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BASIC CONCEPTS OF COMPUTER SIMULATION OF PLANT GROWTH

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ABSTRACT

The experimental study of plant growth and architecture requires two consecutive and complementary approaches. The first one is qualitative and botanical. Through this qualitative analysis, it is possible to divide a tree into botanically homogeneous subunits. The second one is quantitative. Modelling of the functioning of meristems based on stochastic processes has been carried out in the Laboratoire de Modélisation of CIRAD (1980-1999) in combination with extensive experimental work on temperate and tropical plants. Calculations involved in the tree simulations from field data are based on the probabilistic Monte Carlo method for the topological part and on analytical geometry for the morphological part. Data, such as length, angles, elasticities, tropism, are necessary for geometric construction of the plant. The growth model, together with the geometric calculations enables a random plant simulation in 3-D according to geometry for the morphological one. Computer graphics methods are then used to visualize the computed plant (perspective, colours, texture, shadows); they require special programs and graphic computers.

INTRODUCTION

Much progress has been made in understanding tree growth and architecture over the past 30 years. In 1970, a school specialized in morphological descriptions of tree architecture was founded by Hallé in Montpellier, a city known for its botanical studies for over 10 centuries. Hallé *et al.* (1978), defined the basic concepts of architectural analysis, i.e. the architectural model and reiteration, which we will discuss further on. Botanists of this school developed a rational scientific method for visual representation, which is capable of expressing the main elements and growth strategies of trees.

In the field of computer-generated images, computer graphics of trees generated from algorithms already exist : specific branching processes (Kawaguchi, 1982; Aono and Kuniik, 1984), graftals (Smith, 1984), paracladial systems (Lindenmayer, 1976, Prusinkiewicz and Hanan, 1989), fractals (Oppenheimer, 1986), combinatorial trees (Eyrolles *et al.* 1986) and thin transparent ellipsoids (Gardner, 1984).

Although these models are interesting from an algorithmic point of view as well as far their graphic results, they lack through botanical base and an experimental approach. Except for the case of small plants which are obviously easier to model (Prusinkiewicz *et al.* 1988), the trees created may only be seen from far, since details of the mathematical algorithm that produced them predominate when the trees are viewed at close quarters.

At CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement), the Modelling Unit has formed a team of 20 researchers specialized in four different fields - botany, agronomy, mathematics and computer sciences - for quantitative approach to this problem. Our belief is that a well-balanced interaction of these disciplines is necessary to establish the fundamental principles of growth simulation and plant architecture (de Reffye *et al.* 1988). In this paper we present the current status of our investigations.

BOTANICAL BASIS OF PLANT ARCHITECTURE

Hallé has grouped all the known vascular plants into less than 30 architectural models according to simple morphological characteristics (samples are shown in Figure 1). Each of these models corresponds to a particular combination of the different possible types of axes.

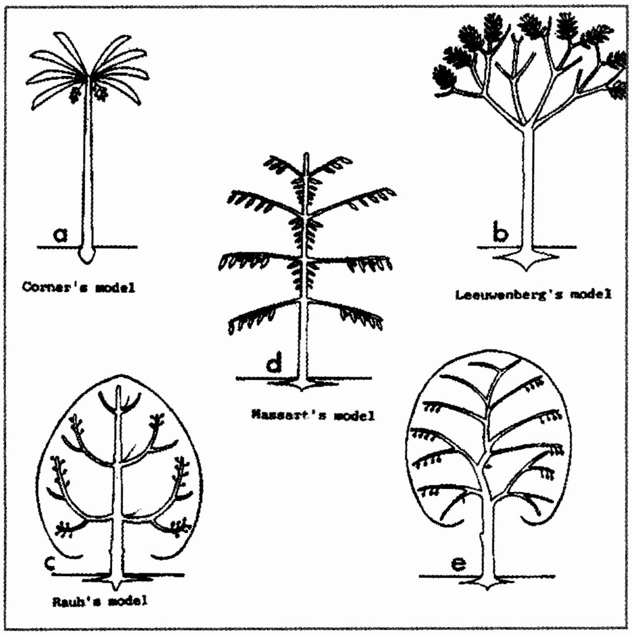


Figure 1. Architectural models.

This concept does not correspond to the conventional concept of habit since several models can exhibit a similar shape even though they function differently.

The hierarchy existing between axes clearly illustrates the concept of branching order (Figure 2) in monopodial trees, studied in particular by Edelin (1984). The trunk is, by definition, an order 1 axis and the axes it bears are order 2 axes, etc. The different axes of a given tree have specific morphological features and can thus be grouped into categories. The description of all the categories of axes of a tree belonging to a given architectural model represent its specific architectural unit. These categories of axes are often linked to the concept of branching order.

