UVED Resource

Plant Growth Architecture and Production Dynamics

Preliminary Course: Eco-Physiology

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Contents and Objectives

Presentation

This section presents an overview of plant eco-physiological concepts involved in crop modelling. Plant physiology is a sub-discipline of botany concerned with the functioning, or physiology, of individual plants.

Closely related fields include plant morphology (structure of plants), plant ecology (interactions with the plant community), phytochemistry (plant biochemistry), cell biology, genetics, biophysics and molecular biology.

Relevant concepts in the development of plant and crop models are mainly related to plant eco-physiology.

Course Objectives

The aim of this course is to enable students to:

Identify climatic factors affecting plant growth
Understand how temperature and light intensity affect biomass production
Understand the principles of biomass production and allocation among organs at the crop scale
Learn about the principles of a crop model

Map

Contents

In this sub-chapter, the following concepts are described:

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

Light interception: PAR, LAI and Beer-Lambert Law
Only part of light energy is used in plant crops. A limited fraction of the light spectrum is absorbed by leaves; this part is constrained by 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 the Light Use Efficiency.

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

Biomass common pool
Assumption: 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.

Process-based models.
Process-based models or crop models are designed to model and simulate biomass production.

Course content map

Factors affecting plant growth

Plant growth results from both endogenous processes and environmental factors.

The endogenous process: plant structure establishment

The plant structure establishment strategy arises from endogenous processes.

The differentiation and production of various organs can be expressed from rules applied to successive metamers.

Environmental factors

Environmental factors such as water, mineral nutrients, CO_2 and light are resources; their supply availability affects plant growth, and thus determines organ sizes.
Temperature affects growth.
In most plants, the structure development steps are governed by the thermal energy received.

Temperature thus affects the rate of structure development and light affects biomass accumulation.

The endogenous process

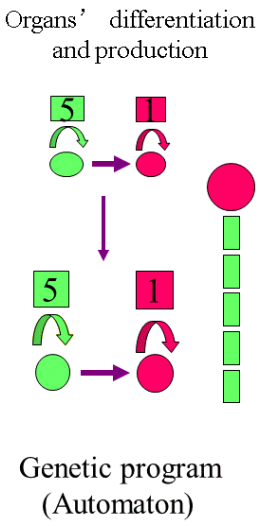
The endogenous process: plant structure establishment

Plant structure establishment is the final result of the endogenous process.

The differentiation and production of the various organs can be expressed from rules applied to successive metamers.

Such rules can be simulated with an automaton.

In the illustrated example the structure is built from five consecutive metamers at the same stage of differentiation. The terminal bud then reaches a flowering stage; the growth is thus determinate. (Drawing P. de Reffye, CIRAD)



Environmental Factors

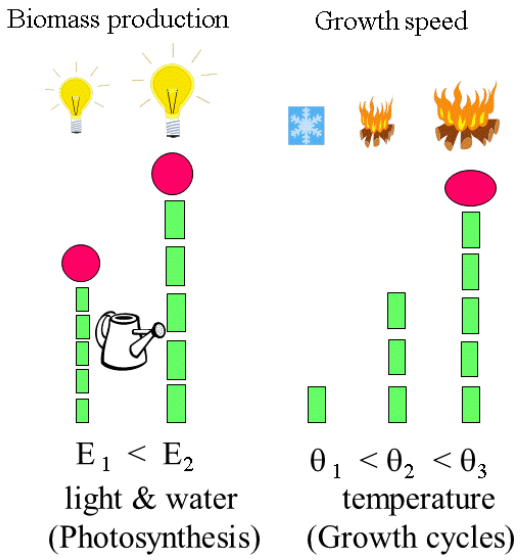
Environmental factors also impact on plant growth.
Resources, and more precisely the water and light supply, affect organ biomass accumulation and thus organ size.

- Light produces photosynthates via green leaf functioning. Empirically, the effect of incident light is well known. According to the light intensity, a linear effect can be seen gradually reaching saturation. Light also has a strong influence on plant plasticity. It can modify plant development by affecting meristem production rules.

- Water is taken up by roots from the root environment and evaporates by transpiration at leaf level. As both transpiration and photosynthesis are strongly influenced by stomata aperture, often a close relationship is found between crop transpiration and biomass production. Plant transpiration depends primarily on radiation and leaf area. It can be limited by water shortages in the root environment (stomata will close). The cumulative effect of water transpiration over the long term is often linearly related to plant biomass production.

