthesis process converts absorbed light energy into biomass with a ratio proportional to Light Use Efficiency.

#### **Biomass common pool**

Biomass produced by the source organs (leaves) builds a common storage pool, to be shared among all competing growing organs.

#### **Organ competition. Sinks**

Growing organs compete for biomass allocation. They are sinks.

#### **Density effect**

At individual plant level, density limits light absorption capabilities, and thus dynamically limits biomass production.

## Eco-physiology reminders

### Thermal Time

Temperature controls both organogenesis (organ appearance) and organ growth. Thermal Time  $T_t$  is measured by calculating the daily accumulations of heat using temperature data. Thermal time is expressed in Growing Degree Days (GDD).

$$T_t = \sum_{d=1,n} (T_d - T_o)$$

where

$T_d$  is the average daily temperature

$T_o$  is the developmental threshold or base temperature under which the development rate is zero.

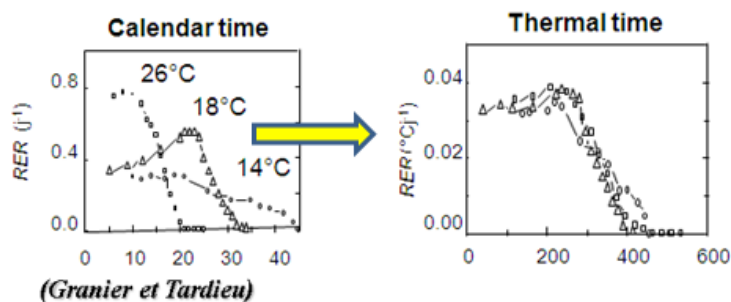
The base temperature varies with the plant species: 8 °C for wheat, barley, soybean, up to 10 °C for maize, rice.

It is assumed that  $T_d \geq T_o$ , if not,  $T_d$  is set to  $T_o$ .

### Thermal Time and Development.

It has been shown that biomass increases are proportional to thermal time.

Normalizing the development time with thermal time (instead of calendar time) allows development comparisons, as illustrated below on root elongations.



This example illustrates the Root Elongation Rate (RER) (Graph Granier and Tardieu, INRA)

RER was measured according to calendar time (per day) compared to thermal time (expressed in °C per day).

## Light interception (reminder).

### PAR

Leaves intercept the light. Chlorophyll, the most abundant plant pigment, is most efficient in capturing red and blue light. Photosynthetically active radiation, often abbreviated **PAR**, designates the spectral range of solar radiation (from 400 to 700 nanometres) that photosynthetic organisms are able to use in the photosynthesis process.

This spectral region corresponds more or less to the range of light visible to the human eye.

### LAI

The **LAI** or Leaf Area Index is the ratio of total upper leaf surface of vegetation divided by the surface area of the land on which the vegetation grows. LAI is a dimensionless value, typically ranging from 0 for bare ground to 9 for a dense forest.

### Beer-Lambert Law

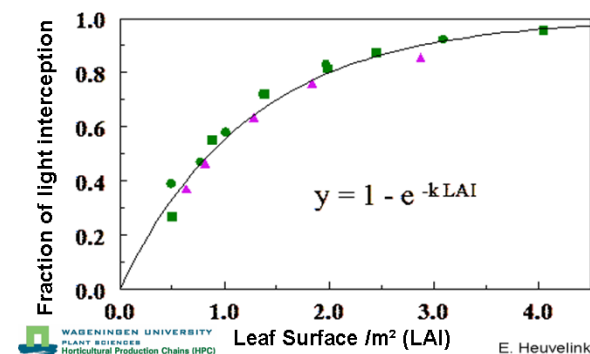
Detailed numerical simulation of radiation absorption has shown that the following approximation is excellent, and never deviates more than 1 or 2% from a detailed simulation with sunlit and shaded leaves:

$$I_{absLAI} = I_0 (1 - e^{-k \cdot LAI})$$

In this formula, called the Beer-Lambert law,  $k$  stands for the extinction coefficient,  $I_{absLAI}$  and  $I_0$  for the radiation level at canopy depth LAI (expressed in overlying LAI) and at depth 0 above the canopy, respectively.

Typical values for  $k$  are in the range of 0.5 to 0.9

For a LAI above a value of 3, almost 90% of PAR is absorbed by the canopy. White cover on the soil surface may reflect 50 to 80% of PAR and increase crop photosynthesis by at least 7% for a LAI of 3 (as long as CO<sub>2</sub> is not a limiting factor) (Gijzen, 1995a).



*Influence of the Leaf Area Index on the fraction of light intercepted by a tomato crop (Graph E. Heuvelink, WAGENINGEN UNIVERSITY)*

*In this example, the extinction coefficient  $k$  is experimentally found from three sets of data respectively, represented by the green and pink symbols.*

## Bibliography

**Gijzen, H.** 1995. CO<sub>2</sub> uptake by the crop. Crop growth and development. In: J.C. Bakker, G. P. A. Bot, H. Challa, and Van de Braak, N.J. (eds), Greenhouse climate control-an integrated approach, Wageningen Pers, The Netherlands. pp. 16-35

## Photosynthesis (reminder)

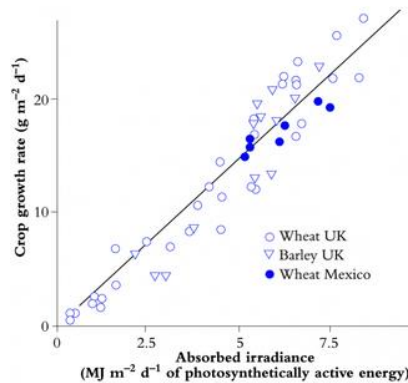
### Light Use Efficiency

In agronomy, the result of photosynthesis activity, i.e. biomass production, is simply quantified by weight.

