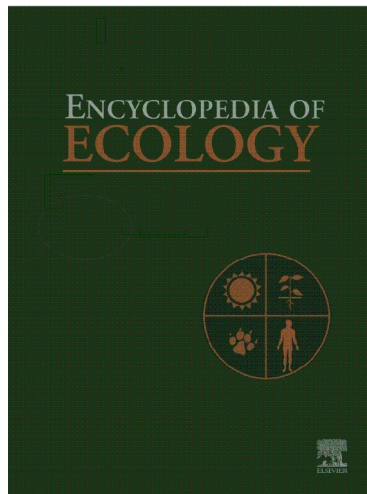


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Plant Growth Models

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Introduction

A Simplified Overview of Plant Composition

Plant Morphogenesis: Necessary and Sufficient

Knowledge for Plant Growth Modeling

Modeling Plant Development and Plant Growth

Conclusion

Further Reading

Introduction

This article attempts to describe the state of the art in building efficient dynamical plant growth and architecture models that contain the basic knowledge coming from botany, ecophysiology, agronomy, applied mathematics, and computer science.

The world of flowering plants is incredibly diverse with over 250 000–300 000 species on Earth. Even inside a family (e.g., Dilleniaceae) one can find trees, shrubs, creepers, and herbs. Despite this diversity, plant architecture is always made of the same kind of basic botanical elements, namely leaves, stems, fruits, roots, etc., whose functions are always the same as sources and sinks for biomass production and partitioning. Important studies to model and simulate the underlying complex mechanisms of plant morphology and physiology have been carried out at the end of the twentieth century in two opposite directions. One tries to simulate with high precision the knowledge of plant physiology taking into consideration plant structure and even gene action; meanwhile, others try to simplify the upper level of the scale (i.e., the level of plant architecture) and find the emergent properties of the system that allows building mathematical plant growth models. To

understand such a complex system as plant growth and development, knowledge about botany (plant structure organization) and physiology (action of environmental parameters, water transport, respiration, and photosynthesis) is not sufficient. Statistical correlations or empirical functions between variables such as temperature, light, or measurements such as plant height or plant weight are also not sufficient mathematically speaking, because these measures are themselves the result of a complex functioning that involves the hidden parameters of an underlying mathematical model that is to be built.

Identifying the relevant parameters that bridge together the various disciplines results in ‘translating the reality into a mathematical model’ that will allow plant behavior study. Mathematical modeling needs to simplify a lot of the complexity of the real world and this is achieved by a dialog between biologists, who have the qualitative knowledge, and mathematicians, who handle quantitative relationships through equations. Results will be more or less accurate according to the validity of the model, and the minimum number of parameters that fulfill the research work should give the best model, since the powerful tools of applied mathematics cannot run properly with too many (overparametrized models).

Computing the numerical values of the hidden parameters from measurements on real plant architecture is what is called an inverse problem. Engineering applications for agriculture can be worked out only if this problem is solved. Otherwise the model remains at a speculative stage. Plant architecture results from both meristem functioning (organogenesis) and photosynthesis (biomass production and partitioning) and it may be assumed that plant architectural development concerns the growth process trajectory keeping at any time in its memory the underlying structure. Thus the hope is to trace back the growth process from measurements on plant architecture in given environmental conditions, and furthermore to control the plant behavior from acting on the environmental parameters. The research work may be considered as fulfilled if it is possible to simulate the growth process with a minimum number of parameters and to build step by step the plant architecture with all the organs in the right place inside the plant structure and with the correct biomass content. Such important problems as optimizing the use of resources (water, fertilizers in fields, temperature and light in glasshouses) and cultivation systems (planting density, pruning) can then be successfully solved.

A Simplified Overview of Plant Composition

A plant is a multiscale network of botanical entities and organs (leaves, internodes, fruits, roots) connected together to build its architecture and whose functioning results in biomass production and partitioning. All organs may be a source of biomass (even sometimes internodes). The seed contains the first reserve for the initial growth, and the leaves are usually the specialized organs for biomass production. Conversely all organs may be sinks for biomass, because they use it for their expansion. For the production of biomass, plants take water and nutrients from the soil through the root system and carbon dioxide from the atmosphere through their leaves.

Roles of Organs

- Leaves ensure light interception, and intercepted light results in biomass production through photosynthesis. The produced biomass allows the formation of new organs by the meristems and their further expansion. Thin leaf blades are optimized for efficient light captivation. Individual leaf-functioning duration is almost never indefinite. It may be short (less than 1 month for most cultivated Poaceae) or long (several years for some conifers) and may depend on environmental factors.

- Stems are basic elements of the plant structure and play a mechanical role for its stability. Produced by the

functioning of apical meristems they may branch and give rise to specific branching patterns. Their expansion in length is called primary growth and it is generally short in time; meanwhile, their expansion in diameter, also called secondary growth in trees, may be indefinite through stems or plant life span. Stems also play a functioning role in conducting the water absorbed by roots through the hydraulic plant architecture till the tips of the axes network. Conversely, they transport the sugars produced by the leaves through the comprehensive plant structure.

- Fruits arise from flowers, after fertilization and fruit set, and are reproductive organs. Their sink can be so big that they may drastically reduce the initiation and/or the expansion of the other organs, as in the case of sunflower. Fruits' sink duration varies with plant species.

- Roots take water and nutrients from their environment. The whole root system is here considered as a single organ whose sink lasts the entire plant growth duration.

Plant Biomass Composition

Fresh matter is roughly composed of 85% of water that comes from the soil and 15% structural dry matter that comes from leaf photosynthesis. Sugars (CH_2O) derived from photosynthesis have several roles. They may be used for plant structure construction when included in cell walls or they may be stored as reserve or even another part, used as energy for the plant's general functioning (respiration). Less than 5% of the fresh weight comes from nutrients (N, K, P, etc.) contained in the sap and as component of dry matter, so they are not considered as a relevant component of the plant architecture; their roles are entirely devoted to plant functioning (mainly enzymes).

Dry matter consists mainly of carbohydrates, lignins, oils/fats, organic acids, and proteins, and primarily originates from sugars produced via the photosynthetic process. Dry matter is obtained once the water is extracted from the fresh organs. As extremes, dry matter may be 95% of the fresh one for seeds and 3.5% for a cucumber fruit, but plant dry matter content ratio is generally about 15% of the fresh weight and in this article it is assumed that the ratio of dry weight to fresh weight remains constant.

Plant Morphogenesis: Necessary and Sufficient Knowledge for Plant Growth Modeling

Botany and Plant Development

Plant development is the result of meristem production (organogenesis) that creates new organs such as leaves, internodes, fruits, rings inside branches, or roots.

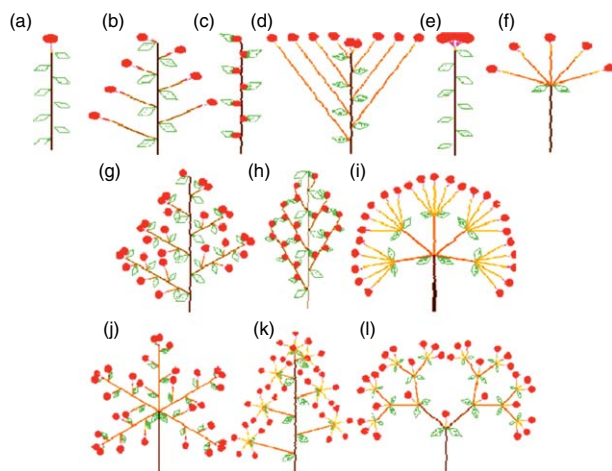


Figure 1 Inflorescence types simulated by VisualPlant software (Zhao Xing, LIAMA) : (a) solitary flower, (b) raceme, (c) spike, (d) corymb, (e) capitulum (f) umbel, (g) compound raceme (panicle), (h) raceme of spikes, (i) compound umbel, (j) umbel of racemes, (k) raceme of umbels, and (l) cyme.