- Temperature also affects growth.
In most plants, the structure development steps are governed by the thermal energy received. Temperature controls the rate of shoot development and the duration of organ expansion. Within a certain temperature range (i.e., when the development rate is linearly related to temperature), there is a linear relationship between the number of phytomers formed on a shoot and the sum of daily effective temperatures received by the plant.

To sum up, temperature affects the rate of structure development and light and water affect biomass growth.



Environmental factors illustrating the growth dynamics with two levels of resources and three levels of temperature (Drawing P. de Reffye, CIRAD).

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).

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

where

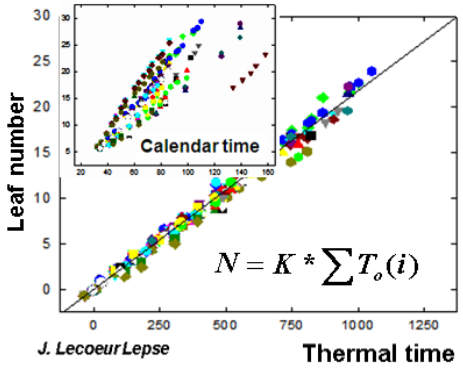
T_d is the average daily temperature

T_o is the developmental threshold or base temperature under which the development rate is zero. The base temperature varies with the plant species: 0 ° C for wheat, 4 ° C for barley, 8 ° C for soybean, and 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 Organogenesis

It has been shown that the number of organogenesis cycles is proportional to the thermal time. The following example illustrates this property on leaf appearance.

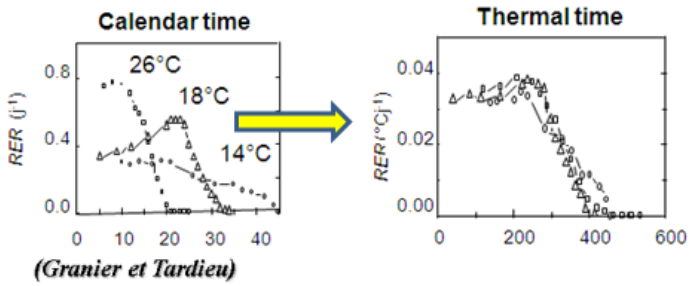


Number of leaves produced in successive periods at various temperatures (Graph: J. Lecoeur, SYGENTA)
Graphs according to calendar time (top left) and to thermal time (bottom).
On the calendar time data, leaf appearance alignments are spread on the graph, with high temperatures on the left, and low ones on the right.
Normalizing the period duration to thermal time (right) leads to a single linear leaf appearance rate.

Thermal Time and Development

This rule can also be applied to organ size increase.
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 Relative Elongation Rate (RER) measured according to calendar time (per day) compared to thermal time (expressed in °C per day).(Graph: Granier and Tardieu, INRA)

Bibliography

Interesting reading related to thermal time:

Granier, C., Massonnet, C., Turc, O., Muller, B., Chenu, K., and Tardieu, F. 2002. Individual Leaf Development in Arabidopsis thaliana: a Stable Thermal-time-based Programme. Annals of Botany (2002) 89 (5): pp. 595-604 (access to paper and pdf)

Lecœur J., Ney B. 2003. Change with time in potential radiation use efficiency in field pea, European Journal of Agronomy. vol. 19, pp. 91-105

Light interaction

Photosynthetic active radiation (PAR)

Leaves intercept light.
Chlorophyll, the most abundant plant pigment, is most efficient in capturing red and blue light.

Photosynthetically active radiation, 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.

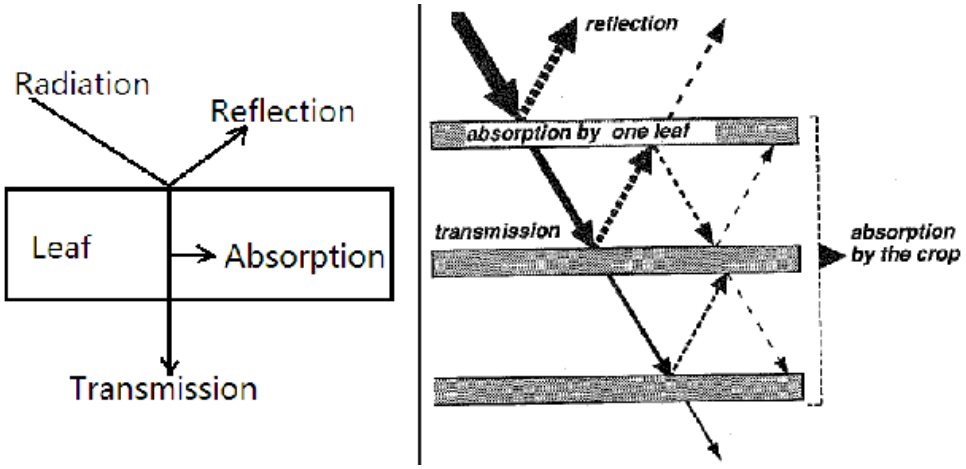
This spectral region corresponds more or less to the range of light visible to the human eye.