It has been shown that the biomass growth rate, expressed in grams of dry matter per square metre per day ( $\text{g.m}^{-2}.\text{d}^{-1}$ ) is linearly related to absorbed irradiance ( $\text{MJ.m}^{-2}.\text{d}^{-1}$ ) for a wide range of crop communities.

This relationship between biomass growth and absorbed irradiance ([PAR](#)) defines Light Use Efficiency, abbreviated as [LUE](#).

Note. When considering total irradiance, this ratio is called Radiation Light Use Efficiency, abbreviated as [RUE](#).



*Light Use Efficiency on common crops.*

*Light Use Efficiency (in  $\text{g.MJ}^{-1}$ ) is represented by the slope of this relationship.*

*It is equivalent to  $3 \text{ g.MJ}^{-1}$  in this example (based on Evans 1993).*

Hence, when the LUE and irradiance exposure are known, a simple growth crop model can be defined.

### A simple LUE Model

On a daily basis, dry biomass growth can be expressed as follows:

$$dW = LUE \cdot PAR \cdot (1 - e^{-k LAI})$$

where:

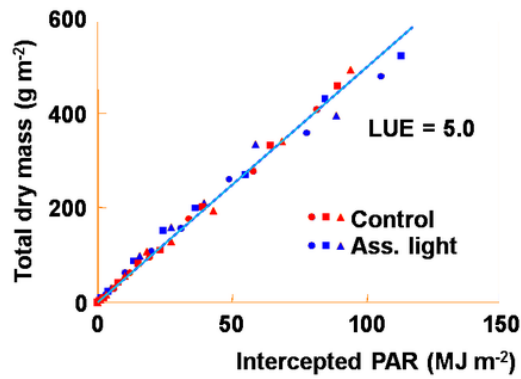
$dW$  = biomass growth rate ( in  $\text{g.m}^{-2}.\text{d}^{-1}$ )

$LUE$  = light use efficiency ( in  $\text{g.MJ}^{-1}$ )

$k$  = extinction coefficient

$LAI$  = leaf area index

$PAR$  = Photosynthetic Active Radiation incident on the crop ( $\text{MJ.m}^{-2}.\text{d}^{-1}$ )



Light use efficiency reported in winter on 3 plant densities with and without light assimilation for cut chrysanthemum (Graph E. Heuvelink, WAGENINGEN UNIVERSITY)

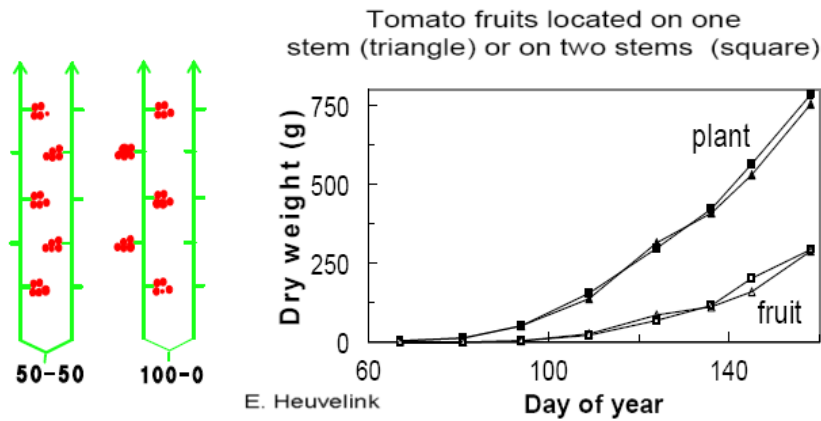
#### Notes

1. Many applications assume constant LUE values as show in the above figure, but LUE can be made dependent on CO<sub>2</sub>, temperature, light intensity, etc.
2. In the GreenLab model, LUE is defined from the fresh biomass weight, on the basis of 80% water concentration.

### Biomass common pool (reminder)

The biomass produced is stored in a common pool to be shared by competing organs.

Biomass distribution is not related to an assimilate transportation pathway in the plant structure. The following experiment carried out on tomato double stems illustrates this.



*Biomass distribution (Drawing and Graph E. Heuvelink, WAGENINGEN UNIVERSITY)*

*On the first tomato plant 50 % of young fruits are pruned.*

*On the second plant, all fruits of the second stem are pruned.*

*As shown in the graph, this pruning did not affect biomass production which was spread among the various organs.*

Shoots with leaves without chlorophyll grow normally, taking up assimilates from the common pool of biomass.

In this case, the leaves are only sinks and no longer sources.



*Ivy chimera, with white leaves (Photo P. de Reffye, CIRAD)*

*Note the distribution and the size of the white leaves are similar to those of the functional ones.*



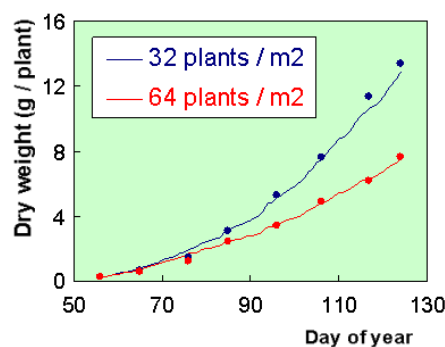
### Density effect (reminder)

Plant density greatly affects overall biomass production due to competition for light, water, and nutrient resources. In controlled environments, competition mainly involves the light resource. At low density, or early growing stages, competition for light between plants is reduced. As plants grow, the canopy closes, reducing the light resource, until reaching complete canopy cover. At this point, experiments have shown that biomass production reaches a stable maximum. The overall change in biomass production is therefore different if considered at plant level or at crop level.

#### Density effect at plant level

At the canopy closure stage, biomass production is stable.

