UVED Resource

Plant Growth Architecture and Production Dynamics

GreenLab Course: Overview

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Contents and Objectives

Presentation

Plant structure and production models offer a wide range of applications from 3D representation to crop optimizing.

Plants grow slowly and they seem frozen in their architecture.
By modelling the development of their structure and the growth of their organs, by simulating them on computers, we can grasp these dynamics and predict and optimize plant production.

Real-time 3D landscape mock-up produced by the LandSim3D® tool (BIONATICS SA) with IGN BDTopo® and BDOrtho® data, and the AMAP virtual plant generator. (© Bionatics and IGN).
To simulate virtual plants, computer models can be defined from botanical studies, and introduced in virtual landscapes with automated planting software tools. By introducing the basis of eco-physiology and agronomy, it is possible to differentiate growth simulation according to environmental conditions, such as temperature and light availability.

This section provides an overview of such approaches, highlighting the following aspects:

- Plant growth results from two processes: establishment of the structure (plant architecture), and the increase in the size of its components (biomass production).
- The structure is established by way of a space conquering strategy, which can be described by botanical architectural concepts and simulated by computerized rules.
- Biomass production results from leaf functioning and can be modelled by compartment dynamic models.
- Modelling both structural and functional aspects defines structural functional models.
- In the GreenLab model, for each growth cycle the organs compete for biomass stored in a common pool.
- All organs of the same age and same morphological stage share the same fate.
- This model can thus be efficiently factorized, expressed by mathematical equations, and can then be easily reversed.
- A wide range of applications may arise from structural functional plant models:
  - from simple 3D representations derived from computational approaches
  - to agronomic optimization, using model reversion.

Course Objectives

The aim of this course is to enable students to:

- Discover plant growth structural and functional modelling and its interests
- Understand that plant growth reflects both structure establishment and biomass production
- Learn that structure establishment can be modelled from botanical architectural concepts
- Learn that biomass production can be modelled from eco-physiological concepts
- Understand that, under specific hypotheses, mathematical factorization can be used to model structure and biomass production
- See that plant structural functional models range from simple simulation outputs (3D plant representations) to complex model inversion (agronomic optimization).

Map and Contents

Contents

This section introduces an overview of such functional structural plant models, highlighting the following aspects:

- Plant growth results from both structure establishment and biomass production.
- Structure establishment can be described by botanical architectural concepts and simulated by computerized rules.
- Biomass production can be modelled by compartment dynamic models.
- Modelling both aspects defines structural functional models that can be efficiently factorized.
- A wide range of applications from simple 3D representations to agronomic optimization.

Course content map

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Sub-Chapter map

Growth: development and expansion

Plant Structure establishment

Plant biomass production

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Growth

Plants are alive! Plants grow slowly and seem frozen in their architecture.

Plant growth: a dual mechanism

On a cell scale, two processes are basically involved in plant growth:
cell multiplication in apical meristems, inside buds, building the various organs (leaves, internodes, wood rings, roots, etc.),
and the expansion of these cells, allowing organ growth.

On a whole plant scale, growth thus results from this dual mechanism.

The organ creation phase is called **organogenesis** or development stage, with the establishment of the plant architecture from new axes.
While organ growth up to maturation, under the effect of photosynthesis, is called **expansion** or simply **growth**.
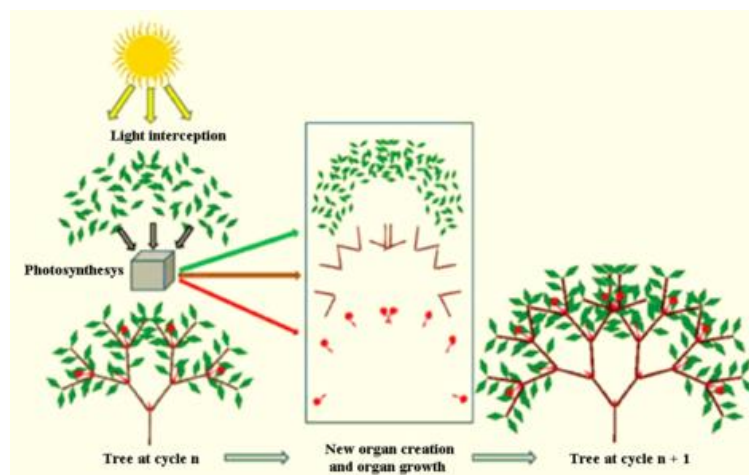
Plant growth and Plant architecture. (© Liama).
Leaves intercept light and produce biomass through the photosynthesis process.
Biomass is used for organ growth (size development) and for the creation of new organs in regular cycles.
These new organs build the plant's architecture.

