# CHAPTER 14

# GRAAL: GROWTH, ARCHITECTURE, ALLOCATION

*A functional-structural model integrating processes of growth and processes of assimilate allocation from the organ level to the whole-plant level*

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**Abstract.** An integrated functional-structural model, called GRAAL, has been developed to simulate and analyse the interactions between morphogenetic processes and assimilate partitioning during the vegetative development of individual plants. GRAAL associates models of plant morphogenesis and models simulating the growth of plant compartments as related to assimilate availability. Using object-oriented methods, knowledge is formalized at the organ level (i.e., local rules of development and functioning). The behaviour of the plant arises from interactions between the organs and the integration of the processes within the whole plant. Shoot and root organs are initiated as a function of temperature. Using the source–sink concept, organ growth is calculated from its potential growth and assimilate availability within the whole plant. In the case of maize plants as regards carbon assimilates, simulation results indicate that the model reproduces the main features of plant functioning (e.g., kinetics of root:shoot ratio for carbon, changes in priority between organs and plant plasticity to carbon availability). More generally, the model is a generic framework for testing and sorting hypotheses on processes involved in plant development. In this respect, it is an integrated ecophysiological tool for analysing the interactions between genotypic and environmental characteristics affecting plant behaviour.

## INTRODUCTION

Numerous models have been developed to simulate soil–plant–atmosphere fluxes within various agrosystems or ecosystems. Most are based on the assumption that leaf and root distribution are horizontally homogeneous. The goals set by scientists using them justify simplifying plant architecture. However, architecture determines the ability of a plant to capture resources and transport assimilates to its organs. It results from developmental processes linked to assimilate partitioning among shoot and root organs, and depends on organ sink strength. Although there is much information available on individual processes in plants at the organ level (such as photosynthesis, sugar metabolism and cell expansion), partitioning of assimilates at



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the whole-plant level is still poorly understood.

Models are helpful for synthesizing knowledge, describing and understanding complex systems such as plants, as well as for testing hypotheses on interactive mechanisms between plant organs. Among the numerous models that have been developed to reproduce plant development and/or functioning, two principal types can be defined. On one hand, there are architectural models that were initially developed for trees. They use botanical concepts to simulate plant topology and three-dimensional geometry (Diggle 1988; Kurth 1994; Perttunen et al. 1996; De Reffye and Houllier 1997; Prusinkiewicz 1999). By representing each organ explicitly and individually, they focus on developmental processes. However, these models take into consideration either the shoot system (e.g. Fournier and Andrieu 1998) or the root system (e.g. Pagès et al. 1989), an approach that does not allow for the study of integrated functioning of the whole plant. On the other hand, there are plant-functioning models that were largely developed for annual plants. They simulate plant growth as related to resources (carbon, nitrogen) and water availability (e.g. Thornley 1972; Brisson et al. 1998; Tabourel-Tayot and Gastal 1998). But by taking into account plant compartments (all leaves, all stems, all roots, all grains), they cannot reproduce partitioning of assimilates between individual organs (see Lemaire and Millard 1999; Lacointe 2000; Marcelis and Heuvelink, this volume).

Recently, some attempts have been made to integrate functional processes into architectural models (Yan et al. 2004; Eschenbach 2005; Allen et al., this volume). To pursue this line of reasoning, we have developed a modelling tool, called GRAAL (Growth, Architecture and ALlocation), to test various hypotheses of plant functioning by integrating processes from the organ level to the plant level. This implies taking into account competition between plants for resource acquisition and competition between organs for assimilate partitioning within the plant. Hereafter, GRAAL is thoroughly described, including the general concepts of the model, the hypotheses on organ processes and the structure of the model. Then, in the case of maize plants, an illustration of model behaviour and model evaluation is given. We discuss the advantages of describing plants at several organizational levels in order to study plant structure and function in relation to the environment. To conclude, we highlight the generic features of the model. This paper is based on previous work from Drouet and Pagès (2003).

## MODEL DESCRIPTION

### *General concepts of the model*

GRAAL associates two aspects of plant functioning: (i) morphogenetic processes that determine the initiation of new organs and plant topology; and (ii) resource acquisition and assimilate exchange between organs that modulate their extension and growth in assimilate mass (see, e.g., Lemaire and Millard 1999). The model is based on a source–sink approach (Warren-Wilson 1972; see Marcelis 1993; Lacointe 2000) and uses only one simple rule for assimilate partitioning: the

effective growth of a given organ is proportional to its potential growth and to assimilate availability (i.e., ratio between assimilate supply and demand). No predetermined coefficient of partitioning between organs is given. The potential growth of each organ is derived from field experiments carried out under low limiting conditions of growth as regards light, nutrients and water.