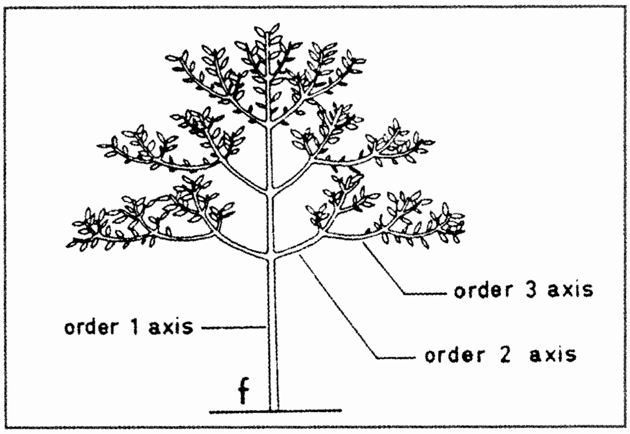


Figure 2. The concept of branching order.

The architectural unit of a tree does not usually allow it to grow past a certain stage. After the tree has reached a certain size it may duplicate its architectural unit according to a specific inherent strategy, referred to as "reiteration" by Oldeman (1974) (Figure 3). A tall tree is thus a stack of reiterations, each of them representing a repetition of the architectural unit.

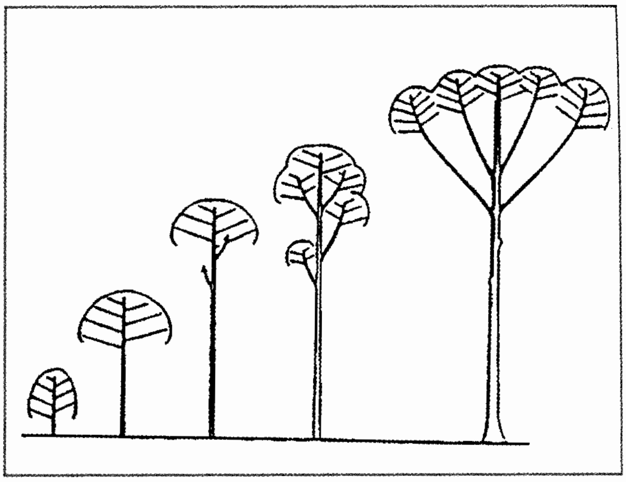


Figure 3. Growth and reiteration.

STOCHASTIC PROCESSES FOR MODELLING THE FUNCTIONAL FEATURES OF MERISTEMS

Qualitative description of meristem structure and functional features

Quantitative modelling can only be based on numbers characterising measurable events. Qualitative analysis, as described earlier, enables grouping of tree axes into homogeneous populations, and provides an essential starting point.

For us, the basic event is the appearance of a new internode at the tip of the leaf axis and its associated node which bears the axillary elements (buds, inflorescences). This event results from terminal meristem activity and it characterises the growth process.

The axillary buds formed in the leaf axis can remain dormant during a certain period of time. Their development into an axis marks the branching process.

During the final phase, the meristems die, and the axes undergo self-pruning. This is the mortality process. Growth, branching, and mortality are the three processes that affect the life of meristems.

Their qualitative formation, described in detail by Rivals (1965), must be observed to model their functional patterns.

Minute embryonic leaves, separated by very short internodes, are produced in the buds by the terminal meristem according to a certain rhythmicity (apical growth). These productions, produced in the bud by organogenesis, are referred to as the preformed part.

The production of new elements is invisible to the observer. Only the elongation and unfolding of the stock of preformed organs (internodes and leaves) can be seen (internodal growth). This elongation may affect some or all existing preformed organs. Elongation is limited by organogenesis. These two types of activity are not necessarily synchronised. The portion of axis that separates two growth cessations of the meristem is referred to as a growth unit (GU).

Random characteristics of meristem activity

This morphological description of terminal meristems corresponds to queuing theory. Apical growth is, by analogy, the law of customers' input ; the stock of internodes produced, those who are waiting in line to be served; elongation, the system's law of customers' output.

In practice, only the law of output can be observed. Experimentally, this law appears to be random. Therefore, if the internodal growth of a population of leaf axes, measured in internodes (belonging to the same clone of the same age), is observed during a given period, we notice that the latter are distributed according to characteristic bell-shaped curves (Figure 4a). Experimentally, it is impossible to predict the number of internodes the meristem will lengthen ahead of time.