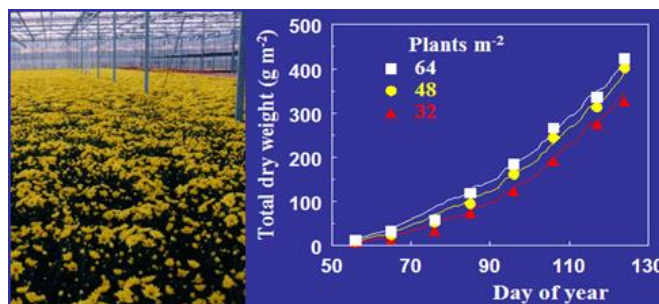
The weight of each individual biomass increase is therefore proportional to the number of plants per square metre, i.e. proportional to the inverse of the density. Considering overall individual production, this proportionality remains true if the cover happens at the early growth stages.



*Chrysanthemum biomass production at plant level at two densities (Graph E. Heuvelink, WAGENINGEN UNIVERSITY). This experiment compared biomass production at plant level at densities of 32 plants per square metre (in blue) and 64 plants per square metre (in red). The graph shows that production was similar for both cases up to 60 days. On that date, the canopy closed at high density, leading to lower individual production. At the mature stage, the individual average weight of the 32 p.m<sup>2</sup> crop was nearly double the individual average weight of the 64 p.m<sup>2</sup> crop.*

#### Density effect at crop level

When considering overall biomass production per area, density has no effect if the canopy is closed at very early stages. However, it does not mean that the fruit is the same: the plant usually adjusts its structure to optimize its production. In general, at early growth stages, canopy cover is not reached, leading to a shift in production profiles when comparing different density experiments.



*Chrysanthemum crop biomass production at three densities. In this case, the same experiments held at Wageningen University on Chrysanthemum compared biomass production at crop level for 32, 48 and 64 plants per m<sup>2</sup>. The production curves, expressed in g per m<sup>2</sup> are similar, staggered by a period corresponding to the different canopy closing dates. (Photo and Graph E. Heuvelink, WAGENINGEN UNIVERSITY)*

## Principles

### Reminder: The growth cycle

#### A discrete model

The GreenLab model evaluates plant structure and production at regular thermal time periods, defined from an average daily temperature sum ratio, called a growth cycle (CG).

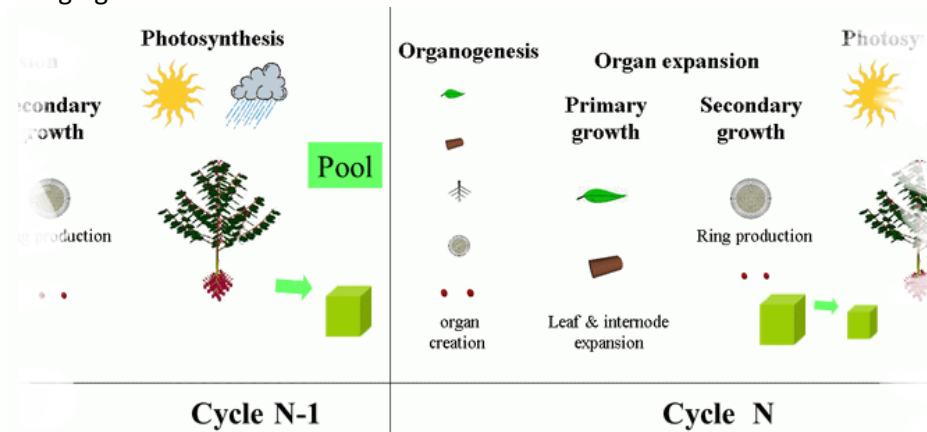
The growth cycle value is usually low compared to a shoot development cycle. Hence:

- \* Thermal time implicitly controls the speed of plant development (organogenesis).
- \* Thermal time implicitly controls organ functioning and expansion durations.
- \* However, organ growth does not depend on temperature, but only on the available biomass to be shared with the other organs from a common biomass pool.

#### The growth and development cycle

- \* For each growth cycle, the model defines organogenesis evolution on a representative of each metamer organ cohort (since all organs in a given cohort share the same chronological and physiological properties).
- \* Biomass production is computed from organ sources and sizes (usually the functional leaf areas).
- \* If organogenesis occurs, new organ cohorts are created.
- \* Biomass demand is then evaluated, for each organ cohort, according to its sink strength value.
- \* The common pool of biomass is then spread among the available functioning organ cohorts, as a proportion if the demand exceeds the pool.
- \* The organ sizes are computed, from their chronological age, their expansion state, and allometry rules
- \* The remaining biomass, if any, is kept in the biomass pool.

The following figure illustrates this scheme.



The GreenLab dynamic model cycle (Illustration P. de Reffye and M. Jaeger, CIRAD)

For each growth cycle:

- 1 - Plant production is computed and stored in the biomass common pool
- 2 - Organogenesis is computed with potentially new organ cohorts
- 3 - Plant demand is evaluated and the required biomass split among the organs in proportion to their sink and the common biomass pool availability

The GreenLab model refines classic process-based models

### *Functioning in GreenLab vs PBM*

#### Computing biomass production

GreenLab is based on the classic production model

$$dW = LUE \cdot PAR \cdot (1 - e^{-k LAI})$$

applying it to successive growth cycles.

The well-known formulation describes production for a unit area (1 m<sup>2</sup>). In the GreenLab model, the unit area is defined as the "plant Area", leading to a unique equation linking production from plant to crop scale.

#### Computing the *LAI*

In PbMs, *LAI* estimation is not obvious. In GreenLab *LAI* computation is replaced by a *total leaf area / plant area* ratio.

At high densities it has been shown that this ratio tends towards the *LAI*.

