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# VIRTUAL PLANT MODELS FOR STUDYING INTERACTIONS BETWEEN CROPS AND ENVIRONMENT

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## KEYWORDS

L-System, Crop Model, Virtual Plant, Ecophysiology,  
Agronomy

## ABSTRACT

Virtual plant models appear as powerful and appealing tools for plant scientists and agronomists, but actual examples demonstrating this usefulness are still rare. This paper presents and evaluates two applications. We developed a model of virtual maize, interacting with physical models for describing the plant environment. This allows simulating the evolution of a population in which growth and development depend on temperature and light availability at the individual plant level. In the first example, the model was used for simulating the evolution of a population, depending on initial conditions (e.g. sowing density) and the weather. The model was able to simulate the emergence of plant to plant variability, as a response to competition for resources. In the second example, model parameters were forced to follow field measurements. Model simulations then were used to investigate the relationships existing at the individual leaf level between light availability and leaf size. We demonstrated simple and robust relationships that point to original directions for the investigation of the physiological processes governing the regulations of leaf size. Finally it is concluded that virtual plant models based on ecophysiological responses, do represent useful tools to improve our understanding of plant functioning and plant-environment interactions. Obviously a lot remains to do to improve the biological realism of virtual plants models. This is a scientific challenge in plant sciences, and virtual plants make it possible to express and test hypotheses. We believe that this approach will help to improve our understanding of how local process results in properties observed at larger scale, and may show that the apparent complexity at these scale can be explained by relatively simple description of local processes and help to identify these processes.

## INTRODUCTION

In the context of agronomy, virtual plant models stand for 3D architectural models of plant development, which integrate, to a certain extent, ecophysiological knowledge of plant functioning. Such a definition apply to a variety of models, including physiological models operating on static 3D structure, probabilistic models of plant 3D morphogenesis

(insensitive to environment), or functional-structural 3D plants that simulate in detail interactions with the environment. The potential of virtual plant modeling in the field of agronomy has been reviewed by several authors (Goel et al. 1990; Room et al. 1996; de Reffye and Houiller 1997; Prusinkiewicz 1998; Hanan 1999). Several workers developed tools or 3D architectural models able of virtual experiments (e.g. Kaitaniemi 1998 and see references in reviews cited above). However, they are only a very few cases where a quantitative assessment of simulations has been considered.

Fournier and Andrieu (1998,1999) developed a 3D model of maize development, ADEL, which integrates known response of the plant to temperature and light intensity. Gautier et al. (2000) developed a 3D clover model including rules for response of individual organs to light quality, and checked whether this enabled to simulate the contrasted plant architectures observed in experiments.

This paper illustrates the interest of virtual plant models in ecophysiology, by considering two case studies in which ADEL was used. In the first case, the ability of the model to reproduce some plant or crop patterns as emergent properties of organ behavior was tested. In the second case, the model was constrained to simulate as close as possible the (measured) reality, and then used to retrieve other unmeasured variables.

## MATERIALS AND METHODS

### Model Description

ADEL-maize is an L-system based model of maize development. The model has been described in details elsewhere (Fournier and Andrieu, 1998, 1999), and only a brief description stands here. ADEL was developed on a modular basis. Main modules are

- A morphogenetic module predicting leaves and stem extension as a function of temperature. This module consists of a set of rules describing the coordination of organ initiation and extension, based on a potential scheme in which resources are not limiting. It takes a few genetic parameters as input and produces a thermal-time based schedule of development as output.
- A 3D geometric model of the shapes of maize organs. This module allows for a 3D representation of the organs as a function of their extension calculated in the previous

module. The 3D model is based on the work of Prévot et al. (1991).

- A simple carbon production and allocation model, which allows for computing mass growth of organs, as a function of light available at the plant level. This module is coupled with the morphogenetic module to introduce regulation of organ extension depending on carbon availability. This is achieved by calculating a carbon balance at each time step, and by applying a set of rules that slow extension in case of carbon shortage. Thus, thinner and shorter leaves are produced. In this simple approach, no remobilization of previously stored carbon is considered: only the carbon produced the same day is available for organ extension.
- Microclimatic models, derived from Cellier et al. (1993) and Chelle and Andrieu (1998), which allow for calculating light availability and temperature for plant development. These models operate on the 3D structure, so that physical variables are available at the individual organ or plant basis, from weather condition and the 3D structure of the set of plants.