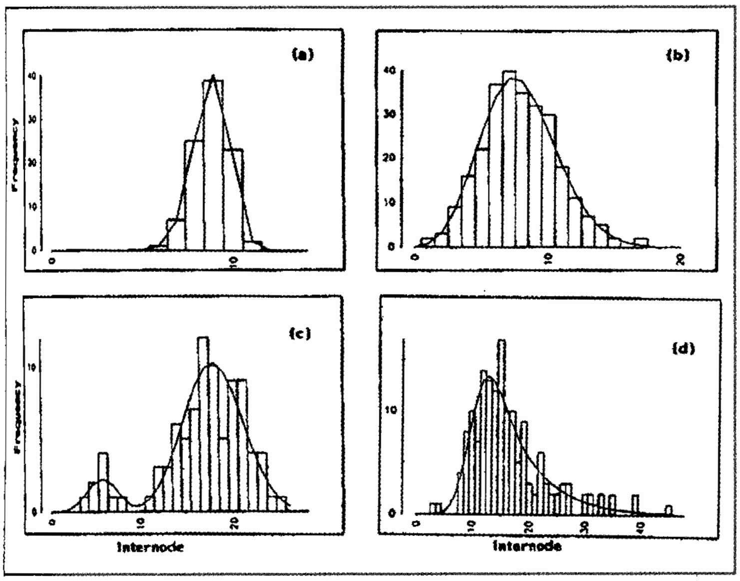


Figure 4. Statistic evolution of number of internodes/GU. (a) Young cocoa tree. (b) Litchi tree. (c) Wild cherry tree. (d) Apricot tree, (I) Frequency; (-), internode.

It is also important to point out that plants are highly dependent on their environment. The development of the aerial structure depends on the soil root system, and atmospheric interactions with the canopy and the environment.

Therefore, the parameters measured are essentially related to exogenous conditions. This phenomenon makes it possible to compare the functional pattern of a given plant under different cropping conditions so as to optimise these conditions.

MATHEMATICAL MODEL AND ITS VALIDATION

Poisson process and its breakdown

When there is a sufficient stock of preformed internodes, two successive internodes can appear almost simultaneously. When this is not the case, a minimum time interval is necessary for production and elongation of the internode.

It should be pointed out that in all cases observed in plants the discretization of time in regular intervals, characteristic of binomial growth, closely approximates the continuous growth process. Moreover, it simplifies the simulation methods (the Poisson distribution can be approached by the binomial distribution).

Interaction between the growth and cessation processes

When the growth process of a population of homogeneous leaf axes is interrupted at the same date, the internodal distribution can be observed directly (Poisson, binomial).

If the growth cessation periods are arranged according to a distribution, we will obtain a mixture arising from the combination of the growth distributions of the subpopulations interrupted at each cessation.

Experimental observations of the number of internodes/GU

There are two main types of growth units from buds of the same physiological age in the trees examined :

- GUs resulting from a single growth period of the meristems. The growth periods are of the same duration. The final distribution of the number of internodes therefore results in a Poisson or binomial distribution (e.g., litchi tree) (figure 4b).
- GUs resulting from several growth cessation periods during development. Several cases illustrate the meristem's aptitude to form a neoformed part after elongation of the preformed part during the springtime growth period (de Reffye et al., 1991b). When the elongation is accomplished, the elongation of the preformed part generally results in a binomial distribution.

Some of the meristems continue functioning as neoformations. Cessation of the neoformation in a tree can be almost simultaneous (e.g., binomial neoformation law in wild cherry tree) (Figure 4c), or staggered (e.g., geometric neoformation law in apricot tree ; in this case, the cessation probability is constant in neoformation) (Figure 4d).

GU metamorphosis in tree architecture

Along a tree's natural botanical gradients (deflection, branching order, acrotony on GU), the neoformed part decreases as the preformed part increases. At the same time, the internodes get shorter. This phenomenon was measured in particular on the elm tree, wild cherry tree, and poplar tree, it characterises the compulsory metamorphosis of a bud from the vegetative to the floral stage (figure 5).

In the trees that were studied, a progressive change of the parameters of the internodal distribution law is observed according to the physiological age of the GUs. Tree uniformity is due to the fact that this law applies to the entire tree, and characterises its functional pattern.