*Hypotheses on processes at the organ level*

*Organ initiation, extension and increase in carbon mass*

Initiation of shoot phytomers (internode and leaf) and roots, potential extension of shoot and root constituents as well as potential increase in carbon mass have already been detailed in Drouet and Pagès (2003). To summarize here, the shoot apical meristem initiates successive phytomers according to a rate function of temperature. Nodal root primordia are produced sequentially above the node of the successive shoot phytomers and the number per phytomer is linearly related to the phyllochron number. The production of lateral roots by branching results from acropetal initiation of lateral primordia close to the apex and then their emergence as root meristems after a given duration.

The extension of each phytomer involves three successive phases: i) from primordium initiation to beginning of leaf elongation; ii) leaf elongation; and iii) internode elongation. The duration of the first period is assumed to depend on temperature and leaf rank. Potential leaf elongation rate depends on temperature only, increasing quasi-linearly with increasing temperature from a base to an optimal temperature, and then decreasing. Profiles of final leaf length as a function of leaf rank are modelled by a bell-shaped curve. Maximal leaf width is derived from final leaf length by an allometric relationship. Duration of leaf elongation is the ratio between final leaf length and leaf elongation rate. Potential internode elongation rate is proportional to potential leaf elongation rate. Profiles of final internode length and diameter are linearly related to internode rank. Duration of internode elongation is the ratio between final internode length and internode elongation rate. Potential root elongation rate increases asymptotically as a function of root apical diameter reflecting root meristem size. Diameter of root apical meristem varies according to carbon availability within the plant.

Total organ carbon mass is the product of organ dimension (area for leaves and volume for internodes and roots) and total organ carbon mass per unit area or volume. For each leaf and internode as well as for each root segment, potential growth in total carbon mass per unit area or volume is assumed to be dependent on air (respectively soil) temperature for shoot (respectively root) organs. It increases linearly between minimal and maximal values determined experimentally.

*Carbon acquisition and partitioning*

Total carbon supply is provided by the seed and photosynthesis. Seed carbon supply is assumed to be a function of the quantity of seed carbon and seed remobilization rate. Gross photosynthesis of the whole plant is the sum of gross photosynthesis for each leaf that is estimated from Photosynthetically Active Radiation (*PAR*) by using

a rectangular hyperbola. Maintenance respiration of the whole plant is the sum of maintenance respiration for each organ (leaves, internodes and roots), which is a function of organ carbon mass and is affected by temperature.

First, carbon supply from seed and photosynthesis is calculated, then maintenance respiration and finally carbon demands for the potential growth of each organ. The rate of growth demand satisfaction in carbon for the whole plant is calculated as the ratio of carbon available (i.e. carbon supply minus maintenance respiration) within the whole plant to the sum of carbon demands for the potential growth in carbon of all organs.

*Effective organ growth*

Effective extension of each organ is a function of temperature alone, except effective root elongation, which depends on carbon availability. Effective growth in carbon mass is the product of organ potential growth in carbon and rate of growth demand satisfaction in carbon. Effective growth in carbon mass per unit area (respectively volume) of a given organ is calculated as the ratio between its effective growth in carbon mass and its effective growth in surface (respectively volume).