The total leaf area results from organogenesis that defines the number of new leaves for each cycle, and their respective areas computed from biomass partitioning

#### Organ compartments

In classic PbMs, biomass is spread among the different organ compartments, defined by organ types.

In GreenLab, each organ compartment is in fact split into several compartments related to their ages:

- their physiological age, as defined in botanical architecture
- their ontogenetic age (in other words the date they appear)

Under these conditions, each GreenLab organ compartment, called cohorts (see next page), contains organs with the same physiological properties, the same age and constrained by the same environmental conditions.

#### Organ expansion dynamics

Organ expansion dynamics are often assumed to be stable (for instance expressed as a ratio between existing organs)

In this model, the function defining the ability to store biomass is considered as a non-constant, hidden function, showing a generic shape, related to genetics and fitted from the model applications on real measurements.

#### Model expression

The GreenLab model can be fully expressed by a set of mathematical expressions allowing:

- theoretical model studies; in particular equilibrium production conditions can be analysed (see study case in Applications)
- parameter identification
- reversing parameters and variables; for instance, finding the density from the measurements on plants already modelled.

Reminder.

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

### *GreenLab Organ cohorts (reminder)*

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 models uses this assumption, evaluating biomass demand and biomass consumption from a single representative of each cohort, multiplied by the number of organs  $N_o(p, t)$  of 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 minimized 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  $d_a$  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).

Note

Two cohorts  $C_o(p, d_a, d_c)$  and  $C_o(p, d_a+i, d_c+i)$  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.

### *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  $C_o(p, d_a, d_{c+n})$ , 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  $C_o(p, d_a, d_{a+l})$ , born on date  $d_a$ , built for the full organ life span  $l$ , defines the chronological organic series of  $o$ , born on date  $d_a$ , 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 of series built from organs on the same axis, from tip to insertion, allow structural statistical properties to be expressed.

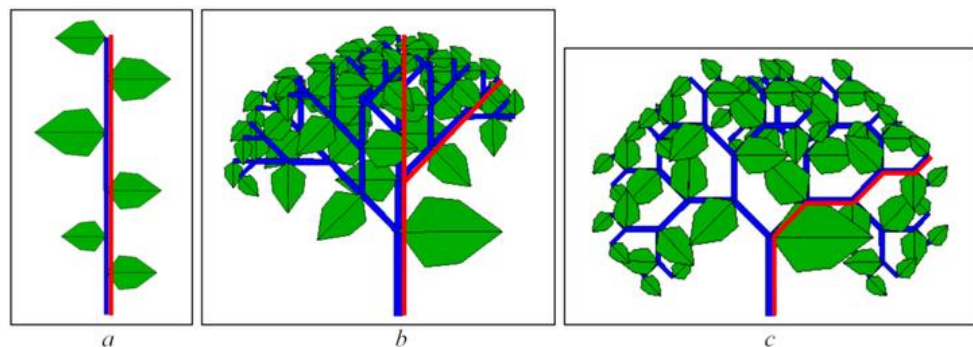
In this case, the series is built from representatives of cohorts on successive appearance dates, corresponding to successive ranks of organ insertion along the axis.

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

From top to bottom, each organ position defines a rank in the different cohort sets.

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

Both organic series are independent from structure architectural considerations as shown below.



Organ Series in plant structures (Image 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.*

### 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](#))

The GreenLab model refines classic process-based models but is not a process-based model or a functional structural plant model

### *Functioning: GreenLab vs PbM & FSPM*

#### Computing biomass production

Photosynthesis is simplified compared to classic PbMs:

In particular, LUE and PAR are not model inputs, an aggregate  $E(n)$  parameter standing for environmental conditions is used instead. However, this point can be refined.

Photosynthesis is simplified compared to classical FSPM:

Production is not differentiated in the plant. The Beer Lambert law is applied on the whole plant. For instance, radiation studies at different plant heights, which are classic in FSPM, cannot be operated on the GreenLab model

#### Respiration

Respiration is ignored in the GreenLab model, and poorly studied so far.

However, if respiration is considered as a fixed structural cost, the model will implicitly integrate its effect through the existing parameter to be fitted on measurements.

Maintenance costs could be integrated into the current model without any particular difficulties.

#### Spatial/structural heterogeneity

GreenLab assumptions related to the Beer Lambert Law and organ cohorts consider the plant level as a whole.

The finest functional level is defined by the organ cohorts. Variance at this level can be simulated (for instance arising from the stochastic number of organs in cohorts) but not explained.

Thus, if cohorts are explicitly related to structural and geometrical aspects, spatial and structural heterogeneity can be studied. For instance, pruning all axes borne on a given date is easy to model and simulate.

However, geometrical and structural gradients cannot usually be considered. For instance, the case of the effects of mechanics, or pruning at a given height cannot be taken into account.

#### Interaction with other models

As far as external models can be expressed at the lowest GreenLab level, i.e. according to organ cohort indexes with the growth cycle as a synchronizing scheduler, interactions with other models are possible.

For example, pest attacks, if located according to plant phenology (leaf age, physiological age, etc.) can even be closely integrated as:

- external organ sinks
- biomass production reducers

## Biomass partitioning

### *Organs, Sinks and Sources*

Organs, considered within their specific cohorts, are in competition during their growth.

For a given organ, the ability to accumulate biomass is characterized by its sink strength. We can consider that all organs show this capability. They are sinks.

#### *Assumption*

Organs are sinks during their expansion. The sink strength function, characterizing organ biomass demand during organ development (a given number of growth cycles) is usually not constant, but becomes null when expansion is finished.

This means that there is no organ maintenance "cost" in this model.

Conversely, some organs are considered as having the ability to produce biomass.

They are sources. They show this capability as soon they appear, and until they reach their functioning time. The capability of the source is characterized by its source strength.