PAR measurement is widely used in agriculture, forestry and oceanography. PAR sensors stationed at various levels of the forest canopy measure the pattern of PAR availability and utilization.
The photosynthetic rate and related parameters can be measured non-destructively using a photosynthesis system, and these instruments measure PAR and sometimes control PAR at set intensities.

PAR is normally quantified as µmol photons per $m^{-2}.s^{-1}$, which is a measurement of the photosynthetic photon flux (area) density.

In Agronomy, PAR is often expressed in energy units as irradiance per area (in $W.m^{-2}$, *1 $W.m^{-2}$ = 4.57 µmol . $m^{-2}.s^{-1}$*).

At leaf level, part of light energy is reflected, the other part is partially absorbed, and the remaining energy is transmitted.
In a crop, the available light energy thus decreases according to the depth of the leaves in the canopy. A common method characterizes leaf depths by successive layers.



Distribution of radiation inside a leaf (left) and inside a canopy (right). (Drawing Ep. Heuvelink, WUR)

Light absorption

LAI

The LAI or **Leaf Area Index** is the ratio of total leaf area 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.

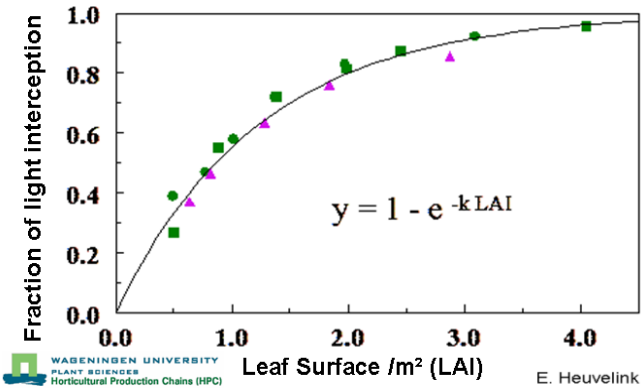
Beer-Lambert Law

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:

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

In this formula, called the **Beer-Lambert Law**,
k stands for the extinction coefficient,
I_{absLAI} stands for the radiation level at canopy depth LAI (expressed in overlying LAI).
I_0 stands for the radiation level at depth 0 above the canopy.
p parameter stands for the value of the canopy reflection coefficient.
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 the PAR and increase crop photosynthesis by at least 7% for a LAI of 3 (as long as CO_2 is not a limiting factor) (Gijzen, 1995a).



Influence of the Leaf Area Index (LAI) on the fraction of light intercepted by a tomato crop.
In this example, the extinction coefficient k is experimentally found from three sets of data respectively represented by the green and pink symbols. (Graph: E. Heuveulink, Wageningen University)

As extinction depends on both the direction of radiation and the geometry of leaf position and orientation, more detailed models have been developed (De Wit, 1965; Ross, 1981).
For horizontal leaves, the fraction of radiation intercepted by any leaf will be proportional to the leaf area itself, independent of the radiation direction.

At leaf level, absorption of PAR by green leaves is about 80 to 85% (Moss and Loomis, 1952; Heuvelink, 1996b). At canopy level, the resulting absorption is greater because radiation is scattered and leaves may have multiple opportunities to absorb.