*Structure of the model*

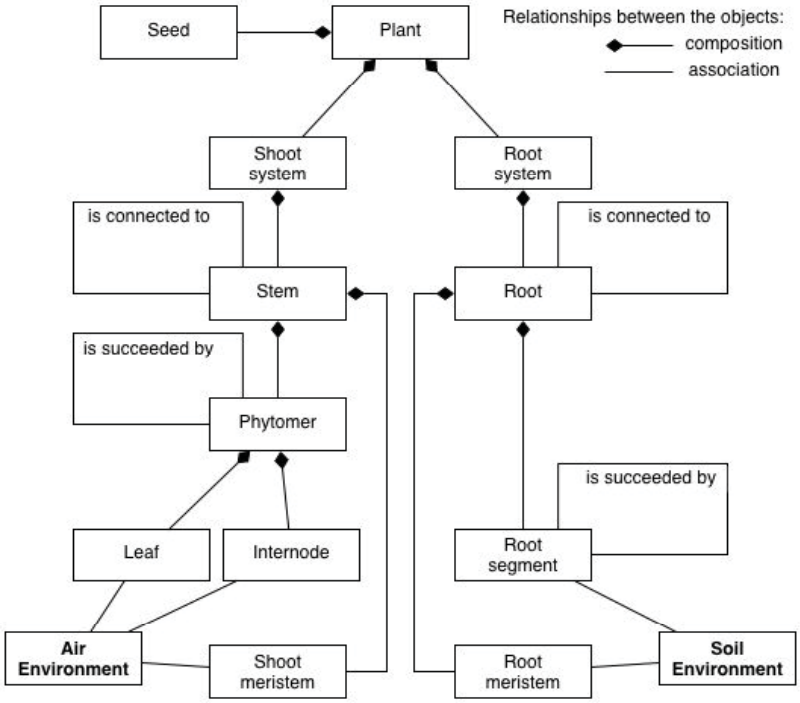


***Figure 1.*** *Class-object diagram (formalized using the Unified Modelling Language, UML) of the GRAAL model integrating processes from the organ level to the whole-plant level*

The model was formalized using object-oriented methods (UML approach, Unified Modelling Language; Muller and Gaertner 2003) that are useful for integrating complex processes. The general principle (Figure 1) is to divide the studied system (the plant) into entities (or objects). Objects are linked by relationships of composition (e.g., a stem consists of phytomers) or association (e.g., a lamina is associated with air temperature). Each root is divided into successive root segments, each segment corresponding to the root part elongated during one time step of the model.

## ILLUSTRATION OF MODEL BEHAVIOUR AND MODEL EVALUATION

### *Illustration of model behaviour*

GRAAL was parameterized for maize plants essentially from literature data (see Drouet and Pagès 2003). For our purposes, the time step of the model is one day. Day length is 12 h. To simplify the analysis of the results, air (respectively soil) temperature was kept constant: 20°C (respectively 18°C) for all simulations. The duration of each simulation is 80 days corresponding to the silking stage. Two contrasting radiation regimes were determined from results obtained by Drouet et al. (1999) within a stand of 10 maize plants $m^{-2}$: for one plant from sowing to silking, daily average *PAR* per unit leaf area decreased exponentially from 530 (respectively 810) μmol $m^{-2}$ $s^{-1}$ to 20 (respectively 90) μmol $m^{-2}$ $s^{-1}$. These two *PAR* regimes are now referred to as 'low' and 'high' *PAR* respectively.

GRAAL simulates organ and plant morphogenesis and has been designed to be coupled with three-dimensional (3D) models of the shoot (Drouet 2003) and root (Pagès et al. 1989) systems (Figure 2). Then, this coupled model can be associated with a light model (Chelle and Andrieu, this volume) and a soil model to investigate the exchanges between plant and environment at the organ level. The model also simulates the dynamics of dry-mass partitioning between individual organs within the plant and accounts for changes in dry-mass partitioning according to *PAR* (Figure 3).

### *Model evaluation*

This type of model allows the generation of detailed virtual plants, and many outputs can be obtained at various scales, from the organ to the plant and crop. Its full evaluation is a long and complicated task and should be guided by the specific objectives of any given study. As a general strategy, we suggest several steps in any one evaluation procedure. First, sensitivity analyses are required to analyse the general behaviour of the simulated plants in relation to changes in carbon availability (Figure 3 serving as an example). Moreover, qualitative comparisons are possible by using the large number of experimental results from the literature.

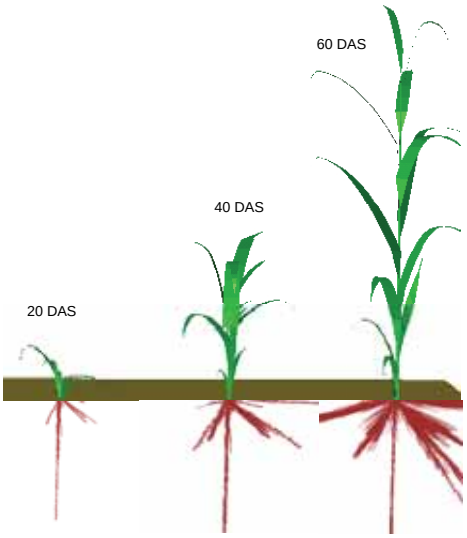


***Figure 2.*** *Simulation of organ and plant morphogenesis by GRAAL coupled with 3D geometrical models of shoots and roots. Presented results are for three developmental stages (20, 40 and 60 days after sowing, DAS) of maize plants grown at low PAR (see text for details). Plants are visualized using the Freeware program Geomview (http://www.geomview.org/)*