### *Assumption*

In our model presentation (and implementation), we consider that only leaves show the ability to be sources.

The functioning time is assumed to be greater than the expansion time.

In theory, each sink organ could also be a source and the model formalism could easily be extended to allow it.

Beta laws are often used to express sink and source strength functions, giving a wide range of shapes from two single parameters (see further in equation sub-section)

### *Typical organs in the GreenLab model*

The list of organs is not exhaustive.

While leaves are the only source organ, usual sink organs are internodes, leaves, female and male fruits, rings, roots.

However, their respective number of cohorts, numbers within cohort and sink strength may be significantly different from each other.

#### *Roots*

In this model, the root system defines a single unique organ.

Its sink strength is defined by a single constant ratio (typically 15 to 20%) of plant demand.

Despite this crude approach, the model show satisfactory results on agricultural plants such as beetroot.

### Female and male fruits

On some crop plants, it may be convenient to distinguish between male and female sexual organs. Their phenology can be quite different as well as their relative ability accumulate biomass. Thus, their relative sink strength may be significantly different, in terms of both strength and dynamics. For instance on maize, tassels and cobs should be considered as different organs.

### Internodes

Internodes are sink organs and not considered as being potential sources.  
The biomass allocated to internodes defines in fact the pith volume (and its dimensions).  
Internode organs do not include wood rings, resulting from another process.

### (Wood) Rings

Secondary growth, and especially ring width establishment, may be a critical biomass consumer, and must thus be considered as a sink organ.  
Computation of the biomass allocated to wood rings is rather complex (see elements below)

### Other specific organs

As an example, on cotton, the leaf organ must be split into two organs, the blade (sink and source) and the petiole (sink only). Such should be the case for all plants whose petioles are significant biomass consumers and show a different sink strength function compared to the blade.



## Organ growth

Biomass partitioning or allocation is the distribution of growth over the different organs (roots, leaves, stems, fruits, rings).

Biomass partitioning among organ cohorts is not constant and results from competition.

Organs, considered within their specific cohorts, are in competition during their growth.

For a given organ, the ability to accumulate biomass is characterized by a sink, expressed by a value for a given duration, i.e. the organ expansion time.

The set of sink values during organ expansion defines the organ sink strength function,  $\varphi_o$ .

On a given date  $t$ , organ sizes results from biomass accumulation.

Each biomass increase  $q(t)$  is defined from the total available biomass  $Q(t)$ , and the relative ratio of the organ sink  $\varphi_o / \sum_j \varphi_j$ , with  $j$  respectively standing for all the different organ types (all roots, all leaves, etc.).

$$q(t) = Q(t) \cdot \varphi_o / \sum_j \varphi_j$$

The value of the sink strength function has to be expressed according to organ expansion, i.e. its age.

Definition of the sink strength function is compatible with definition of the cohort, and can thus be associated with the cohort parameters:

all organs belonging to a given cohort show the same sink value, on any date.

Beta laws are often used to express sink functions, giving a wide range of shapes from two single parameters (see below in the equation sub-section)

## Organ weight

We have seen that plant growth is modelled step by step, integrating processes during growth cycles. Expansion periods are thus expressed as a number of growth cycles.

The sum of all the biomass increments of an organ gives its weight.

The total biomass allocated to a given organ  $o$  is thus:

$$Q_{o,p}(n) = \sum_{j=n-l;n} q_{o,p}(j)$$

where

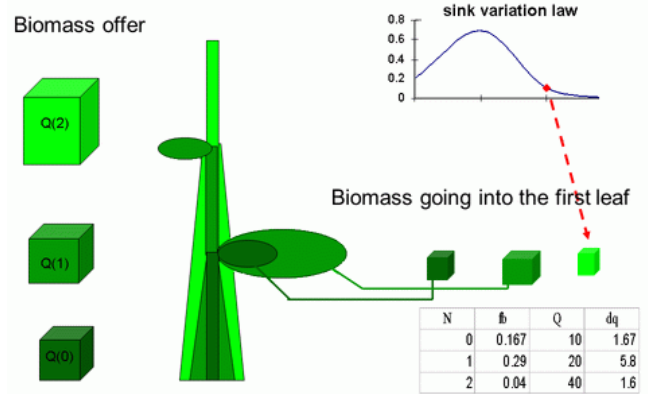
$n-l$  stands for the first appearance cycle of the current organ.

$l$  stands for the expansion duration (in number of cycles) of the current organ.

Organ weight thus results from a dynamic process:

- it results from iterative biomass allocations during all organ expansion periods
- each allocation is defined from the available biomass in the common pool and the organ sink strength
- the organ sink strength varies during organ expansion

Organ weight is thus a convolution, as illustrated in the small example below.



This example shows the growth of the first leaf of a simple plant, over three growth cycles (Images and animation P. de Reffye, CIRAD)

## Organ dimension. Organ weight and sizes

The sum of all the biomass increments of an organ gives its weight.

In the GreenLab model, the relation relating sizes to fresh biomass is defined from [allometries](#). Allometric equations take the general form  $Y = u \cdot M^w$ , where  $Y$  is some biological variable,  $M$  is a measurement of body size,  $u$  a global scaling factor and  $w$  is some scaling exponent.

Using allometric equations thus makes it possible to evaluate organ dimensions.

On the assumption of an average stable density  $d_{org}$ , and simple organ shapes, the organ dimension can be defined from the allometric general form, where  $M$  stands for the volume  $v_{org}$  (i.e. the density that divides the biomass  $q_{org}$ ) and  $Y$  a metric or metric relation.