Bibliography

Gijzen, H. 1995. CO_2 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

Heuvelink E. 1996. Dry matter partitioning in tomato: validation of a dynamic simulation model. Annals of Botany - London 77, pp. 71-80 (access to pdf)

Moss, R.A, and Loomis, W.E. 1952. Absorption Spectra of Leaves. I. The Visible Spectrum. Plant Physiology. April 1952, 27, pp. 370-391. (pdf)

Ross, J. 1981. The radiation regime and architecture of plant Stands. Tasks for Vegetation sciences. 3, Dr. W Junk Publ., The Hague.

de Wit C.T. 1965. Photosynthesis of leaf canopies. Centre for Agricultural Publications and Documentation, Wageningen, 1965, 63 p. (pdf)

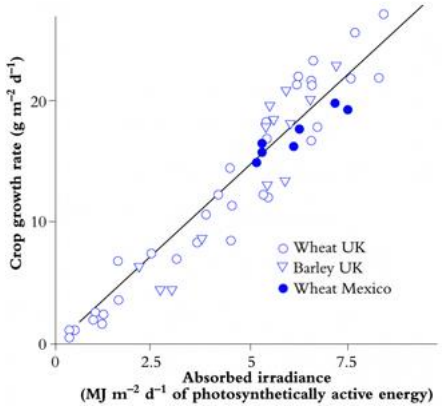
Photosynthesis

Light Use Efficiency

In agronomy, 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 ($g.m^{-2}.d^{-1}$) is linearly related to the irradiance absorbed ($MJ.m^{-2}.d^{-1}$) for a wide range of plant communities.

The relationship between biomass and absorbed irradiance (PAR) defines **Light Use Efficiency**, abbreviated as **LUE**.

Note. When considering total irradiance, this ratio is called **Radiation Light Efficiency**, abbreviated as **RUE**.



Light Use Efficiency on common crops.
Light Use Efficiency (in $g.MJ^{-1}$) is represented by the slope of this relationship.
It is equivalent to 3 $g.MJ^{-1}$ in this example (based on Evans 1993).

Growth & Maintenance respiration

Plant functioning corresponds to growth and maintenance of the living structure.

Taking into account environmental factors, biomass production at the level of square metres per unit of time is summarized by the following equation:

$$dW/dt = Yg (Pg - Rm)$$

where

Pg is gross photosynthesis,
Rm is the cost of structure maintenance,
Yg is growth conversion efficiency,
and *dW/dt* is biomass production in the crop per square metre per unit of time.

Rm is assumed to have priority over growth
If *Rm* > *Pg* then *Rm* is set equal to *Pg* and biomass production is thus zero.

Yg, growth conversion efficiency, depends on the chemical composition; it stands for the costs of converting sugars into fats, organic acids, etc.
Typical values for *Yg* are 0.35 for oil-rich seeds, 0.6 for leaves and stem, up to 0.8 for the root of sugar beet.

Note that under stress conditions (e.g., soil salinity), the main share of sugars is used to fight against osmotic stress and thus the growth process can be greatly reduced.

Maintenance respiration

Maintenance respiration (*Rm* variable on previous page) refers to the carbon dioxide (CO_2) released, or oxygen (O_2) consumed during the generation of usable energy (mainly ATP, NADPH, and NADH) and metabolic intermediates used to:

- resynthesize compounds that undergo renewal (turnover) in the normal process of metabolism (examples are enzymatic proteins, ribonucleic acids, and membrane lipids)
- maintain chemical gradients of ions and metabolites across cellular membranes that are necessary for cellular integrity and plant health
- operate metabolic processes involved in physiological adjustment (i.e., acclimation) to a change in the plant's environment.

The metabolic costs of repairing injury from biotic or abiotic stress may also be considered a part of maintenance respiration.

Maintenance respiration is essential for the biological health and growth of plants.

It is estimated that about half of the respiration carried out by terrestrial plants during their lifetime is for the support of maintenance processes.
Typically, more than half of global terrestrial plant photosynthesis (or gross primary production) is used for plant respiration, more than one quarter of global terrestrial plant photosynthesis is presumably consumed in maintenance respiration.

Modelling maintenance respiration

Maintenance respiration is a key component of most physiologically based mathematical models of plant growth, including models of crop growth and yield and models of ecosystem primary production and carbon balance.

Maintenance respiration mainly depends on biomass and temperature.
The following model is common:

Rm = Coef * Dry Biomass Weight

Here the coefficient *Coef* is computed from a reference coefficient (for instance at 25°C) and a power function.