The rules described above result in a key plant-environment interaction in which plant architecture both depends of previously acquired resources and determines the ability to acquire new resources. The real interaction involves several positive and negative feed-back loops and is not fully understood. Here it is approximated as a purely positive feed back loop, in which a shortage in resources decreases the ability of foraging further resources.

## Presentation of Case Studies

The first case study is the simulation of the competition for light between plants. The objective was to test whether the simple carbon balance model and the approximation of leaf size being depending on carbon limitation could reproduce known pattern of maize architecture when the sowing density (pl./m<sup>2</sup>) is varied. Weather data and genotype parameters were taken identical to a field experiment in which maize was sown at a range of density (Sonohat Popa 1997). Then model simulations were compared to experimental measurements of plant architecture.

In the second case, the aim was to further investigate the processes responsible for the regulation in leaf size that had been observed in the multi-density experiment. Thus, the loop simulating the regulation of leaf extension by carbon balance was deactivated. Instead, to achieve an almost exact simulation of the field experiment, measured data (final leaf size and information on kinetics of leaf appearance) were used to constrain the model. Thus, ADEL was used for reconstructing as close as possible the time course of plant architectures, based on measurements at discrete periods of time. Then evolution of light climate on individual leaves was calculated with a model simulating the distribution of light on the 3D structure. Finally, relations between observed leaf width and light available at the whole plant and/or the individual leaf basis were investigated.

## RESULTS

### Simulation of the Competition for Light

The model was tested by considering two effects of competition: mean effect on plant morphology and structuration of the population.

The effects of sowing density on morphology of leaves depend on their position along the stem (Sonohat Popa 1997). The size of basal leaves is not affected by plant density, as these leaves are the first to expand, i.e. extension takes place at a time when even high plant population does not result in significant depletion of resources. The higher the leaf, the larger the reduction in size. The model reproduces the observed trend quite well (figure 1). Model simulations show that expansion of higher leaves take place at increasing levels of competition for light between plants, and also at increasing levels of competition for resources between organs within a plant, due to the onset of stem extension. Finally, the model enabled to quantitatively relate the main spatial patterns to the timing of events: the observed effect of density on the vertical gradient of final leaf size can be explained by the time of organ extension, relatively to the timing of resources depletion and that of the evolution of number of active sinks in the plant. Some discrepancies exist however between simulation and measurements: irregular patterns in the simulated size for successive leaves result from numerical instabilities. It can also be seen that the model tends to underestimate the size of leaves, and that the effect of density first appears on a more basal phytomer in the reality (leaf 6) than in the experiment (leaf 9). Possible reasons for these discrepancies will be discussed later.

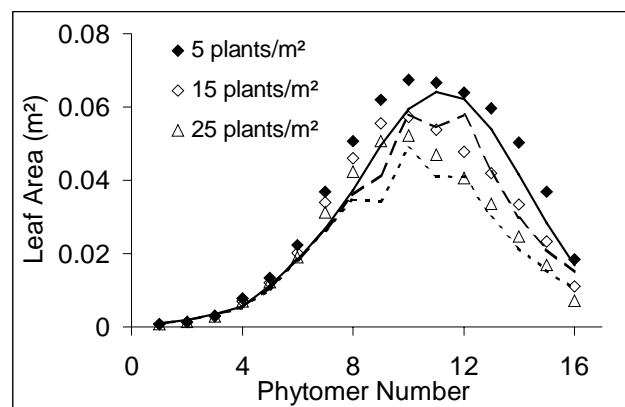


Figure 1: Leaf Area as a Function of Leaf Position for Plant Grown at Three Densities. Symbols are for Experimental Data and Lines for Simulated Values