The general organ allometry is thus:

$$Y_{org} = u \cdot (q_{org} / d_{org})^w = u \cdot v_{org}^w$$

## Usual organ shapes and their dimensions

### Fruits

For fruits, the basic shape to consider can be the sphere, characterized by its radius  $r$

We thus have  $v_f = 4/3 \cdot \pi \cdot r^3$  giving  
 $r = (3 \cdot v_f / (4 \pi))^{1/3}$

This approach can be extended to an ellipsoid shape defined by 3 axes

$r_1 = r$ ,  $r_2 = a \cdot r$  and  $r_3 = b \cdot r$

We thus have

$v_f = 4/3 \cdot \pi \cdot r_1 \cdot r_2 \cdot r_3 = 4/3 \cdot \pi \cdot a \cdot b \cdot r^3$  giving

$$r = (3 \cdot v_f / (4 \cdot a \cdot b \cdot \pi))^{1/3}$$

### Internodes

The internode can be represented by a cylinder defined by its height  $h$  and its section  $s$ .

In the general allometry form, let us consider the allometry between height and section with  $b$  as a lengthening scaling factor, and  $\gamma$  as the scaling exponent:

$$h / s = b \cdot (v_i)^\gamma$$

The cylinder height and section can then be expressed from the volume  $v_i$  as follows:

$$\begin{aligned} \text{for height: } h &= b^{1/2} \cdot (v_i)^{(1+\gamma)/2} \text{ and} \\ \text{for section: } s &= b^{-1/2} \cdot (v_i)^{(1-\gamma)/2} \end{aligned}$$

### Note

If  $\gamma = 1$  then the section  $s$  is constant and height  $h$  becomes proportional to the volume.

If  $\gamma = -1$  then the height  $h$  is constant and section  $s$  becomes proportional to the volume.

If  $\gamma = 2/3$  then the ratio height  $h$  on diameter is constant.

## Leaves

For leaves, this scaling factor is defined from the Specific Leaf Weight -[SLW](#)- (or the inverse of the Specific Leaf Area, -[SLA](#)-).

This variable, noted  $e$ , representing leaf (or blade) thickness, is usually considered constant during expansion.

The allometry rules defining organ dimensions from their volume (i.e. from their biomass) is summarised here:

$s = \frac{v_l}{e}$	Leaf: simple area $s$ of thickness $e$
$r = \sqrt[3]{\frac{3v_f}{a b \pi}}$	Fruit: ellipsoïd shape ( $r, r_a, r_b$ )
$height = \sqrt{b} (v_i)^{\frac{1+\gamma}{2}}$	Internode: cylinder with lengthening $b$ and allometry $\frac{height}{section} = b v_i^\gamma$
$section = \sqrt{\frac{1}{b}} (v_i)^{\frac{1-\gamma}{2}}$	

Organ allometry relations in the GreenLab model

## GreenLab Functional Equations

### *GreenLab equation summary*

Starting from the production equation of the classic process-based model, the GreenLab model is introduced, scaling down the equation to the single plant.

Biomass allocation to a given organ is then introduced. Summarizing the allocation of all organs leads to the definition of plant demand.

At organ level, the successive biomass increments define its geometry. We can thus specifically define the leaf area.

Moreover, the formalisation of organogenesis allows us to define an equation for the number of phytomers produced.

To sum up, the GreenLab model is expressed as a set of 6 basic equations.

This section is divided up as follows:

- Expression of the classic crop model at single plant level
- Biomass allocation. Plant demand
- Organ weight. Organ sizes. Leaf Area
- Explicit production equation and its interpretation
- Development equations (reminder)
- The GreenLab model

## The production equation

The equation for production at crop level

We have seen that crop-based models may express biomass growth per unit area,  $m^2$ , as follows:

$$dW = LUE \cdot PAR \cdot (1 - \exp(-k LAI))$$

where:

$LUE$  is the Light Use Efficiency,

$LAI$  the Leaf Area Index

$PAR$  the Photosynthetic Active Radiation incident on the crop (per  $m^2$ )

## Expression of the crop model at single plant level

Let  $d$  define plant density.

Then  $S_d = 1/d$  represents the potential available area at single plant level.

Let  $S_l$  also define the total area of functional leaves. We can then write:

$$LAI = S_l / S_d$$

The production equation can thus be expressed as:

$$dW = LUE \cdot PAR \cdot S_d (1 - \exp(-k S_l / S_d))$$

Now, at low density, we introduce  $S_p$ , a virtual surface area such that:

$S_p = F(S_d)$  with  $F(S_d) \rightarrow S_d$  when the crop cover closes (at a significant density value).

Moreover, we can integrate these equations over the duration of a growth cycle.

Assuming that the leaf area remains constant during a growth cycle, we obtain the first GreenLab equation, defining fresh biomass production as follows:

$$Q(n) = \frac{E(n) \cdot S_p}{r} \left( 1 - \exp\left(-k \frac{S_l(n)}{S_p}\right) \right) \quad (\text{equation 1})$$

where:

$Q(n)$  is the fresh biomass produced at cycle  $n$

$E(n)$  is an aggregate variable standing for environmental resource conditions, typically  $LUE$  and  $PAR$

$r$  represents the water resource, proportional to the Water Use Efficiency inverse ( $WUE^{-1}$ )

$k$  stands for the Beer Law extinction coefficient

$S_p$  stands for the projection area, as defined above

$S_l(n)$  stands for the total functional leaf area

## Biomass Allocation. Plant Demand.

### Biomass allocation

Biomass allocation is driven by the sinks of all expanding organs.

We have seen that, on a given date  $t$ , the biomass increase  $q(t)$  is defined from the total available biomass  $Q(t)$ , and the relative ratio of the organ sink  $\varphi_o / \sum_j \varphi_j$ , with  $j$  respectively standing for all the different organ types (all roots, all leaves, etc.); the sum of all organ sinks (  $\sum_j \varphi_j$  ) builds plant demand  $D(t)$ .