Plant components

A plant is composed of 80% water, 15% sugars and 5% trace elements.
The photosynthesis process produces sugars, which are necessary as an energy source and for building the material for its growth.

Plant production material is called **biomass**.

The organogenesis and expansion processes both require new biological material, i.e. production of new biomass.

Building plant components

Water is taken up from the soil by the roots.

Sugars (cellulose), composed of water and CO_2 from the atmosphere, are synthetized by the leaves.

It should be remembered that components such as trace elements (phosphorus, potassium, nitrate,) are necessary to cell mechanisms, but secondary in biomass production.

Sugar production requires energy. This energy is light, intercepted by the leaves.
The sugar production process is called **Photosynthesis**.

A specific point is that sugars arising from photosynthesis are both
- fuels for plant functioning
- the basis of plant building material (cellulose)

The ration allocated to both functions may vary and depend on environmental conditions.
For example, under saline conditions, more sugars are devoted to limiting salinity pressure, potentially stopping cellulose production.

Plant Architecture

Plant structure: architectural botany

In the 70s, botanists Francis Hallé and Roelof Oldeman extended the inflorescence structural pattern classification to tree structures.
They created a new approach to Botany: Architectural Botany.
Inflorescence patterns where classified according to their regular geometrical patterns.

In architectural botany, plant structure is described according to a specific axis typology, according to axis traits:
- the axis building mode: continuous or rhythmic
- the position of sexuality: lateral or terminal
- the branching occurrence pattern: immediate or delayed
- the branching pattern into shoots
- the direction of axis development (vertical with branches developing in a spiral / horizontally with branches developing in a plane)
- ...

In young trees, a different axis typology can be observed, showing different morphological stages: vigorous shoots on trunk, up to a short axis usually bearing sexuality.
They are qualified by a **physiological age** (1 for the trunk, 2 for vigorous branches, 3 for branches, 4 for short axes, etc.)
A specific axis typology may be found at several places in the plant structure.

These different axes develop according to a specific combination, or strategy, following one of the 23 **architectural models** defined by the botanist community.

Each plant species expresses its architectural model with its own specific parameters, defining its **architectural unit**.
The architectural unit can be considered as a stable plant genetic development scheme.

When the tree matures and becomes older, the plant structure duplicates its architectural unit, either fully or partially.
This process, called **reiteration**, allows the building of huge complex crowns.

In the botanical architectural approach, plant structure is not considered as static.
Plant structure results from the dynamics of leafy shoot formation, derived from terminal and lateral buds.

Simulating plant structure

The architectural unit defines a basis for plant structure modelling and simulation.

Plant structure can be generated by a computer program, using a procedural approach.
Successive development stages are obtained by applying rules to the terminal and axillary buds of the existing structure.

Rules are defined for each physiological age, translating the botanical branching patterns, sexuality

occurrence and growth modes.

They may introduce stochastic aspects, including dormancy and viability aspects.
Rules can be implemented by automatons, grammars or dedicated procedures.
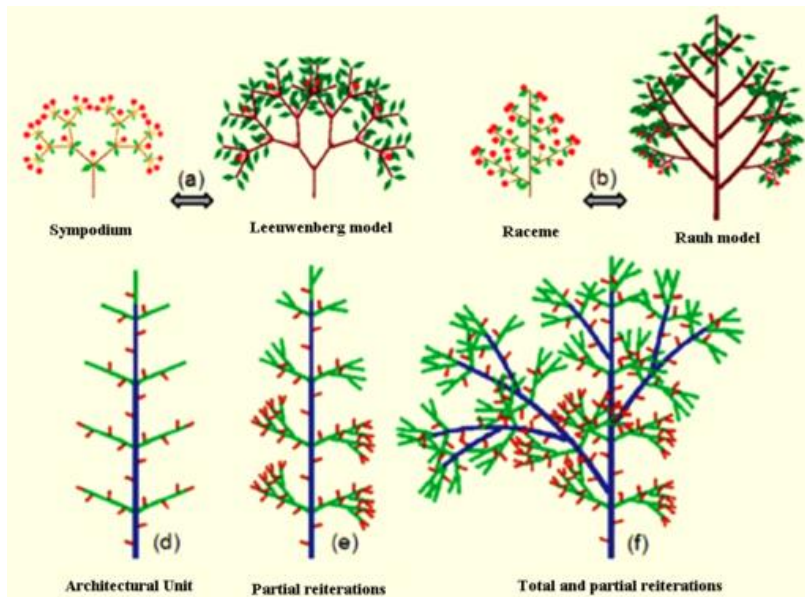
Plant architecture (© Liama).