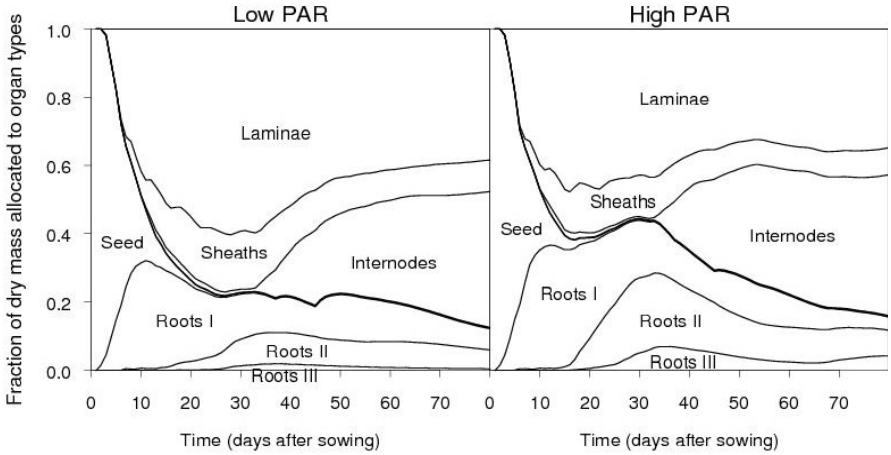


***Figure 3.*** *Simulation of dynamics of dry mass allocated to organ types of maize plants grown at low and high PAR. The area between curves corresponds to the dry mass allocated to the indicated organ types: laminae, sheaths, internodes and roots of first, second and third order*

Second, it is important to validate such a model as regards its ability to predict the kinetics of global variables like root and shoot biomass (or root:shoot ratio). This can be done by comparing model outputs with literature data and with outputs from other models like CERES (see Figure 4 left). Third, evaluation at the organ level on given genotypes and under given environmental conditions requires specific experiments in which plant development is monitored (Figure 4 right).

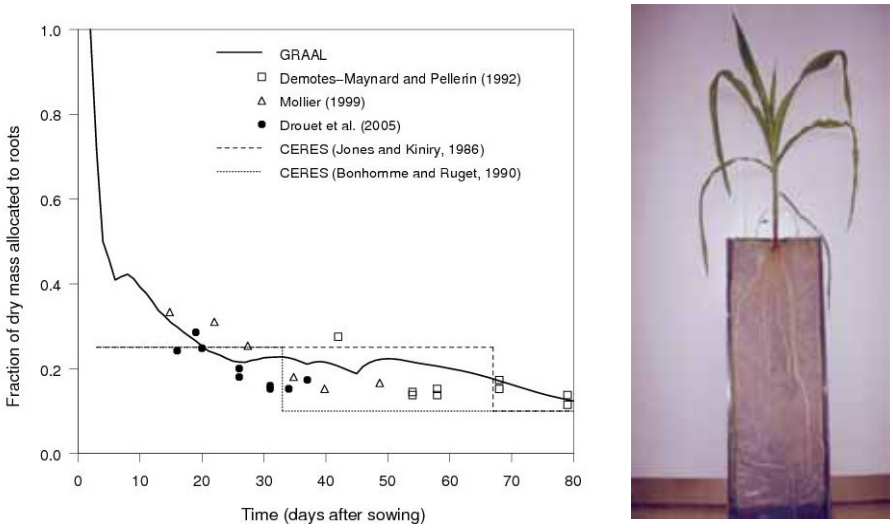


***Figure 4***. *(left) Evaluation of the model for dry mass allocated to roots and shoots; (right) experimental design using rhizotron in a controlled growth chamber to monitor plant development (e.g., maize plant at 37 days after sowing)*