Competition for resources also results in hierarchies, with dominant and dominated plants. Thus, in a plant population, variability between plants increases with plant density. It is difficult however to assess the role of individual capabilities (genetic parameters), initial conditions (e.g. late or soon emergence) or just “chance” in the development of these hierarchies. Here, starting from a population of identical plants (same model parameters) with minimal differences in

initial conditions, (same date of emergence, but some variability in leaf orientation) the model described above was able to simulate the development of heterogeneity between plants (Figure 2). The model also predicts that higher density results in higher variability and that, for the range of density considered here, the variability starts developing at the onset of stem extension (day 20 in figure 2). All this is consistent with field observation. The search for homogeneity in plant genotype, and the definition of field preparation and crop management methods ensuring homogeneous conditions have been an important aspect in agronomic research. This is still the case, although the trend also exists today to cope with variability, in order to reduce environmental costs. The model illustrates that small and unavoidable variability, which may be seen as “just chance”, may eventually results in large differences, when many individual are competing for limited resources. Finally this example shows that individual-based plant model can help to a better understanding of the processes involved in the behavior at the population level.

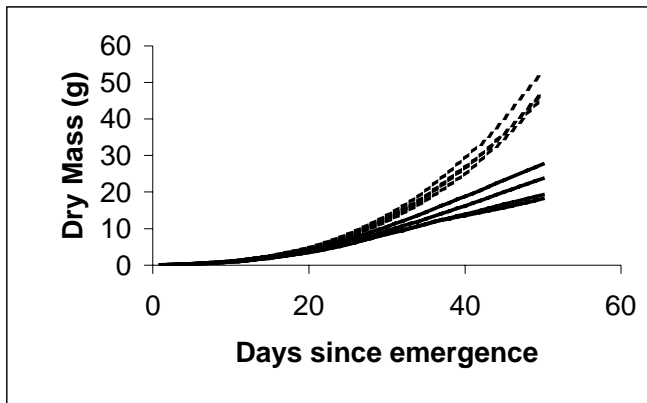


Figure 2: Simulated Dry Mass Accumulation of 4 Plants Grown at two Densities: 5 pl./m<sup>2</sup> (dotted lines) and 25 pl./m<sup>2</sup> (plain lines)

### Interpretation of Leaf Width Variation with Density

Variation in leaf area with plant density (Fig.1) is a known regulation observed in maize and a lot of other grasses. Narrowing of leaves, much more than shortening, causes the reduction in leaf area. In the previous section we have seen that a model in which leaf size was reduced according to daily carbon acquisition at the plant level gave a reasonably good account of leaf width measured in a multidensity experiment. However leaf narrowing, although correlated with resource depletion, may not or not only, be due to resources depletion. Plants have developed light sensors so that several adaptive processes take place before resource shortage, and actually enable to avoid, or to adapt to, this shortage. There is thus no proof that carbon availability, rather than, e.g., sensing of light is the responsible for regulation of leaf width. Moreover, regulating leaf width with carbon availability rises the question of multiple possible ways of evaluating available carbon and distributing it between growing organs. For instance, some authors have demonstrated that correlations exist between the size of a leaf initium, and the width of the mature leaf, so “initial conditions” probably play a role in the later distribution of resources. Moreover carbon stored in older organs could be

remobilized to sustain the growth of new leaves. Here we investigated the relations between the width of the mature leaf and the history of light climate on the leaf. For this, we suppressed the calculation of leaf width and length and instead the model parameters were forced so that model simulations reproduced as close as possible the experiment. Thus the model was used as a tool to reproduce the time course of the actual 3D structure. Then, using the light model, the amount of light on each leaf was calculated on a daily basis. The whole field is about 500 plants, and figure 3 shows a detail of the simulation. The field was organized in a circular pattern and distance between plants decrease from the border to the center.