Top: Inflorescence patterns and architectural models.
Botanists have defined 23 architectural models to characterize a plant structure development strategy
Leeuwenberg's model corresponds to a Symposium inflorescence pattern.
Rauh's model is one expression of a Raceme inflorescence pattern.

Bottom: A simulated young tree and older stages with partial and total reiterations
Left: The young tree expresses its architectural unit
Middle: Partial reiteration appears
Right: Total reiterations appear, developing the crown
The colour stands for the various physiological ages: vigorous axes in blue, branches in green, short axis bearing sexuality in red.

Biomass production

Plant production

Plant production (biomass) modelling sets out to predict plant crops quantitatively, and to optimize crop management sequences.

Plant production modelling: a macro-scale approach

Plant crop models were introduced by the Dutch researcher de Witt in 1970.

Plant crop models involve various climatic and vegetation parameters, indexes and data:
- climatic parameters (light, water, temperature)
- leaf indexes (such as leaf area per m^2)
- yield indexes (the ratio of biomass related to the crop compared to the total biomass)
- etc.

Such models try to express the photosynthesis process by an equation summarizing a daily dry biomass production per unit area (m^2).

In those models, also called **crop models**, biomass production is considered for a unit area (m^2) level, not on an individual plant level.

Field experiments have shown relations (laws) explaining macroscopic functional behaviour in plants, without considering the deeply complex physiological processes of photosynthesis or respiration, or considering aspects at cell level.

Agronomic laws

Thermal time

One noteworthy empirical law at plant level is the notion of thermal time.

Thermal time corresponds to the sum of average daily temperatures received by the plant.

Experiments have proved that plant organ development (both for organogenesis and expansion) appears unstable depending on calendar time, but becomes linear with thermal time.

In other words, the occurrence of germination, flowering, new leaf emissions from terminal buds takes place beyond a specific sum of temperatures.

Thermal time therefore drives development sequences in plants.

Thermal time thus defines the growth cycle steps (rather than a calendar schedule) in most agronomic crop models.

Light interception

The other point to consider in the production of dry matter (*DM*) is the relationship between growth and light interception.

In its simplest form, this relationship can be expressed by the following equation:

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

where

LUE is Light Use Efficiency, i.e. the efficiency of light conversion to dry matter for the active part of the radiation (*PAR*) received by the cover.
LAI is the Leaf Area Index, i.e. the leaf area per m^2 in the crop.
The higher this index is, the more light is intercepted by the foliage.
The coefficient *k* is determined empirically.
This exponential term models how the leaves cover each other, reducing light efficiency.

This formalism based on the light intercepted by the foliage is the **Beer-Lambert law**.

Notes
1. Beyond a LAI value of 4, all the light is intercepted and dry matter production saturates. Additional leaves are no longer effective and increasing the planting density is pointless.
2. Under favourable conditions barely more than 20 grams of dry matter can be produced per day per m^2.

Functional Structural Plant Models

Modelling plant production

Plant production (biomass) modelling may be complex, especially if structural aspects are also considered.

Plant production modelling simplified
Sound simplifications, demonstrated by agronomic experiments, are of major interest for defining efficient models.

At crop level, taking into account the architecture of the plant is not always necessary. However, knowing the distribution of the various organs at respective occurrence times and physiological ages is a key point.
In other words, geometrical aspects may be ignored, but not the quantitative composition of the structure.
We postulate the existence of a **common biomass** pool.

Similarly, we can consider only net photosynthesis, i.e. the proportion of sugars involved as construction materials in the dry matter of the organs.

Plant modelling principles
In general, dry matter production is divided into compartments (leaves, stems, roots, fruits) whose proportions are **sinks** for storage of the biomass produced.
In fact, some organs produce biomass, such as leaves and seeds, are **sources**, while others consume, and are **sinks,** such as internodes and fruits.