Although the structures of inflorescence show regular patterns (Figure 1), which have been described already long ago, the development of shrubs and trees looks more complicated and was not carefully studied before the apparition of plant architecture analysis that allows botanists to understand the link between bud functioning and the resulting three-dimensional (3-D) plant geometry and topology. Through relevant simplifications, the botanists Hallé and Oldeman introduced in 1970 the fundamental criteria for classification, giving birth to 23 models of plant architecture (Figure 2). These condensed criteria concern inflorescence position, axis growth pattern and differentiation, and branching patterns. They allow classifying any kind of tree in one of the described models that is supposed to correspond to the stable endogenous developmental pattern of a given plant species.

Each architectural model is an outline of the plant organization. To go further, the so-called architectural unit concept was defined; it refines the plant description and represents the precise and specific expression of the architectural model of a species. According to this concept, axes of a plant may be grouped into a few numbers of categories that are not obligatorily related to branching order, that is, a same type of axis can be found at different precise places in the tree structure according to developmental stages or specific phenomena like acrotony.

This gives a multiscale organization to the plant structure that gives birth to a stack of substructures analog to fractal models, but not necessarily links to autosimilarity. In the last two decades, coupled with precise morphological observations, architectural analyses of several plant species revealed that, under given environmental

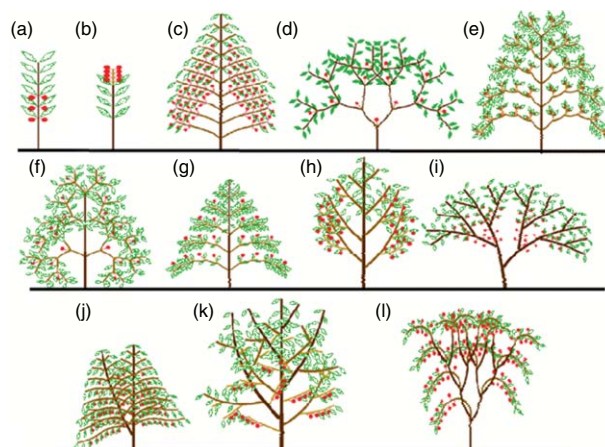


Figure 2 Computer simulations of some tree architectural models with VisualPlant software (Zhao Xing, LIAMA) : (a) Corner model, (b) Holttum model, (c) Roux model, (d) Leeuwenberg model, (e) Aubréville model, (f) Scarrone model, (g) Prévost model, (h) Rauh model, (i) Troll model, (j) reiteration of Roux model, (k) reiteration of Rauh model, (l) reiteration of Mangenot model. Modified from Hallé F and Oldemann RAA (1970) *Essai Sur l'Architecture et la Dynamique de Croissance des Arbres Tropicaux*. Paris: Masson.

conditions, the structure and features of a particular elementary botanical entity (metamer or phytomer, growth unit, annual shoot, etc.) are predictable and strongly dependent on both: (1) its topological location in the comprehensive architecture of a plant and (2) the ontogenetic stage of the plant. At the level of the whole plant, the 'morphogenetic gradients' notion was defined in order to take into account the intrinsic organization rules of plant structure and was shown to be a powerful concept to explain the observed structure and series of modifications of botanical entities during the ontogeny of any plant species. Features and structure of botanical entities produced by meristems may progressively change along an axis or during plant aging. Powerful botanical notion of 'physiological age of meristems' (PA) describes the state of differentiation of the meristems generating axes and allows clarifying the understanding and interpretation of tree architecture and organization along time (Figure 3). To each PA corresponds a resulting type of generated axis or axis element. Apical meristems can remain in the same state along the branch construction until they mute in another older one. Lateral meristems are usually created with an 'older' PA than the main apical meristems or the same PA may be reproduced by two meristems in case of a reiteration (i.e., duplication of the initial elementary architecture).

Botanists can identify the type of axes and their associated physiological ages even in the complex architecture of mature trees. This leads to a sampling strategy for collecting data and calibrating plant development.

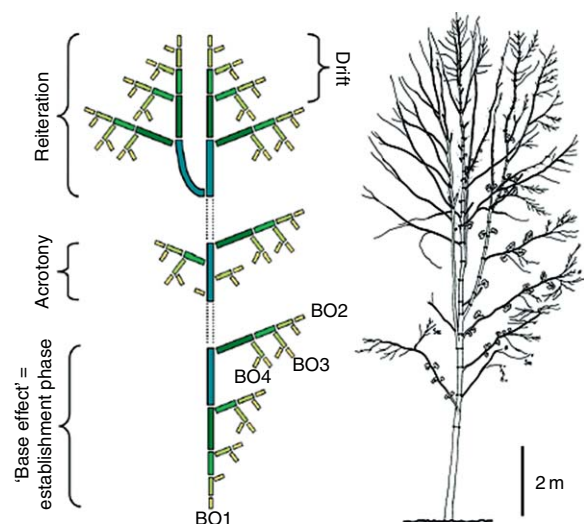


Figure 3 Left: Theoretical and diagrammatic representation of tree structure organization according to 'morphogenetic gradients' and 'physiological age of meristems' and (b) mature beech tree architecture. (Left) After Barthélémy D, Caraglio Y, and Costes E (1997) *Architecture, gradients morphogénétiques et âge physiologique chez les végétaux*. In: Bouchon J, Reffye de P, and Barthélémy D (eds.) *Modélisation et Simulation de L'architecture des Végétaux*, pp. 81–136. Paris: INRA (Sciences update, Editions). (Right) From Nicolini E (1997) *Approche morphologique du développement du hêtre (Fagus sylvatica L.)*, 185pp. PhD Thesis, University Montpellier, France.

Ecophysiology and Plant Functioning

Plant growth results from biomass production (photosynthesis) and its partitioning among organs. Both environmental factors and organ functioning are involved. Growth may occur independent from development, that is, organs may still expand when no further organogenesis occurs as is the case for sunflower or chrysanthemum after the terminal inflorescence has been initiated. Studies based on explanatory models linking environmental factors to crop production started in agronomy with C. T. de Wit in the 1960s.

Role of environmental factors

The main driving factors for plant growth are light, temperature, water, and CO₂; secondary ones are nitrogen, potassium, and other essential elements. A challenge is to compute the climate effect on growth potential and to find, by inverse problem, the parameters of efficient empirical functions that can assess biomass production in a variable environment. In order to simplify, we consider here the cumulated effect of the environmental factors on plant growth that is relevant for biomass production, rather than the instantaneous one, where things are much more complicated.