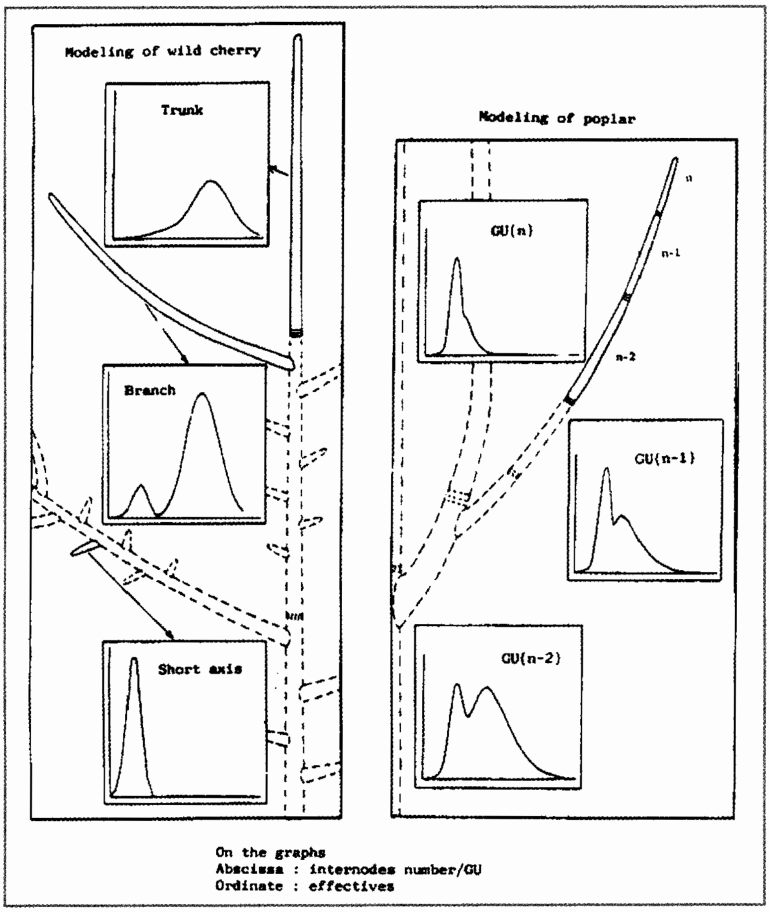


Figure 5. Distribution at different branching orders.

Appearance law for new GUs

Appearance of new GUs is similar to internode elongation, but at a different scale. In tropical trees (litchi, rubber tree), the process from GU to GU is close to a binomial process. The coffee tree is a special case since its GU has only one internode. Binomial growth was studied for the first time with coffee trees.

The time interval between two successive GUs is variable: 15 days for the coffee tree. and up to several months for the litchi and rubber trees. For temperate plants, except for the juvenile polycyclisms, it is 1 year long.

The GUs are the visible marks of a tree's growth periods. In general, the separation between two GUs is marked by scars which remain visible for several years. For single trees, it is preferable to manage time according to the appearance of GUs.

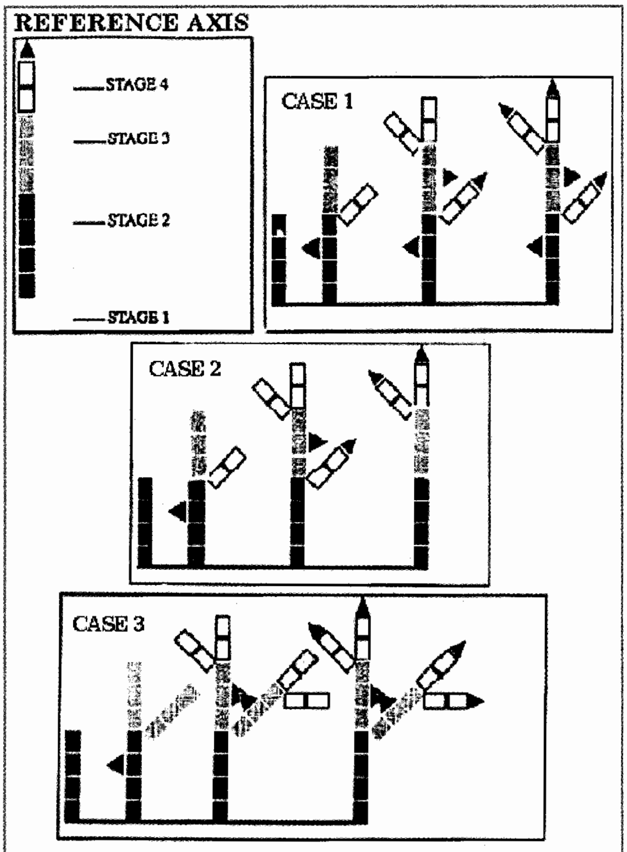
Branching process

The new internodes produced by the terminal meristem bear nodes with axillary buds at the leafy axes. Branching can be instantaneous (sylleptic branching) or delayed (proleptic branching). So, there is a budding probability for dormant buds in terms of time. With sylleptic branching, the branching test is done only once. If it is not positive, it will never bud. With proleptic branching, the budding probability is tested at each dimension unit.