In experiments, it has been shown that this coefficient value may double for every 10°C increase in temperature. Hence the following model:

$$Coef = Coef_{25} * Q_{10}^{(t-25)/10}$$

Setting the Q_{10} value to 2.0 simulates the experiment results.
$Coef_{25}$ values lie typically in the range [0.01, 0.02]

A Light Use Efficiency Model

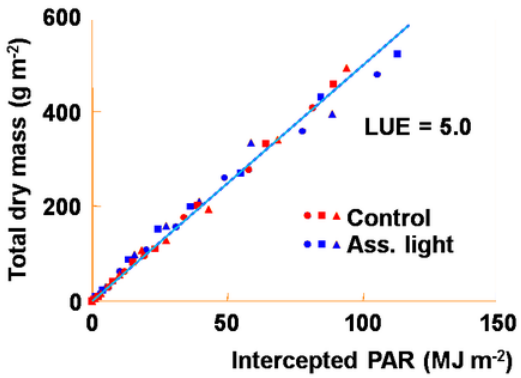
Knowing the LUE and the irradiance intercepted, a simple crop growth model can be defined.

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

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

where:

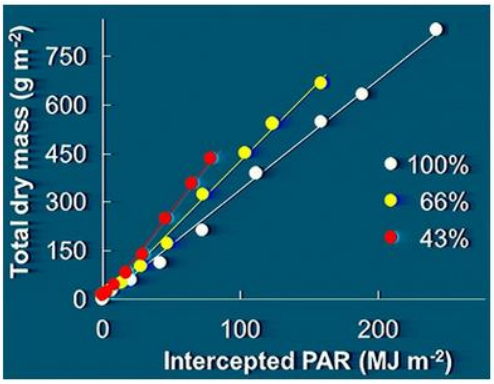
dW is the biomass growth rate (in $g.m^{-2}.d^{-1}$)
LUE is Light Use Efficiency (in $g.MJ^{-1}$)
k is the extinction coefficient
LAI is Leaf Area Index
PAR is Photosynthetic Active Radiation incident on the crop ($MJ.m^{-2}.d^{-1}$)



Light use efficiency determined in winter for 3 plant densities with and without light assimilation for cut chrysanthemum. (Graph: E. Heuvelink, Wageningen University)

Notes:

1. In some models, such as the GreenLab model, LUE is defined on a fresh biomass weight base with 80% water content.
2. Many applications assume constant LUE value, as shown in the figure below, but LUE can be made dependent on CO_2, temperature, light intensity, etc..



Light use efficiency determined for 3 light intensity experiments for cut chrysanthemum. (Graph: E. Heuvelink, Wageningen University)

Density effect

Plant density greatly affects overall biomass production due to competition for light, water, and nutrient resources.

In controlled environments (i.e. in greenhouses), competition is mainly for light.

At low density, or early growing stages, competition for light between plants is reduced.
As plants grow, the canopy closes, reducing the light resource, up to reaching complete canopy cover.

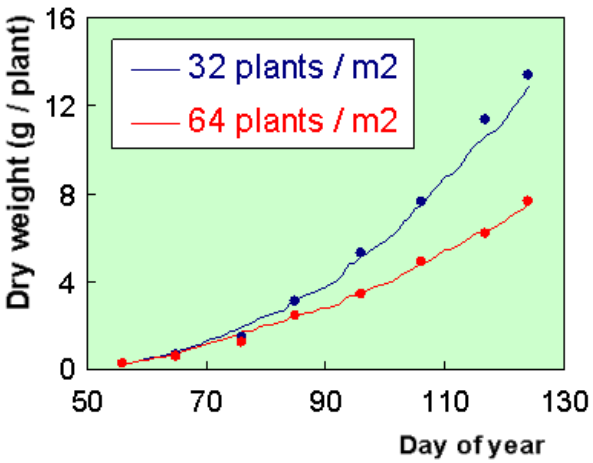
At this point, experiments have shown that biomass production reaches a stable maximum.
As a consequence, the variation in overall biomass production is therefore different if considered at plant level or at crop level.

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 occurs at early growth stages.



Chrysanthemum biomass production at plant level at two densities. (Graph: E. Heuvelink, WAGENINGEN UNIVERSITY)
This experiment, carried out at Wageningen University on Chrysanthemum 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^2 crop was nearly twice the individual average weight of the 64 p.m^2 crop.