Temperature controls the speed of shoot development and the duration of organ expansion (Figure 4a). Within a certain temperature range (i.e., when development rate is

linearly related to temperature), there is a linear relationship between the number of phytomers developed on a shoot and the sum of daily effective temperatures received by the plant. This corresponds to the so-called 'temperature sum' factor, and allows the definition of a 'thermal time' that is linearly related to development. It is different from the 'calendar time', with the use of which the observed speed of development (the phyllochron) may be variable depending on temperature.

- Light produces photosynthates via green leaf functioning. Empirically, the effect of incident light is well known. According to light intensity, one can observe a linear effect coming progressively to saturation. Light has also a strong influence on plant plasticity. It can modify plant development by affecting meristems' rules of production. It can also change sink values and organ allometries. In shadow conditions for instance, internodes will have greater biomass and length, and consequently other organs will be reduced.

- Water is taken up by roots from the root environment and evaporates by transpiration at the leaf level. As both transpiration and photosynthesis are strongly influenced by light intensity, often a close relation between crop transpiration and biomass production is observed. Plant transpiration depends primarily on radiation and leaf area. It can be limited by water shortage in the root environment (stomata will close). Cumulated effect of water transpiration at long term is often linearly related with plant biomass production and allows the definition of the so-called 'water-use efficiency' (Figure 4b). It should be noticed that this relationship is not functional but statistical, and it should be used with caution. Under normal conditions, more than 90% of the water withdrawn from the soil will be evaporated out of the leaf surface and only 10% results in fresh mass increase. The water efficiency depends on the plant species. For example, the production of 10 kg of fresh potato requires 600 l of water whereas that of 10 kg of fresh maize cob needs 250 l of water. So the proportion is quite variable according to the plant species, but fortunately it is quite stable for a given cultivated plant in field conditions from year to year. Water stress mainly reduces the growth and has usually little impact on biomass partitioning between shoots and roots.

Plant functioning (respiration)

Plant functioning corresponds to growth and maintenance of the living structure. Taking into account environmental factors, the biomass production at the level of square meters per time unit is summarized by the following equation:

$$\frac{dW}{dt} = Y_g (P_g - R_m) \quad [1]$$

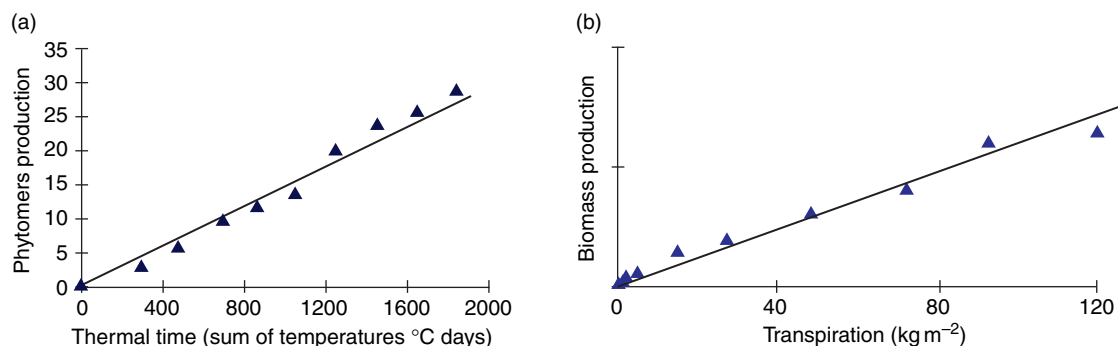


Figure 4 (a) Speed of plant development depending on daily average temperatures ($^{\circ}\text{C}$ days for each phytomer; base temperature is 15°C). (b) Biomass production depending on plant transpiration. Data for cotton from Guo Yan, Chinese Agricultural University, 2002.

Here, P_g is the gross photosynthesis, R_m is the cost of the structure maintenance, Y_g the growth conversion efficiency, and dW/dt the biomass production in the crop per square meter per unit time.

In a stress condition (e.g., soil salinity), the main part of sugars is used to fight against the external salt concentration and the growth process can be very much reduced. To simplify, we consider that plant growth is proportional to the amount of sugars produced.

A common pool of biomass

The branching system of a plant may be quite complex. Each leaf has its own functioning, in its local environment, and its biomass production has to spread to each organ according to its sink and through the complex network of branches.

This induces us to consider both topological and geometrical structures to ensure the connection between organs and the matter transport. Fortunately, ecophysiol-ogists have proved for many crops that the final balance of the source and sink relationships for a long term is similar to the action of a common pool of biomass that enables us to skip the details of the transport resistance system of the biomass. One can consider that each organ is connected

directly and independently from others to a virtual reserve from which it withdraws biomass as a sink or provides biomass as a source (Figures 5 and 6). Direct or indirect proof of this comes from skilled experiments on crops, but in the case of a big structure (trees), this assumption could fail as it has been demonstrated that growth in thickness at a particular point is proportional to the leaf surface seen above this point. However, in most cases, the assumption of a common assimilate pool is valid. In the case of big trees, the actual sink of an organ becomes proportional at the same time to its own strength multiplied by its possibility to access to the sources that is proportional to the leaf surface it ‘sees’ above its position.

Dry matter partitioning

Keeping the notion of a common pool of biomass, we can skip the study of a complex transport path resistance of the sugars within a complex plant topological and geometrical structure. In this case, we can define the sink strength as the ‘potential demand of an organ for biomass accumulation’. Although this demand, S_o , is absolute and follows usually a bell-shaped curve as a function of organ developmental stage, one may consider that it is relative,

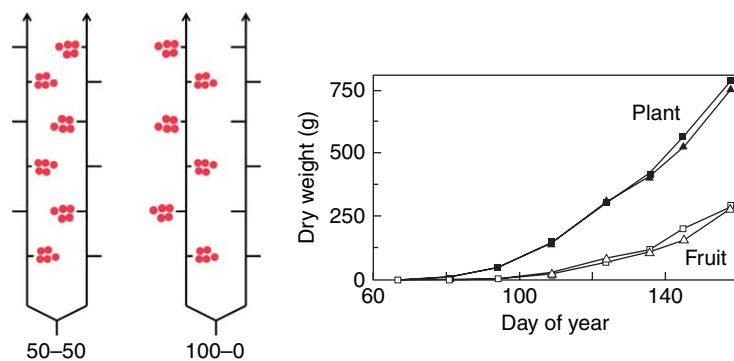


Figure 5 Cumulative total (closed symbols) and fruit (open symbols) dry weight per plant as a function of day of the year (day 1 = 1 January). Plants were decapitated above cotyledons and had two equal stems originating from the axillary buds of the cotyledons. Tomatoes located on one stem (100-0; triangles) or two stems (50-50; squares). Details are given in Heuvelink E (1995) Dry matter partitioning in a tomato plant: One common assimilate pool? *Journal of Experimental Botany* 46: 1025–1033.



Figure 6 Growth of a nonphotosynthetic shoot of *Hedera helix* (ivy) using the common pool of biomass. Here leaves are no more source but only sink organs.

because it has to be balanced by the sum of the plant sinks $\sum S$ that is the total plant demand. Eventually, the relative sink strength, f_o , can be written:

$$f_o = S_o / \sum S \quad [2]$$

where f_o represents the fraction of assimilates partitioned to an organ with sink strength S_o .

Roles of organs in the plant functioning

Each organ contributes to the plant processes, during its functioning period, in different ways. Leaves ensure light interception and biomass production; stems with their constitutive internodes build the hydraulic plant architecture for the water transport from the root to the leaves and for transport of assimilates from sources to sinks. All organs (even those that can also be sources like leaves) are sinks during their expansion and are thus involved in biomass partitioning.