Considering now the period of a growing cycle  $n$ , the biomass allocated to organ  $o$ , of physiological age  $p$ , can be written as follows:

$$q_{o,p}(n) = Q(n-1) \cdot \varphi_{o,p}(i) / D(n) \quad (\text{equation 2})$$

where

$n$  is the current growing cycle

$o$  stands for the organ type

$p$  stands for the physiological age

$i$  stands for the organ age (expressed in cycles since the beginning of expansion)

$\varphi_{o,p}$  defines the sink function of organ  $o$  at physiological age  $p$

$D(n)$  is the total plant demand at cycle  $n$  (the sum of all sinks of organs in expansion)

$Q(n-1)$  is the available biomass in the common pool. By definition  $Q(0)$  defines the seed biomass.

### Plant demand

Plant demand, at a given cycle  $n$ , called  $D(n)$ , can be computed from the sum of all cohort demands:

$$D(n) = \sum_{o,p} D_{o,p}(n)$$

where

$D_{o,p}(n)$  is the demand of organ  $o$ , at physiological age  $p$ .

$$D_{o,p}(n) = \sum_{t1=n-l;n} N_{o,p}(t1) \cdot \varphi_{o,p}(t1-n+l)$$

giving the expression of demand:

$$D(n) = \sum_{o,p} \sum_{t1=n-l;n} N_{o,p}(t1) \cdot \varphi_{o,p}(t1-n+l) \quad (\text{equation 3})$$

where:

$n$  is the current cycle

$o$  is the organ type (internode, leaf, fruit, ring, root, etc.)

$p$  is the physiological age

$t1$  stands for the different appearance cycles of cohort  $C_{o,p}$

$t1$  stands for the different appearance cycles of cohort  $C_{o,p}$

$t1-n+l$  is therefore the age of the organ (belonging to  $[0..l]$ )

$N_{o,p}(t1)$  stands for the number of organs appeared at cycle  $t1$

## Organ dimensions

### Organ geometry & organ weight

We have seen that the weight is the total biomass allocated to a given organ  $o$ :

$$Q_{o,p}(n) = \sum_{j=n-l;n} q_{o,p}(j)$$

where

$n-l$  stands for the first appearance cycle of the current organ.

$l$  stands for the expansion duration (in number of cycles) of the current organ.

Using [\(equation 2\)](#) describing organ biomass allocation we can then write:

$$Q_{o,p}(n) = \sum_{j=n-l;n} q_{o,p}(j) = \sum_{j=n-l;n} Q(j-1) \cdot \varphi_{o,p}(j-n+l) / D(j)$$

where

$n$  is the current growing cycle

$o$  stands for the organ type

$p$  stands for the physiological age

$n-l$  stands for the first appearance cycle of the current organ.

$j-n+l (= j-(n-l))$  stands for the organ age (expressed in cycles since the beginning of its expansion)

$D(j)$  is the total plant demand at cycle  $j$  (the sum of all sinks of organs in expansion)

$Q(n-1)$  is the available biomass in the common pool. By definition  $Q(0)$  defines the seed biomass.

In this expression, production is expressed according to the cycle number, as well as the sink function. An alternate writing is to express these quantities relatively to organ age:

$$Q_{o,p}(n) = \sum_{j=1;l} \varphi_{o,p}(j) \cdot Q(j+n-l-1) / D(j+n-l) \quad (\text{equation 4})$$

### Organ sizes

In the GreenLab model, the relation relating sizes to fresh biomass is defined from allometries (see [here](#)). A reminder of the allometry rules defining organ dimensions from their volume (i.e. from their biomass) is given here:

$s = \frac{v_l}{e}$	Leaf: simple area $s$ of thickness $e$
$r = \sqrt[3]{\frac{3v_f}{a b \pi}}$	Fruit: ellipsoid shape ( $r, ra, rb$ )
height = $\sqrt{b} (v_i)^{\frac{1+\gamma}{2}}$	Internode: cylinder with lengthening $b$ and allometry $\frac{\text{height}}{\text{section}} = b v_i^\gamma$
section = $\sqrt{\frac{1}{b}} (v_i)^{\frac{1-\gamma}{2}}$	

Organ allometry relations in the GreenLab model



## Blade Area

With a constant leaf thickness  $e$ , the total functioning blade area  $S(n)$  at cycle  $n$  can then be expressed as follows:

$$S(n) = \frac{1}{e} \left( \sum_{i=1; T_b} \left( \sum_{j=1; i} \varphi_b(j) \frac{Q(n-i+j-1)}{D(n-i+j)} \right) \right) \quad (\text{equation 5})$$

where:

$\varphi_b(j)$  stands for the leaf blade sink function at age  $j$

$i, j$  stands for the blade age with  $T_b \geq i \geq j$

$T_b$  is the number of cycles before the leaf becomes senescent (i.e. the number of functional cycles)

$e$  is the blade thickness (the SLW)

### GreenLab production equation

Equation expression

Replacing the functional leaf Area  $S(n)$  in eq. 1 by its detailed expression as defined in eq. 5, defines the explicit GreenLab production equation:

$$Q(n) = \frac{E(n) \cdot S_p}{r} \left( 1 - \exp \left( - \frac{k}{e \cdot S_p} \sum_{i=1; \tau_b} \sum_{j=1; i} N_b(i) \varphi_b(j) \frac{Q(n-i+j-1)}{D(n-i+j)} \right) \right) \quad (\text{equation 6})$$

where:

$Q(n)$  is the fresh biomass produced at cycle  $n$

$E(n)$  is an aggregate variable standing for the Environmental resource conditions at cycle  $n$ , typically LUE and PAR

$r$  represents the water resource, proportional to the Water Use Efficiency inverse ( $WUE^{-1}$ )