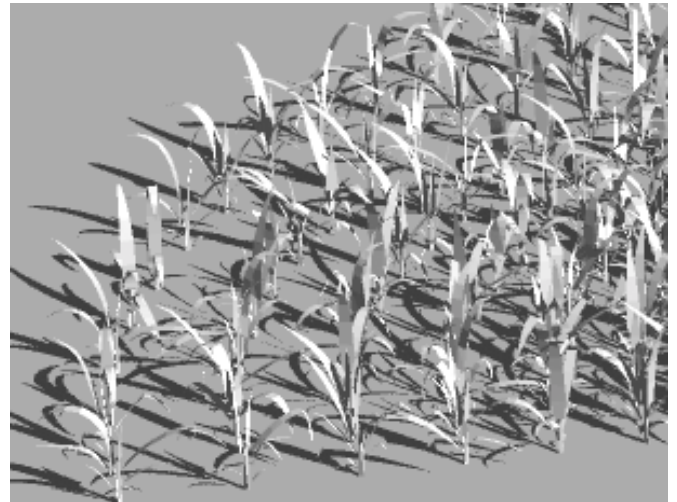


Figure 3: Computer Simulation of the Field Experiment, Shown on Day 40 after Emergence. For Clarity, just a Fraction of the Virtual Field is Shown

A simple relation was found between the final width of a leaf and the irradiance cumulated on that leaf from initiation to the end of the width extension. Relation holds for irradiance in photosynthetically active spectral domain (PAR : 400nm – 700 nm). Precisely, the final width of any leaf in the multidensity experiment could be expressed as

$$W_n = 0,139 \cdot \emptyset_n \cdot \text{Log}(E/E_0) \quad (r^2 = 0,943)$$

Where  $W_n$  is the measured width of a leaf,  $E$  is the calculated cumulated PAR irradiance on that leaf (MJ/cm<sup>2</sup>), subscript  $n$  refers to the phytomer number,  $E_0$  is a fitted constant ( $E_0 = 0,01434$  MJ/cm<sup>2</sup>), and  $\emptyset_n$  is a fitted function of  $n$ .

This finding can be interpreted as the final leaf width being the product of a potential depending on phytomer number (function  $\emptyset_n$ ), and of a function of the course of light climate on that leaf during the time of extension. Figure 4 shows the normalized leaf width ( $W_n/\emptyset_n$ ) as a function of  $E/E_0$ . Figure 5 shows the fitted function  $\emptyset_n$ . Interestingly,  $\emptyset_n$  resembles much to data of apex diameter at leaf initiation published by Bassiri et al (1992) (see inset in Fig. 5). Finally, this analysis enabled to find a simple and accurate empirical function to estimate variation of leaf width with density. Use of this function requires however to be able to calculate light climate on individual leaf, and thus necessitates a 3D plant model coupled with a light model. The simplicity and accuracy of the relation points to the physiological processes that could be responsible of this. No calculation of plant carbon balance

was required, simply the knowledge of the light climate on individual leaves. Moreover a log relation with irradiance was found, which is reminiscent to the log shape of response curve to signals that have been found for other physiological processes.

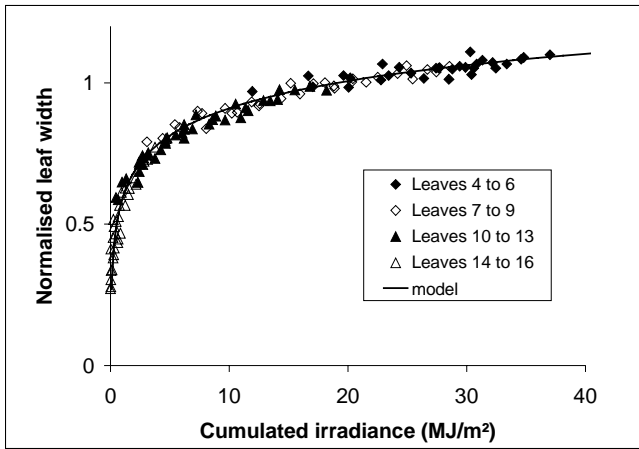


Figure 3: Normalized Leaf Width ( $W_n/\phi_n$ ) as a Function of Cumulated Irradiance