Role of leaves

Crop light interception is no more proportional to leaf area when the canopy is dense. In homogeneous

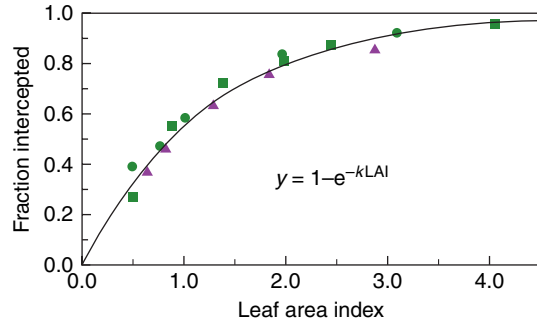


Figure 7 Light interception of young tomato plants arranged at different plant densities in order to vary LAI. Measurements – three symbols for three different dates/plant sizes. Line represents regression equation $y = 1 - e^{-0.83x}$. Details are given in Heuvelink E (1996) *Tomato Growth and Yield: Quantitative Analysis and Synthesis*. PhD Thesis, Wageningen University.

conditions (that is to say most cases), a crop can be considered as a turbid environment and light interception is well described by Lambert–Beer law (Figure 7). At the stand level, the number of leaves overlapping is controlled by a simple parameter, the leaf area index (LAI = leaf area per square meter), and the fraction of intercepted light (FIL) is deduced from the relationship

$$FIL = (1 - \exp(-k \cdot LAI)) \quad [3]$$

The light extinction coefficient k depends on leaf orientation and reflectance and transparency, that can be assessed by measurements inside a crop. Biomass production can be calculated as the product of FIL, incident light (PAR, photosynthetically active radiation), and light-use efficiency (LUE; $g MJ^{-1} PAR$). LUE is a robust parameter, and its value is species dependent and also prone to environmental influences (e.g., CO_2 concentration), but often a value between 2 and 3 $g MJ^{-1} PAR$ is reported. For low planting densities, the biomass production per unit of ground area is proportional to the LAI (and the number of plants). At highest densities, the production per square meter of ground area becomes independent of the plant density (Figure 8).

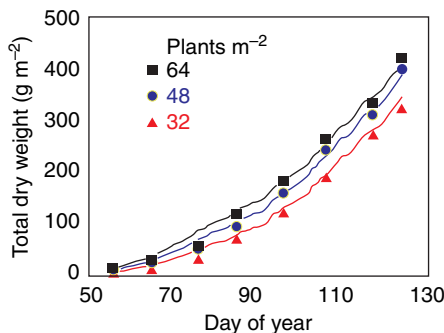
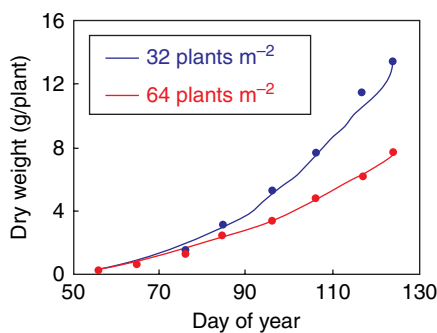


Figure 8 Effect of density on plant weight and biomass production per square meter for *Chrysanthemum*. The individual weight is lower at higher planting density, but the biomass production per square meter per day is independent of density, once the LAI reaches a high value. From Lee J-H, Heuvelink E, and Ortega L (unpublished) (Wageningen University).

The photosynthetic active functioning duration of a leaf is limited. For a plant, the highest resistance to water transpiration is located at the leaf surface level, where the water changes from liquid to vapor phase. For a 10-year-old poplar tree, the leaf area represents 95% of the resistance to transpiration monitored by the hydric potential between soil and atmosphere.

The ratio between the leaf weight and the leaf surface is called specific leaf weight (SLW). A low value means thin leaves and this favors in a young crop the fast buildup of light-intercepting capacity and hence growth.

Role of stems and their constitutive internodes

Beyond the mechanical role that ensures plant stability, stems play a functional role for transport of water and assimilates and form a hydraulic network. Resistance to water flow of the hydraulic architecture for the above-mentioned 10-year-old poplar is low and assessed to be only 3% of the total resistance. For most crops it may thus be considered as quite negligible. For mature trees it can increase and consequently reduce water transpiration and photosynthesis. Stems in woody plants have secondary growth that increases their diameters. Eventually, stems contained a pith and a stack of rings. The pith has a variable sink linked to the phytomer; meanwhile, the rings belong to the whole plant architecture and can be considered as a single big sink for biomass that is always in expansion.

Role of fruits

Fruits (reproductive organs) are sinks during their whole lifetime. They are often the strongest sinks on a plant and can reduce dramatically the expansion of the other organs such as in sunflower (the inflorescence) and maize (the cob). They have no significant influence on the biomass production that depends on the LAI. However, an indirect influence occurs when leaf area development is drastically reduced because of the strong sink capacity of the reproductive organs.

The place where fruits can occur in the plant structure depends on the plant species; for example, in a sweet pepper plant typically there is a flower in every leaf axil, whereas a tomato plant produces a truss after every three leaves and internodes. Whether a flower turns into a fruit or not depends on the assimilate status of the plant (source/sink ratio) but besides assimilate availability, hormonal regulation also plays a separate role.

Role of roots

The root system is seldom accessible to measurements. The weight ratio shoot/root is supposed to be constant by default. In the case of loose soil where the roots can find their way, the root system can be considered as a single sink. For the above-mentioned 10-year-old poplar tree, its resistance to water transport is considered negligible and assessed at about 2%.

Modeling Plant Development and Plant Growth

Knowledge from botany and ecophysiology has to be adapted and integrated properly inside a mathematical model. The effort to simplify the complexity is an important part of the modeling work. It leads to the identification of the relevant parameters that are used in the equations that control plant morphogenesis and functioning. As previously mentioned, a detailed qualitative knowledge alone is not sufficient to understand such a complex system as plant development and growth. Plant functioning has to be grasped through the behavior of the equations. Thanks to these, we can hope to solve the inverse problem that leads to the calibration of the model parameters in real situations. The final goal is to monitor plant growth in variable climate conditions and to optimize crop production.

Depending on methods, aims, and processes concerned, three main classes of models may be distinguished. They are currently referred to as geometrical models (GMs), process-based models (PBMs), and functional structural models (FSMs).

GMs and the Simulation of Plant Development

GMs are only concerned with the 3-D representation of plants and plant development (i.e., the meristem functioning). The model of plant development (often in a grammar shape) can be more or less faithful to botany; what is important there is to obtain a good geometry. GMs produce organs whose sizes are fixed from empirical observations on real plants. Moreover, information about branching angles, phyllotaxy, and tropisms has to be included to increase the realism. Simulation of plant development uses schedulers and parallelism to simulate bud functioning and this leads to heavy computations for big trees due to a cumbersome topological structure. GMs are used in town and landscaping, advertising, even in botany or agronomy for getting nice 3-D mockups.

GMs (L-systems, Amap) have developed special tools to simulate plants faithful to botany. Using the physiological age to control the meristem differentiation and stochastic processes to follow the meristem behavior, and adding an empirical geometry, it is possible to obtain an accurate organogenesis and realistic plant architecture. Sampling complex architecture thanks to the physiological age allows collecting data on which it is possible to calibrate the parameters of plant development.