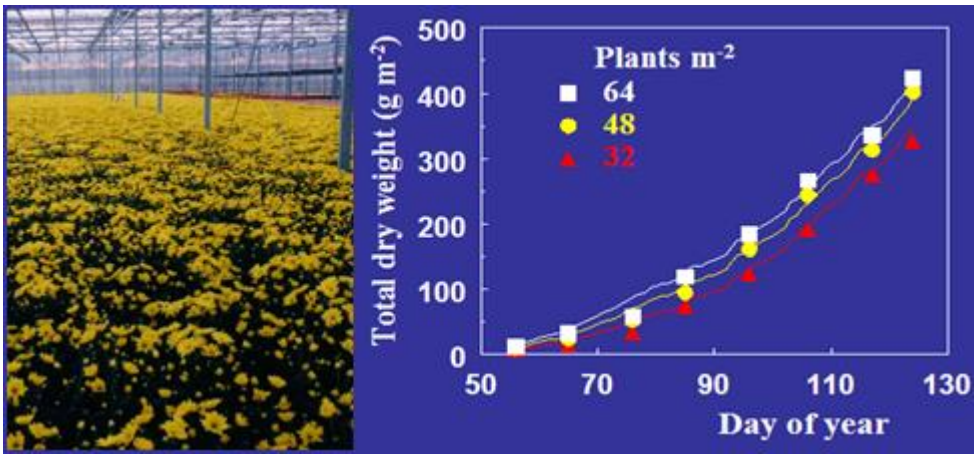
We have seen that, at single plant level, the biomass of each individual increment is inversely proportional to the number of plants per square metre.

Density effect at field level

When considering total biomass production per area, the 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.



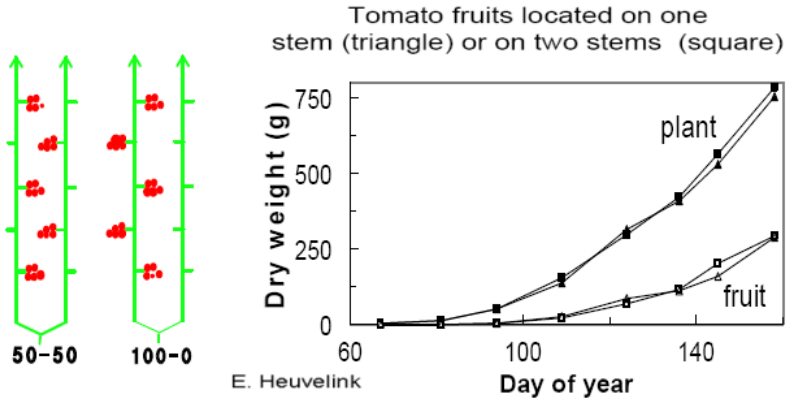
Chrysanthemum crop biomass production at three densities. (Photo and graph: E. Heuvelink, WAGENINGEN UNIVERSITY)
These experiments, carried out at Wageningen University on Chrysanthemum compared biomass production at crop level for densities of 32, 48 and 64 plants per m^2.
The production curves, expressed in g . m^{-2} are similar, staggered by a period corresponding to the different canopy closing dates.

Biomass

Biomass Common Pool

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

Biomass partitioning is not related to an assimilate transportation pathway in the plant structure.
The following experiment carried out on tomato double stems illustrates this.
This assumption can be assessed on many crops, but fails when plant structure becomes complex (i.e. on big trees). However, in our context, this assumption is kept in the definition of our models.



The Biomass Common Pool. (Drawing and graph: E. Heuvelink, WAGENINGEN UNIVERSITY)
Experiment carried out on double stem tomato plants.
On the first tomato plant 50% of young fruits were pruned on both stems.
On the second plant, all fruits of the second stem were pruned.
As shown in the graph, pruning did not affect biomass production at either the fruit or whole plant levels.

Shoots with albino leaves (without chlorophyll) grow normally, taking up assimilates from the biomass common pool.
In this case, leaves are only sinks and no longer sources.

This is illustrated here on an Ivy chimera.

Ivy chimera, with albino leaves. (Photo: P. de Reffye, CIRAD)
Note the distribution and size of the white leaves are similar to those of functional ones.

Biomass partitioning, Sinks

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

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

Organs are in competition for assimilates (or biomass) during their growth.

For a given organ, the ability to accumulate biomass is characterized by its sink strength, expressed by a dynamic value for a given duration, i.e. the organ expansion time.
The set of sink values during organ expansion defines the organ **sink function**, φ_o.

On a given date *t*, organ size results from biomass accumulation.