In models predicting crops, equation (1) defines the basic framework.
Indeed, it accumulates dry matter in the compartment of interest, day after day, processing the energy received by the canopy, and sharing the dry matter among sinks.

Functional Structural Plant models (FSPM)

Functional structural plant models are designed to model and simulate both plant structure establishment and biomass production.

They are therefore centred on individual plants.

Development of the architecture is controlled by a grammar or automaton that pilots organogenesis vs. time (ideally vs thermal time).
Branches consist of **phytomers**, the elementary axis entity, consisting of an internode, one or more axillary buds and its leaves.
Axillary buds may give rise to branches or fruit.

Most FSPM approaches use the (dynamically computed) plant structure as a biomass transportation pathway.

Production is thus not computed at organ compartment level, but at each individual organ level.
Depending on its nature, each source organ may diffuse matter within the structure pathway, and/or, conversely, may consume biomass.

In such approaches, local pools of biomass are locally stored and managed.

FSPM implementation is based on a mesh that allows a geometric representation of the plant with polygons (these leaves will intercept light), or other shapes.
An underlying graph structure reflects the plant architecture in order to compute the propagation of sugar and water in the structure. Source organs send the biomass they produce into the network and the sink organs intercept it according to their sink strength.

The FSPM approach mimics the morphogenesis process in its entirety.

Such systems provide a better understanding of the plant, but cannot address simulations on the scale of agricultural production.

Indeed, simulation time and memory costs usually become substantial, which, added to a large number of parameters to be identified, may usually not be lead to convenient model calibration under true field conditions.

Modelling principles

GreenLab specificity

From individual plant to crop level

FSPM approaches show heavy reliance on production computation, since they use the plant structure as a biomass storing and transportation pathway.

The main specificity of the GreenLab models lies in the fact that structure is only used as an organ compartment classifier, and not as a transportation network.

Indeed, an interesting way of overcoming this difficulty is to use the crop production model approach, defined at m^2 level to estimate photosynthesis.
The structural approach precisely defines organ compartments sharing the same fate, making biomass allocation easier, but does not require exhaustive definition, be it topological (graph), or geometrical.

This positioning, between individual plant and crop models, is specific to the GreenLab model.

Taking into account the simplifications established by agronomists from experimental studies, i.e. the common biomass pool, the use of net photosynthesis and biomass computation from Beer's Law, this approach does away with use of the topological structure in production computation.
The classic crop model equation (Eq. 1) is adapted to the plant scale as follows:

$$Q = LUE \cdot PAR \cdot Sp \cdot (1 - e^{-k\, Sf/Sp}) \qquad \text{(Eq. 2)}$$

where
Q is the increase in biomass of the plant cycle
Sf is the leaf area of the plant
Sp is a parameter which has the dimension of a surface
Sp allows equation (2) to operate even when the canopy is not very dense.

In an high density d stand, the canopy is uniform and Sp verifies:

$$Sp = 1\,/\,d \quad \text{(Eq. 3)}$$

This relation has been verified experimentally on crops (see below).
Equations (Eq. 1) and (Eq. 2) are thus equivalent, but the formula (Eq. 2) allows a switch from the individual plant to the plant stand.

Organogenesis

In the GreenLab model, organogenesis is modelled by meristem production equations, according to their physiological age, and deduced from observations.
Growth, mortality and branching processes are described by probability laws.

For each cycle of growth, new organ population (cohort) occurrences are simulated.

Each organ takes up biomass from the common biomass pool according to the strength of its sink function; (this function varies during organ maturation).

Since all organs of the same cohort and of the same type are in the same state, efficient factorization can be applied. For instance, plant demand D is simply the sum of the demand of all the cohorts.