GMs are sufficient to build the plant architecture, if there is no need to assess the plant biomass production (**Figure 9**).

PBMs and the Simulation of Plant Growth

PBMs focus on plant functioning. The goal is to assess the crop production per square meter based on environmental

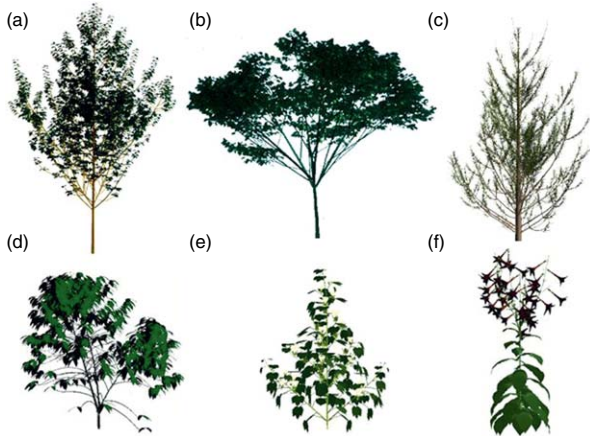


Figure 9 Simulations of geometrical plant models simulated with AMAPsim software (J. F. Barczi, CIRAD): (a) wild cherry tree (Fournier), (b) zelkova tree (Barthélémy), (c) young Aleppo pine (Carraglio), (d) coffee tree (de Reffye), (e) cotton plant (de Reffye), (f) ornamental tobacco plant (Rey). The parameters for plant development and geometry have been assessed from measurements on real plants.

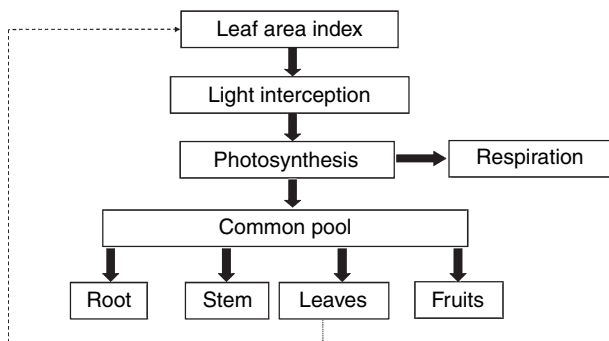


Figure 10 Flowchart of a PBM for plant growth.

conditions, and not its 3-D representation. For such an attempt, the plants are considered only at the minimal level of organ compartments. PBMs rely more on computation than on computer simulation and represent the engineer's point of view of agronomists.

PBMs are used to simulate crops production in either fields (i.e., Ceres model) or greenhouse conditions (i.e., Tomsim model; **Figure 10**). They take account of the simplifications seen previously:

- light interception based on the Lambert–Beer law: this way of using LAI is quite efficient to compute and skip the cumbersome plant leaf canopy;
- biomass production according to eqn [1] (see above): parameter Y_g and processes P_g and R_m are computed from empirical knowledge and relationships with the environmental parameters (radiation, temperature, CO_2);
- using the common pool of biomass (transport resistance for assimilates is neglected), the biomass partitioning is

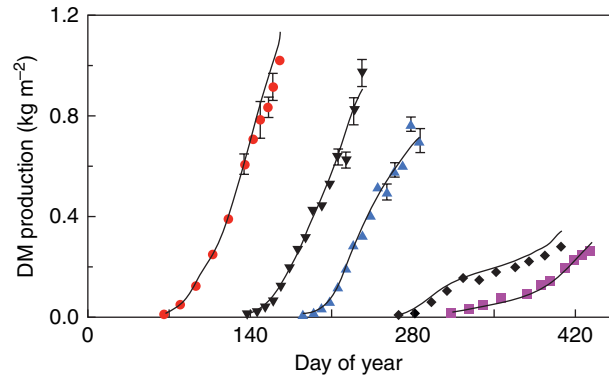


Figure 11 Measured (symbols) and simulated (model TOMSIM: lines) dry matter production for five tomato crops differing in planting date (first data point). Hourly averages for measured global radiation outside the greenhouse, greenhouse temperature, and CO_2 concentration were input to the model. Details are given in Heuvelink E (1995) Dry matter production in a tomato crop: Measurements and simulation. *Annals of Botany* 75: 369–379.

performed according to the relative values of the sink strength of organs (some experiments allow assessing them directly);

- sources and sinks have no significant direct interaction.

PBMs perform the computation of both biomass production (dry matter) and biomass partitioning. They are dynamical models that follow the step-by-step plant functioning. They rely on eqn [2] and on the assessed sinks of the different plant compartments thanks to direct measurements.

Such models work fairly well in normal conditions (**Figure 11**). Nevertheless, some bottlenecks of PBMs and FSMs appear for different reasons:

- For ornamental crops, a 3-D output is relevant to assess the resulting plant architecture (plant external quality).
- A lack of prediction of the SLW according to different environmental conditions (climate, density) prevents a good estimation of the leaf area.
- There is neither a good prediction about organ abortion, nor about dry matter contents.
- No consideration is taken of the statistical variations among the yield.

PBMs often summarize the whole plant architecture in four compartments (leaf, stem, fruit, and root) for samples collected on the crop at each step of time. This makes fitting models easy and misleading, since an infinite number of plant architectures could correspond to a plant fitted with a PBM.

It is generally recognized that these drawbacks come from ignoring the plant architecture and its plasticity, such as the interactions between growth and development at phytomer level. Typically, the number of phytomers

produced by a bud building an annual shoot depends on the biomass production of the previous year in temperate trees.

Functional Structural Models and the Simulation of Plant Growth and Development

Two different strategies are explored in the development of functional structural models. The first one focuses mainly on the ability of computers to simulate complex systems and seems more attractive for physiologists and computer scientists. The attempt here is to imitate as closely as possible the details of the plant architectural development, including the parallel functioning of meristems, and the plant physiological functioning, including the biomass circulation in the plant topological and geometrical structure. Eventually the 3-D geometric representation of the plant is obtained as a result of its functioning. In such models, the plant physiology is sometimes described down to the cell level (e.g., stomata functioning).

To cope with such a level of detail, complex simulation software is developed. These models integrate in detail the components of plant morphogenesis and since they consider smaller scales, they do not take into account the relevant simplifications underscored by agronomists at plant scale (simplifications recalled in the previous sections, like the concept of common pool). A bottleneck of this approach is hit when the geometrical and topological structures become too complex, as in trees, since each meristem is dealt with individually to determine organogenesis and the whole plant structure and geometry have to be explored to compute light interception and matter circulation.

Although these type of models are still far from providing practical applications for agronomy, forestry, or ecology, they remain interesting for plant physiologists as tools of knowledge capitalization for teaching and research.

The second strategy endeavors building mathematical models, solving inverse problems, and developing optimization methods, and is of particular interest for agronomists and automation specialists. It aims at extrapolating PBMs at organ level by merging the botanical knowledge on plant development with the functional equations. It has led to mathematical models of plant growth and development. Contrary to the simulation models, the computation of the plant physiological functioning bypasses the exploration of the whole plant structure. And yet, if necessary, the complete plant architecture can be built.