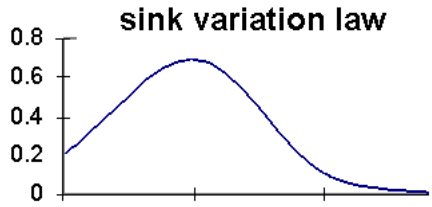
Each biomass increase *q(t)* is defined from the total available biomass *Q(t)*, and the relative ratio of the organ sink $\varphi_o / \Sigma_j \varphi_j$, with *j* respectively standing for all the different organ types (all roots, all leaves, etc.).

$$q(t) = Q(t) \cdot \phi_o / \Sigma_j \phi_j$$

The total sink on date *t*, more precisely the sum of all organ sinks ($\Sigma_j \varphi_j$), defines **plant demand** *D(t)* on date *t*.

Sink function definition.

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



A typical sink function (leaf), defined for an expansion period of duration 3. (Graph: P. de Reffye, CIRAD)

Sources

Sources
Organs producing biomass (usually restricted to functioning leaves) are called **source organs**. The ability of **the source** to produce biomass also depends on time; it increases with organ growth before reaching a stable value. The source function is therefore expressed in terms of a functioning duration, usually longer than the organ expansion duration.

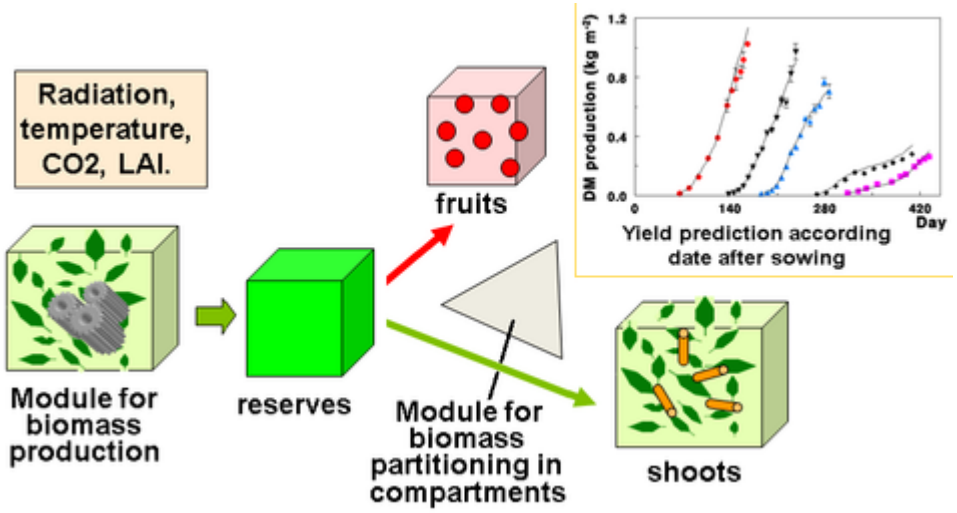
Source function definition
The source function values are defined as a function of the organ age. Beta laws can be used to express these functions, giving a wide range of shapes from two single parameters, from the appearance time to final expansion. At this final stage, the source value is based on the remaining functioning duration.

Crop Models

Process-based models

Process-based models or process-based crop models, called **PBM**, are designed to predict yield from simulations of plant functioning according to endogenous plant properties and environmental conditions.

The **harvest index** is a typical output of such models. It is the ratio of the crop yield (harvested grain) to total biomass. A process-based model therefore operates on organ compartments.
Such a model is built from several dedicated fundamental processes connected together. It classically involves a biomass production model and a biomass partitioning (or allocation) model.



A typical process-based model application. (Drawing and Graph E. Heuvelink, WUR and P. de Reffye, CIRAD)

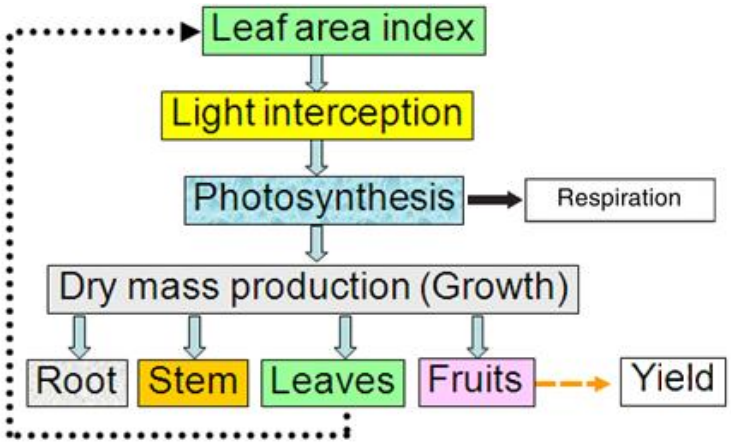
The biomass production model computes the biomass produced by the leaf compartment from the LAI and environmental conditions.
The partitioning models then allocate the biomass among the fruits and the other organ compartments.
The model then loops for a new development cycle.
In this application, four tomato plants are compared, corresponding to four different sowing dates.