## DISCUSSION

GRAAL associates processes of organ production and processes of carbon partitioning between organs and integrates them from the organ level to the whole-plant level. In this respect, GRAAL contrasts with plant models that consider either morphogenetic processes alone (e.g. Diggle 1988; Kurth 1994; Perttunen et al. 1996; De Reffye and Houllier 1997; Prusinkiewicz 1999) or assimilate-partitioning processes without taking into account changes in plant morphology (e.g. Thornley 1972; Jones et al. 1986; Brisson et al. 1998; Tabourel-Tayot and Gastal 1998; Lemaire and Millard 1999). In addition to environmental limitations (e.g., temperature, soil resistance), source–sink limitations (e.g., light, $CO_2$, nitrogen nutrition) strongly determine organ development and plant plasticity. Organs represent numerous sinks competing for assimilates and differ in their relative sink strength and relative source activity. Since carbon assimilates are required within the whole plant, it was important to consider from the onset the shoot and root systems at a comparable level of detail. This feature makes GRAAL very different from most

architectural models that consider either the shoot system (e.g., for maize Fournier and Andrieu 1998) or the root system (e.g., for maize Pagès et al. 1989), but not both simultaneously.

In GRAAL, processes are formalized for each individual organ characterized by its specific properties: initiation rate (e.g., functioning of primary meristems essentially depends on temperature), growth processes (e.g., growth in length and carbon exchange), status (source or sink) and architectural position (e.g., leaf 11 is above leaf 10 and roots of the upper phytomers are larger). Since the organs have a different status at a given date, pooling them into plant compartments (leaves, internodes, roots; e.g., Thornley 1972; Jones et al. 1986; McCown et al. 1996; Brisson et al. 1998) precludes heterogeneity among compartments. By contrast, our approach emphasizes the fact that organs are well-defined entities that can be characterized through experiments by measuring variables and estimating parameters of clear morphological significance (e.g., final leaf length and root branching density).

Integrating morphogenetic development and allocation processes for shoot and root systems described at the organ level implies that a large number of processes are formalized. One could argue that the multiplication of the number of parameters may involve cumbersome experimentation and a risk of cumulated errors. These drawbacks are to a large extent overcome because this formalism, at the organ level, makes it possible to estimate more stable parameters. GRAAL hypotheses for organ initiation, organ extension and organ increase in carbon mass are relatively simple: each type of organ (leaves, internodes, roots) has a single curve for potential extension, and the shape of the curve for potential increase in carbon mass is unique for all organs. Only one central hypothesis is considered for carbon partitioning between each sink organ: carbon is allocated according to the potential demand of each organ and the ratio between total carbon availability and total carbon potential demand (i.e. source:sink ratio; see Marcelis 1993; Lacointe 2000). For root organs, potential growth demand depends on the status of the meristem where growth actually occurs, evaluated by the apical diameter (Thaler and Pagès 1998). This approach is acceptable for the root system as long as we are able to assume that all root meristems have the same status and develop identically. Conversely, the shoot system includes various types of meristems (apical meristem, leaf meristems and internode meristems) and such an approach cannot be extended easily at the whole-plant level. Thus, for the shoot system, we used potential growth functions depending on temperature alone. According to all the above hypotheses, the behaviour of the whole plant (architectural development, carbon partitioning, root:shoot ratio) is triggered by the local characteristics of the organs, the interactions between organs, and the integration of the processes at the whole-plant level. By using only a proportional allocation rule for all organs, changes in priority of carbon partitioning between organs result from changes in organ status over time. In this respect, each organ becomes a potential reserve compartment.

## CONCLUSION

GRAAL integrates processes of organ production and carbon partitioning described at the organ level, both interacting at the whole-plant level (i.e. shoot and root systems). It associates the two separate approaches to characterize growth as an increase in surface or volume and as an increase in dry mass. GRAAL is a useful tool for improving our understanding of processes involved in plant functioning and their regulation by environmental and endogenous factors. It has been developed to be generic with concepts and structure transposable to other crops and resources (e.g., nitrogen).

The ascending modelling process of GRAAL is parallel to the structure and function of a real plant and falls into line with the ascending approach used in systems biology. It is a good framework for discussions about processes of plant functioning between partners working in scientific fields ranging from genomics to agronomy and ecology. GRAAL can also contribute to current works aimed at distinguishing the effects of genotype characteristics from the effects of environmental factors involved in plant development (see, e.g., Dingkuhn et al. 2005; Hammer et al. 2005; Tardieu et al. 2005).

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