The mathematical formalism has obvious advantages for applications in agronomy, forestry, and ecology as it makes it possible to study the system behavior, to estimate

model parameters by model inversion, and to perform system optimization and control. For this reason, there is mainly a focus on this approach in this article.

Factorization of plant architecture

Depending on the type of plants, phytomers are set in place rhythmically or continuously. In the rhythmic case, the plant grows by successive shoots of several phytomers produced by buds. The apparition of these shoots defines the architectural growth cycle. A growth unit is the set of phytomers built by a bud during a growth cycle. These can be of different kinds and ordered according to botanical rules, like acrotony. Plant growth is said to be continuous when meristems keep on functioning and generate phytomers one by one. The number of phytomers on a given axis (that is to say generated by the same meristem) is proportional to the sum of daily temperatures received by the plant, as detailed before. The growth cycle is defined as the thermal time unit necessary for a meristem to build a new phytomer.

In both continuous and rhythmic cases, the chronological age of a plant (or of an organ) is defined as the number of growth cycles it has existed for, and the organogenesis is used as the time step to model the plant as a discrete dynamical system.

Quite naturally, owing to the simultaneous functioning of the meristems, parallel rewriting grammars introduced by Lindenmayer (L-systems) are most widely used to model plant organogenesis, both for simulation and mathematical models, but in different ways.

At each growth cycle, cohorts of similar organs are created. Simulation models handle each of them individually, which may lead to cumbersome computation in the case of tree growth simulations, as the number of organs may exceed several millions. However, it is not usually necessary to consider local environmental conditions at the organ level. Thus, we can suppose that all organs of the same kind, created at the same growth cycle, behave identically. From a modeling point of view, it leads to a powerful structural factorization of the plant, based on botanical instantiations derived from the concept of physiological age (see above). Compact inductive equations of organogenesis can thus be deduced.

Let P be the maximum number of physiological ages in the plant. It is generally very small ($P \leq 5$). From the botanical description of the plant, we know that phytomers and buds are the elementary bricks of the plant structure. At growth cycle t , a metamer is characterized by its physiological age p , the physiological age of its axillary branches q (with $q \geq p$), and its chronological age n . It is denoted by $m_{pq}^t(n)$. These three indices p , q , and n are sufficient to describe all the phytomers and their number grows linearly with t . A bud is only characterized by its physiological age p and is denoted by s_p .

The terminal bud of a plant axis produces different kinds of metamers bearing axillary buds of various physiological ages. These buds themselves give birth to axillary branches and so on. A substructure is the complete plant structure that is generated after one or several cycles by a bud. In the deterministic case, all the substructures with the same physiological and chronological ages are identical if they have developed at the same moment in the tree architecture. At cycle t , a substructure is thus characterized by its physiological age p and its chronological age n . It is denoted by $S_p^t(n)$. Since the physiological age of the main trunk is 1, at growth cycle t , the substructure of physiological age 1 and of chronological age t , $S_1^t(t)$, represents the whole plant. **Figure 12** illustrates the way substructures are organized. The total number of different substructures in a plant of chronological age t is very small, usually less than 30, even if the total number of organs is high. Substructures and phytomers are repeated a lot of times in the tree architecture, but they need to be computed only once for each kind (**Figure 12**).

We use the concatenation operator to describe the organization of plant phytomers and substructures and deduce their construction at growth cycle t by induction, as follows:

- substructures of chronological age zero are buds: $S_p^t(0) = s_p$;
- if all substructures of chronological age $n - 1$ are built, we deduce the substructures of chronological age n :

$$S_p^t(n) = \left[\prod_{p \leq q \leq P} \left(m_{pq}^t(n) \right)^{u_{pq}(t+1-n)} \left(S_q^t(n-1) \right)^{b_{pq}(t+1-n)} \right] S_p^t(n-1) \quad [4]$$

For all (p, q) such that $1 \leq p \leq P, p \leq q \leq P$, $(u_{pq}(t))_t$ and $(b_{pq}(t))_t$ are sequences of integers that are characteristic of the plant organogenesis; $u_{pq}(t)$ corresponds to the number of metamers m_{pq} in growth units of physiological age p appearing at growth cycle t ; $b_{pq}(t)$ is the number of axillary substructures of physiological age q in growth units of physiological age p that appeared at growth cycle t . These sequences can be deterministic or stochastic.

In eqn [1], substructure $S_p^t(n)$ is decomposed into:

- its oldest growth unit, called base growth unit:

$$\prod_{p \leq q \leq P} \left(m_{pq}^t(n) \right)^{u_{pq}(t+1-n)}$$

- the lateral substructures borne by the base growth unit (they are one cycle younger):

$$\prod_{p \leq q \leq P} \left(S_q^t(n-1) \right)^{b_{pq}(t+1-n)}$$

- the substructure grown from the apical bud of the base growth unit (also one cycle younger):

$$S_p^t(n-1)$$

Its decomposition is illustrated on $S_1(2)$ in **Figure 12**. If we add geometric rules (internode lengths, branching angles, phyllotaxy) to the construction equations, we obtain the 3-D architecture of a geometrical tree.

The mathematical equations of plant functioning
Biomass acquisition

The practical ecophysiological concepts implemented in PBM, such as modeling of source–sink interactions and

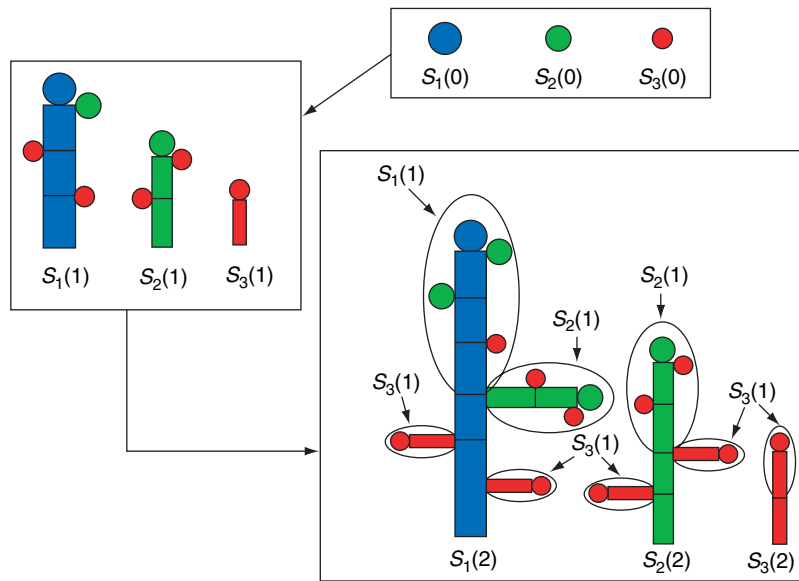


Figure 12 Factorization of the plant development and inductive construction of the substructures for a plant with three physiological ages.

the common pool hypothesis, are adapted to the individual plant, at organ level. We consider two steps at each growth cycle: first, the neat biomass production (dry or fresh), and then, its repartition among all growing organs according to their sink strengths.

For high crop density, eqns [1] and [2] of resource acquisition per unit surface area (m^2) can be summarized by:

$$\frac{dW}{dt} = \lambda I(1 - \exp(-kLAI)) \quad [5]$$

I denotes the light radiation and the intercepted light is computed by the Beer–Lambert law. λ is the light-use efficiency, which is the conversion coefficient of light interception to biomass.