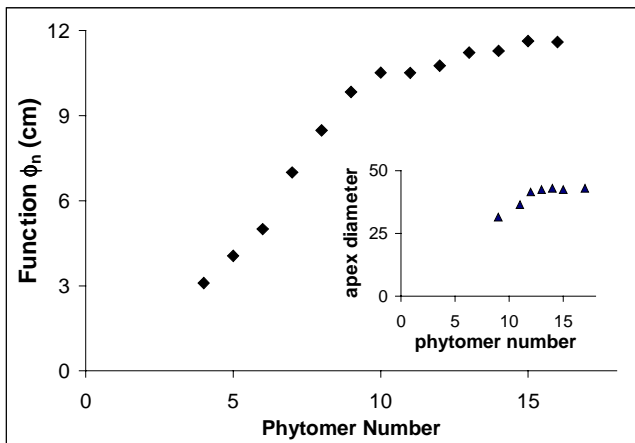


Figure 4: Fitted Function  $\phi_n$ .

Inset : Apex Diameter ( $\mu\text{m}$ ) at the Time of Initiation of Phytomer, from by Bassiri et al (1992).

## DISCUSSION

The model used here simulates the aerial development of maize, which is a relatively well known plant. It took however about 3 years to develop that model, which still ignores major parts of plant functioning, such as response to nitrogen or water. This shows that simulation of multi-specific canopies (for example maize-weeds interactions, or, more generally, ecosystems) with a level of accuracy of interest to agronomists is a long term objective. However, interesting research direction, such as here the possibility of creating hierarchies without significant differences in the potential of individual can rise from even very simplified models. Moreover, preliminary results indicate that, at the scale of organ functioning, similarity between species could be greater than at the scale of the plant as a whole. For example, on wheat (Ljutovac, pers. com.) or on fetuque (Durand, pers. com.), the patterns of organ extension are very

close to those of maize. At a given level of description, some generic rules may even apply to larger groups such as dicots or monocots. We also showed here that modeling plant behavior at the level of organs may not be more complex than modeling at the usual level where canopy is considered as an homogeneous entity. At least some of the ecophysiological responses appear simpler to understand and model when the plant architecture and the microclimate are considered in sufficient details, both for the time and space features.

Finally, the interest of virtual plant for plant scientist is not only in the application of these models, but also in the possibility to test hypotheses and in the research required for the development of the model. The objective of creating a virtual plant model that behaves exactly as its real counterpart is certainly still unrealistic. But this is true for any approach of modeling. We believe that acceptable compromises between complexity and accuracy can be found which will allow in the next future the development of a new generation of crop models, which simulate with more details plant functioning, but with simpler rules introduced in it.

In the short term, one promising application of virtual plant models could be the virtual simulation of experiments, as presented in the second example. It is today difficult to compare experimental results obtained in field experiment to those obtained in controlled conditions. This is, to a large amount, due to an insufficient accuracy in the experimental characterisation of environmental variables. It would be a huge work to monitor experimentally the light climate on all organs of a single plant. On the other hand, the physics of light transfer is sufficiently known so that an accurate description of canopy structure and the knowledge of light source characteristics enable to calculate in detail the distribution of light on a 3D structure. Research in progress aims to generalize this to others aspects of environment such as temperature and humidity. Thus “in silico” reproduction of actual experiments appears to us as a powerful tool to scientists wanting to investigate the biological processes.

## CONCLUSION

The two case studies illustrate two applications of virtual plant for agronomic and ecophysiological issues. Realist rendering allowed by such models might create the confusion that such modeling approach can or should be also totally “exact” from a biological point of view. This is probably too high a requirement, as it would be for other models in biology. However, compared to usual crop models, this approach do enable to better take into account spatial and temporal processes in plant and plant population, and thus the interactions within the plants or between plants and their environment. This allows to better express knowledge or test hypotheses on biological processes, and help making the bridge between several scales, from organ to plant and population. Virtual plants can also be of great help in the interpretation and analysis of real experiments and we believe that this field of application could have a high practical value in quite a short term. Research is needed to make virtual plant models more biologically faithful, robust, easy to fit to measured data, and versatile to a wide range of species. This is of interest, not only for the sake of accuracy

of model prediction, but because it represents a better understanding of processes central to biological sciences.

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