$N_b(i)$  is the number of blades appeared at cycle  $n$

$k$  stands for the Beer Law extinction coefficient

$e$  is the blade thickness (assumed to be constant here)

$\varphi_b(j)$  is the blade sink at age  $j$

$D(n)$  is plant demand at cycle  $n$  as formulated in (eq. 3)

## Equation interpretation

Understanding equation terms

$$Q(n) = \frac{E(n) \cdot S_p}{r} \left( 1 - \exp \left( - \frac{k}{e \cdot S_p} \sum_{i=1; \tau_b} \sum_{j=1; i} N_b(i) \varphi_b(j) \frac{Q(n-i+j-1)}{D(n-i+j)} \right) \right)$$

Terms related to environmental conditions

$E(n)$ : the aggregate variable standing for the environmental resource conditions at cycle  $n$ , typically LUE and PAR

$r$  represents the water resource, proportional to the Water Use Efficiency inverse ( $WUE^{-1}$ )

Terms related to development (plant architecture)

$N_b(i)$  : the number of blades appeared at cycle  $n$

Note that  $D(n)$ , the plant demand at cycle  $n$ , involves the number of organs  $N_o$  in expansion in cycle  $n$

Terms related to organ competition (biomass allocation)

$\varphi_b(j)$  : the blade sink at age  $j$

Note that:

\*  $D(n)$ , the plant demand at cycle  $n$ , involves the sink function of all organs  $N_o$  in expansion in cycle  $n$

\*  $Q(n)$  is the fresh biomass produced at cycle  $n$ , and more precisely the Supply to Demand ratio  $Q(n-1) / D(n)$  defines the potential biomass increment of each organ.

Terms specific to the plant (or plant species)

$S_p$  is the projection area

$k$  : the Beer Law extinction coefficient

$e$  : blade thickness

## GreenLab full model equations

In the following equations:

$n$  is the current cycle

$o$  is the organ type (internode, leaf, fruit, ring, root, etc.)

$p$  is the physiological age

$\varphi_{o,p}$  defines the sink function of organ  $o$  at physiological age  $p$

$Q(n-1)$  is the biomass available in the common pool. By definition  $Q(0)$  defines the seed biomass.

Structure: The Number of organs at cycle  $n$ , appeared at cycle  $t$

$$N_p^t(n) = [ \prod_{p \leq q \leq P} u_{p,q}(t+1-n) (N_q^t(n-1))^{b_{p,q}(t+1-n)} ] N_p^t(n-1)$$

where:

$u_{p,q}$  corresponds to the number of phytomers  $m_{p,q}(t)$  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.

Plant demand at cycle  $n$

$$D(n) = \sum_{o,p} \sum_{t1=n-l;n} N_{o,p}(t1) \cdot \varphi_{o,p}(t1-n+l)$$

where:

$t1$  stands for the different appearance cycles of cohort  $C_{o,p}$

$t1$  stands for the different appearance cycles of cohort  $C_{o,p}$

$t1-n+l$  if therefore the age of the organ (belonging to  $[0..l]$ )

The biomass allocated to organs

$$q_{o,p}(n) = Q(n-1) \cdot \varphi_{o,p}(i) / D(n)$$

where  $i$  stands for the organ age (expressed in cycles since the beginning of expansion)

The total functioning Leaf area  $S(n)$  at cycle  $n$

$$S(n) = \frac{1}{e} \left( \sum_{i=1; T_b} \left( \sum_{j=1; i} \varphi_b(j) \frac{Q(n-i+j-1)}{D(n-i+j)} \right) \right)$$

where:

$\varphi_b(j)$  stands for the leaf blade sink function at age  $j$

$i, j$  stands for the blade age with  $T_b \geq i \geq j$

$T_b$  is the number of cycles before the leaf becomes senescent (the number of functional cycles)

$e$  is blade thickness (the SLW)

The Production equation

$$Q(n) = \frac{E(n) \cdot S_p}{r} \left( 1 - \exp \left( -k \frac{S_l(n)}{S_p} \right) \right)$$

where:

$Q(n)$  is the fresh biomass produced at cycle  $n$

$E(n)$  is an aggregate variable standing for the environmental resource conditions, typically LUE and PAR

$r$  represents the water resource, proportional to the Water Use Efficiency inverse ( $WUE^{-1}$ )

$k$  stands for the Beer law extinction coefficient

$S_p$  stands for the projection area, as defined above

$S_l(n)$  stands for the total functional leaf area

## Supplementary resources

### *Production supplementary resources*

Recommended on-line resources

Eco-physiology for crop modelling course (English)  
[../P1\\_Prelim/EPhysio/Physio\\_intro.html](http://../P1_Prelim/EPhysio/Physio_intro.html)

Introduction to Models (English)  
[../P1\\_Prelim/Model/Model\\_intro.html](http://../P1_Prelim/Model/Model_intro.html)

More detailed GreenLab papers (pdf files)

Relevant qualitative and quantitative choices for building an efficient dynamic plant growth model ([pdf](#))

Plant growth models ([pdf](#))

### *Bibliography*

**De Reffye P., Hu BG**, 2003. Relevant qualitative and quantitative choices for building an efficient dynamic plant growth model: GreenLab case. In Hu BG, Jaeger M (Eds), Plant growth modelling and applications (PMA03), Proceedings of the 2003' International Symposium on Plant Growth Modeling, Simulation, Visualization and Their Applications Tsinghua University Press, Springer; pp. 87-107. ([pdf](#))

**De Reffye P., Heuvelink E, Barthélémy D, Cournède PH**. 2008. Plant growth models. In: Jorgensen S, Fath B (Eds.), Ecological Models, Vol. 4 of Encyclopedia of Ecology (5 volumes), Elsevier (Oxford), pp. 2824-2837. ([pdf](#))