If d is the plant density and $S_d = 1/d$, S_d represents the potential surface area available for each plant. We thus have $LAI = S_f(n)/S_d$, with $S_f(n)$ the total surface area of nonsenescent leaves for the individual plant. Moreover, we can integrate eqn [5] on the whole growth cycle. Thus, we obtain the equation giving at growth cycle n the neat biomass production $Q(n)$ for the individual plant:

$$Q(n) = \lambda I(n)S_d \left(1 - \exp\left(-k \frac{S_f(n)}{S_d}\right) \right) \quad [6]$$

For lower densities, we define a virtual surface area S_p , linked to S_d by a relevant empirical relationship $S_p = F(S_d)$, and eqn [6] is rewritten:

$$Q(n) = \lambda I(n)S_p \left(1 - \exp\left(-k \frac{S_f(n)}{S_p}\right) \right) \quad [7]$$

Biomass distribution

As explained above, biomass allocation is driven by the sink strengths of all expanding organs. The sink value of an organ depends on its physiological age and on its type o ($o = b, p, i, c, f$ for leaf blade, petiole, internode, secondary growth rings on stems, and fruits or flowers, respectively) and its chronological age j . It is denoted by $p_o(i)$ and usually modeled by a parametric function (density function of beta law for example). From the organogenesis equations, we can easily deduce $N_o(j)$ the number of organs of type o and of chronological age j and thus write $D(n)$ the total plant demand at growth cycle n :

$$D(n) = \sum_o \sum_{j=1}^n N_o(j)p_o(j) \quad [8]$$

Consequently, biomass allocated to an organ of type o and of chronological age j is proportional to its sink and to the incremental pool of biomass for distribution, divided by the total plant demand. If we do not consider reserve allocation or remobilization, it is given by:

$$p_o(i)Q(n)/D(n)$$

The sum of all the biomass increments for a given organ gives it weight. Using the SLW ϵ , we can retrieve leaf surface area, which will be used to compute resource acquisition in eqn [7]. If we want to build the plant geometry, we need to compute the fresh weights, from which we can deduce organ volumes, dimensions, and shapes, thanks to allometric rules.

The general equation of plant growth

If we consider a constant SLW at the growth cycle scale, and if T_b denotes the number of growth cycles before a leaf get senescent (also supposed constant for all leaves), we can replace $S_f(n)$ in eqn [7] by its expression as a function of the successive biomass productions and demands, to obtain the general inductive equation [9] in which development and growth are implicit:

$$Q(n) = \lambda I(n)S_p \left(1 - \exp\left(-\frac{k}{e \cdot S_p} \sum_{i=1}^{T_b} N_b(i) \times \sum_{j=1}^i p_b(j) \frac{Q(n-i+j-1)}{D(n-i+j-1)}\right) \right) \quad [9]$$

An important variable emerges from eqn [9] – the ratio of available biomass to demand (Q/D value). It represents the global source–sink balance and the trophic competition during plant growth. It can be used as a key variable to control interactions between growth and development, such as fruit set, bud break, or vigor.

For applications that do not necessitate plant geometrical representation, this equation coupled with the allocation equations can be sufficient to describe the whole plant growth. Such a mathematical formalism provides interesting advantages for estimation of model parameters from experimental data, optimization, and optimal control problems, which makes it suitable for applications in agriculture, forestry, or ecology. The GreenLab model, developed jointly in China, the Netherlands, and France, is based on this set of equations.

Estimation of model parameters from experimental data: From architecture to functioning

The key step for model applications is its validation on real plants, by estimating the specific parameters of a given plant variety, from experimental data. Some model parameters can be measured, while some cannot be directly assessed from experimental observations. It concerns both development (when the rules of organogenetic grammars are too complex) and growth (like the parameters of the sink and source functions). These hidden parameters have to be estimated by model inversion. Since plant growth can be modeled in the form of a dynamical system, classical methods of parameter

estimation can be used, based on the maximum likelihood criteria and Newtonian methods of optimization. The model outputs from which this identification can be achieved are the organ masses, as they can be easily measured on real plants and as they result from the plant functioning and thus keep track of the whole history of source–sink balances (Figure 13).

If we consider a monospecies population, several plants, at different ages, can be used simultaneously to form the observation vector. Complications can be induced if the population has strong intraspecific genetic variability and environmental variability. The amount of data collected is a compromise between the statistical accuracy of estimation and the heaviness of the measurements.

In most cases, the simplifications used in the physiological model are justified by the confrontation of the model to real plants, since a very small number of model parameters are sufficient to predict a large number of data. Even though all the complex phenomena underlying plant growth and development are not accounted for, the prediction ability of such models remains quite good. The reason is that the simple theoretical plant given by the model is such that its architectural trajectory is very close to that of the real complex plant.

Compared to Figure 9, the simulations of Figure 14 are more accurate, because the sizes of organs depend on the biomass production and the biomass partitioning and do not directly result from empirical data sets.

Applications of functional structural models

Functional structural models aiming at simulating detailed physiological functioning, thanks to sophisticated algorithms, are still far from current applications on crops. On the contrary, the ones that are based on dynamical equations share the same applicative philosophy and the same knowledge as PBMs and can easily be used in agriculture or forestry. Their advantage is that populations of organs instead of compartments are considered. More information about the history of growth is thus collected on the plant architecture, which allows more accurate model identification and growth description. This is particularly true when considering plant plasticity:

- Sink values or organ allometry may be modified during plant growth in response to an environmental stress. These effects can be measured and integrated in the dynamical equations quite easily, thus allowing the consideration of plant–environment interaction and stresses (light, temperature, water, density).
- Organogenesis can be strongly modified by growth as a result of growth and development interaction. Plant development may be quantitatively strongly modified and 15-year-old beech trees in the shade or in open field conditions can, for instance, respectively, be 15 cm high, without branch, or 15 m high with a vigorous crown (Figure 15)! According to Q/D value (source/sink ratio), axillary stems may develop or organs may abort, thus allowing a faithful modeling and simulation of plant architectural plasticity.