A Crop Model example

TOMSIM

The following diagram presents the TOMSIM crop simulator main frame, developed by HPC at Wageningen University for a tomato crop (Heuvelink, 1996, 1999).

In this model, the flowchart involves four main computational steps and the LAI is updated from the leaf biomass compartment pool at each growth cycle.



TOMSIM tomato crop simulator workflow. (Chart: E. Heuvelink, WAGENINGEN UNIVERSITY)

Four organ compartments are defined, including the root system.
At each growth cycle, the biomass allocated to leaves allows the LAI update for the next cycle.

Bibliography

Heuvelink E. 1996. Dry matter partitioning in tomato: validation of a dynamic simulation model. Annals of Botany - London 77, pp. 71-80 (access to pdf)

Heuvelink E. 1999. Evaluation of a dynamic simulation model for tomato crop growth and development. Annals of Botany, 83 (4), pp. 413-422

Supplementary resources

Eco-physiology video courses (from Ep Heuvelink, wmv format, in English)

Full slide spport set (pdf) : Simulation_DMprod_full_2pp.pdf

Video (wmv) : Introduction Slides (pdf) : 1a_Simulation_DMprod_Intro_2pp.pdf

Video (wmv) : Models Slides (pdf) : 1b_Simulation_DMprod_About_models_2pp.pdf

Video (wmv) : Light Slides (pdf) : 3a_Simulation_DMprod_Light_interception_2pp.pdf

Video (wmv) : Photosynthesis Slides (pdf) : 3b_Simulation_DMprod_Photosynthesis_2pp.pdf

Video (wmv) : Respiration Slides (pdf) : 4a_Simulation_DMprod_Respiration_2pp.pdf

Video (wmv) : Dry Matter production Slides (pdf) : 4b_Simulation_DMprod_DM-production_2pp.pdf

Video (wmv) : Models-data Slides (pdf) : 4c_Simulation_DMprod_Models_exp-data_2pp.pdf

Video (wmv) : Conclusion Slides (pdf) : 4d_Simulation_DMprod_Concluding_remarks_2pp.pdf

Video (wmv) : Salinity 1

Video (wmv) : Salinity 2 Slides (pdf) : 6b_Simulation_DMprod_Salinity_stress_example_2pp.pdf

Lectures

Guelph Plant University (Canada) (https://www.uoguelph.ca/plant)

Crop physiology : (https://www.uoguelph.ca/plant/courses/pbio-3110/lectures/lec02_08.pdf)

Unreferenced. Light Interception Lecture : ./Light_Interception_Lecture.pdf)

Bibliography

Recommended reading:

Heuvelink E. 1996. Dry matter partitioning in tomato: validation of a dynamic simulation model. Annals of Botany - London 77, pp. 71-80 (access to pdf)

Heuvelink E. 1999. Evaluation of a dynamic simulation model for tomato crop growth and development. Annals of Botany, 83 (4), pp. 413-422

Heuvelink E., Marcelis L., Bakker M., Van der Ploeg A. 2007. Use of crop growth models to evaluate physiological traits in genotypes of horticultural crops. In Scale and Complexity in Plant Systems Research: Gene-Plant-Crop Relations, eds Spiertz JHJ, Struik PC, van Laar HH (Springer, Heidelberg), pp 223-233 (access to pdf)

Jeuffroy M.-H., Ney B. 1997. Crop physiology and productivity, Field Crops Research, Volume 53, Issues 1-3, July 1997, pp. 3-16, ISSN 0378-4290. (pdf)

Johnson I. 2010. PlantMod: exploring the physiology of plant canopies. (pdf)

Wery J. and Lecoeur J. 2000. Learning crop physiology from the development of a crop simulation model. Journal of Natural Resources and Life Sciences Education, 29, pp. 1-7. (pdf)

Web site: University of Queensland (AUS) Plants in Action - Crop growth analysis