The biomass increment Δq of a given organ depends on its sink φ, the available biomass in the common pool Q calculated by equation (Eq. 2) and plant demand D according to the formula:
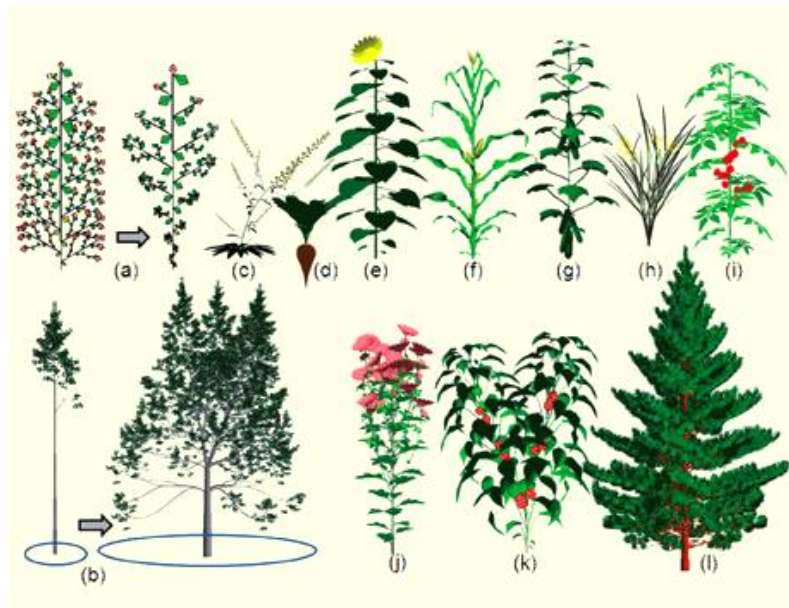
$$\Delta q = \varphi \cdot Q / D \quad \text{(Eq. 4)}$$

Organ weight is then simply defined by summing up the biomass increments (Eq. 4).
Its dimensions (length, diameter, area) are assessed by applying geometric (allometric) rules.
The weight of the organ compartments is obtained by summing up all cohorts of the same organ.
In particular, the total functioning leaf area of the plant Sf is deduced, using equation (Eq. 2).

Simulation of plant growth and structure plasticity with the GreenLab model (© Digiplante and LIAMA). These virtual plants are obtained from field data thanks to the software that takes particular account of how organs (leaves, roots, fruits, etc.) change, which can be very different depending on environmental conditions.
(a) simulating morphological gradients.
The base effect due to low biomass availability at early stages is shown on the right. The left-hand tree is only a structural simulation
(b) structural plasticity simulation on the beech tree.
Left and Right are respectively simulated with the same parameter, except for the Sp (Eq. 2) area value (shown as a grey disk) standing for reversed density.
Other calibrated simulations are for: (c) arabsisdosis, (d) beetroot, (e) sunflower,
(f) maize, (g) cotton, (h) rice, (i) tomato,
(j) chrysanthemum, (k) sweet pepper, (l) Mongolian pine

The GreenLab model is therefore a dynamic model of plant growth which operates by feedback between growth and development.
The calculation of plant production does not need to rely on the details of the architecture, but only on the equations of production and source-sink relations.
Such a model offers efficient computing costs and enables model calibration, optimisation and control methods to be implemented.

Applications

Modelling plant growth offers interesting opportunities for environmental science.

Given its positioning, GreenLab benefits from both structural and crop model applications.

For agriculture, it seeks to provide geneticists with new parameters in order to characterize more precisely the functioning of crops and direct breeding.

The same set of parameters, used in the dynamic equations of the model, can be brought into play to:
- predict crop production under different environmental conditions (temperature, light)
- predict crop production at different densities
- analyse individual variability inside a crop (related for instance to seed weight variations and stochastic structural aspects)
- optimize crop management sequences (irrigation, treatments, etc.).

In the longer term, in landscaping and urban planning, such approaches could design libraries of structural functional plants.

Thus, environmental conditions, retrieved from geographic information systems (GIS), climatic conditions, site positions and orientation will be used to generate 3D plant representations reflecting local conditions. "Virtual landscapes" created by image synthesis will then turn into "functional landscapes" open to different environmental and climate scenarios.

Supplementary resources

More on GreenLab

Recommended on-line resources
Architectural Botany course (English)
../../P1_Prelim/Bota/Bota_intro.html

Eco-physiology for crop modelling course (English)
../../P1_Prelim/EPhysio/Physio_intro.html

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

GreenLab Full Course (English)
../GL_intro.html

More detailed GreenLab overviews (pdf files)

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

Plant growth models (pdf)

Bibliography

Hallé, F., Oldemann, R.A.A. 1970. Essai sur l'architecture et la dynamique de croissance des arbres tropicaux. Paris: Masson.

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

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)

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

GreenLab project Web site: http://GreenLab.cirad.fr/

Une histoire de la modélisation des plantes (French)