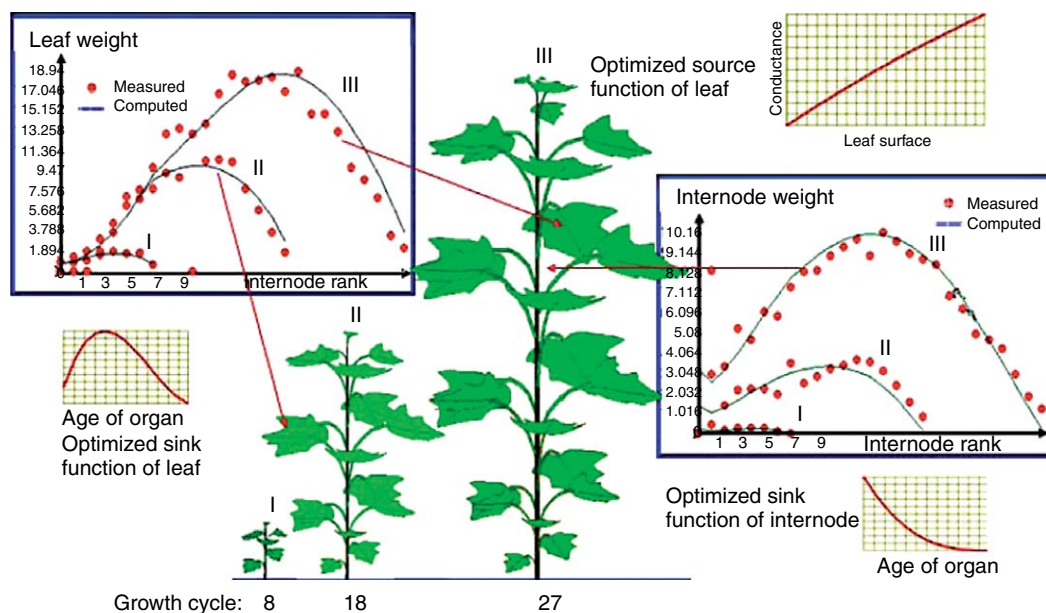


Figure 13 Several growth stages of the same plant are fitted simultaneously at the organ biomass level with an optimized common set of parameters that insure biomass production and biomass partitioning. The organs of different types are fitted together because they share the same plant demand and production. Eventually the plant growth dynamics are controlled by a small set of constant parameters. From Zhan Zhigang, LIAMA.

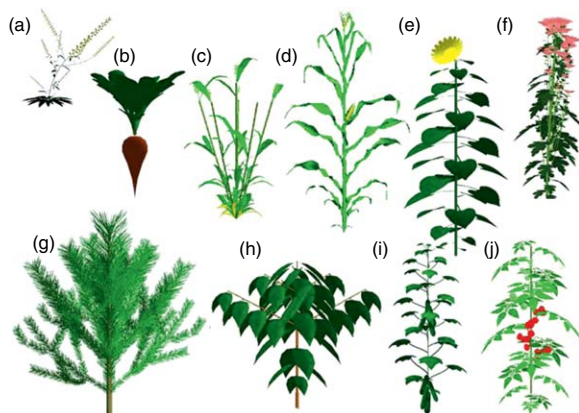


Figure 14 Simulations of 3-D plant architectures including growth and development (GreenLab model: developed at INRIA, ECP, LIAMA, CIRAD): (a) *Arabidopsis* plant, LEPSE (Digiplante software: ECP); (b) beetroot plant, Institut Technique de la Betterave (Digiplante software); (c) wheat plant, Wageningen University (GreenScilab software: LIAMA); (d) maize plant, Chinese Agricultural University (software CAU); (e) sunflower plant: INRA/LEPSE (Digiplante software); (f) *Chrysanthemum* plant, Wageningen University (GreenScilab software); (g) pine tree, Chinese Academy of Forestry (Digiplante software); (h) coffee tree, CIRAD (Digiplante software); (i) cucumber plant, CAU (Digiplante software); (j) tomato plant, CAU (CornerFit software: LIAMA).

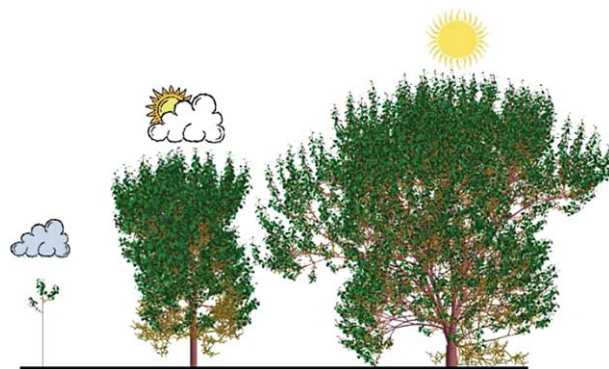


Figure 15 Interaction between plant growth and plant development. In different incident light conditions, the tree architecture can be strongly modified. Parameters for development can be modified depending on the evolution of the ratio supply/demand during the growth process (Amélie Mathieu, Digiplante: ECP).

For applications in agronomy, forestry, or ecology, a key question is raised by the transition from individual-based (plant) models to population-based (crop) models. Competition for space and resources are modeled and the dynamic equations can be written per unit surface area (per square meter), similar to PBMs. Optimization and control of cultivated systems can thus be achieved, like determination of optimal irrigation, fertilization, or densities.

Another important application consists in linking plant growth models with genetic models, since the stable

endogenous parameters of the dynamical model are good candidates for quantitative trait loci detection.

Conclusion

Plant growth and development are very complex phenomena which have challenged modelers for a long time. Botanists, ecophysicists, and agronomists have endeavored to find at the scale of plant architecture the relevant traits and the global empirical laws that enable to simplify the biological knowledge for the purpose of modeling. Thanks to these results, mathematicians are now able to develop specific formalisms and numerical tools to solve problems of parameter estimation and optimization, which gives way to applications in diverse fields of agricultural sciences or ecology.

See also: Plant Competition.

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Plant Physiology

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What Is Physiology? What Is Ecology?

Plant Physiology: Function of Plants and Their Parts

Plant Ecology: All Conditions of Its Existence

Photosynthesis: A Special Case Story

General Importance of Physiological Processes for Fitness at the Community Level

Further Reading

What Is Physiology? What Is Ecology?

A well-known dictionary of the English language says that physiology is “the science of the function of living organisms and their parts” and that ecology is “the branch of biology dealing with the relations of organisms to one another and to their physiological surroundings” and if we follow more closely Ernst Haeckel’s original definition when he first introduced the term ecology in 1866 we have it as “the entire science of the relations of the organism to its surrounding environment, comprising in a broader sense all conditions of its existence.” Hence, if we want to bridge the interface between general ecology and plant physiology we must consider functions of parts and the whole of organisms on the one hand and all conditions of their existence on the other hand and integrate both. It shall be done by looking first at plant physiology and then at ecology and finally by combining both, choosing physiological ecology of photosynthesis as a case study because photosynthesis with its primary production of new biomass from inorganic precursors is of paramount importance for all life on Earth.

Plant Physiology: Function of Plants and Their Parts

The Parts

In a hierarchical order the parts of plants are molecules, membranes, organelles, cells, tissues, and organs. Macromolecules such as polynucleic acids, proteins, polysaccharides (carbohydrates), and lipids may have both

structural and functional roles. Biological membranes composed of lipids and proteins (lipoprotein membranes) border the living cells at their surface (the plasma membrane) and separate and conceal various compartments inside the cells, for example the central cell sap vacuole (the tonoplast) typical of plant cells. Important organelles within cells are the mitochondria and the chloroplasts. The plant cells are surrounded by cell walls composed of polysaccharides, most importantly cellulose. Individual cells can already be independent autotrophic organisms, such as prokaryotic photosynthetically active bacteria and cyanobacteria, which as endosymbionts also have become the evolutionary precursors of chloroplasts, and eukaryotic unicellular algae. In the pluricellular algae, bryophytes, and vascular plants, many cells build up tissues, different tissues form organs and various organs, such as roots, stems, leaves, and flowers make up the whole vascular plant. Eukaryotic plant cells have a nucleus with chromosomes where the central genome is located, but they have two additional genomes in the two organelles, the mitochondria and the chloroplasts, which as original endosymbionts in the phylogenetic history of the eukaryotic cells have retained their own deoxyribonucleic acid (DNA) carrying genetic information.

The Functions

The main concern of plant physiology is the causality of functions. A basic property of life is metabolism. Therefore, we may distinguish functions of biochemistry and functions of development.