In individualized GUs, the branching occurs in particular regions: terminal region, called "acrotony" (e.g., poplar tree, apricot tree) and median region, called "mesotony" (e.g., rubber tree). The branches can be grouped in packets along an axis and show significant correlations between successive branches. Sequences of branches can be analysed by Markoff chains, thus the branching process can be measured like growth and mortality processes.

REFERENCE AXIS

Studies of temperate crops and mature trees indicated the need to extend the concept of ramification order for describing a given plant. A mature order 1 shoot may have the same behaviour as an order 3 or 4 shoot. Similarly, an axis with an order 3 or 4 behaviour can appear on an order 1 axis (figure 6).



Case 1. Growth based on reference axis in the case of a plant presenting no self-pruning.
The trunk covers the whole reference axis step by step.
The jump made by shoots is dictated by an acrotonic gradient.
At each branching area the upper bud takes a jump up to stage 4.
When an axis reaches the last stage of the reference axis, plant stops growing.

Case 2. Same kind of process as in case 1, except that each axis undergoes self-pruning when reaching the end of the reference axis.

Case 3 Self-pruning occurs as in case 2, but the upper bud takes a local jump (reiteration) at every branching area.

Figure 6. Growth principle expressed by means of a reference axis in the case of a theretical plant showing 4 sucessive differentation stages.

The processes are thus described according to a unique, irreversible axis, termed "reference axis". The reference axis translates the theoretical processes that affect a bud from the seed to the flower (de Reffye et al, 1991a).

Laws governing bud activity are expressed as a jump along this axis. Growth is generally a short jump along the axis. Mortality - if it is not accidental - is a jump up to the terminal stage (flower).

The reference axis translates the notion of physiological age associated with a bud. It enables the description of growth strategies and overcomes the problem of reiteration (a reiteration is branching with a small or no jump along the axis).

The concept of the reference axis, which is fundamental to the description of bud activity, can also be extended to the geometric properties of the elements resulting from growth (e.g., angle of insertion of an axis, phyllotaxy, length, wood elasticity).

Simulation techniques

The simulation program is the same whatever the tree species is and is based on the reference axis and age data of the plant. It is divided into two parts: the topological part describes bud activity and the geometric part defines the spatial characteristics of bud activity.

Bud activity is simulated by the Monte-Carlo process in which random numbers are combined with stochastic laws of mortality, pause, and branching.

The simulation software is able to calculate the architecture of any plant defined by its reference axis parameters. Simulations based on different sequences of random numbers can also be compared. They reproduce the variability observed within the same species.

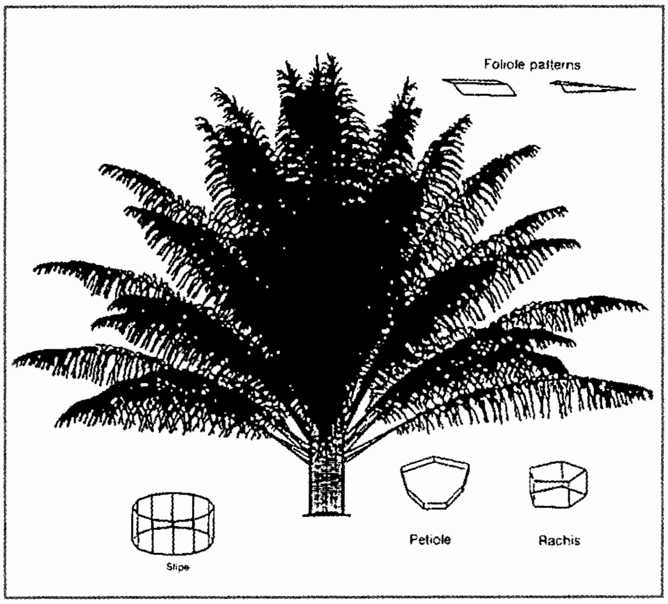


Figure 7. 3-D organs for the oil palm.

Structure of the simulation-based graphic database: the line tree

The simulated topological elements are stored in a line tree file designed by Jaeger (1987). The line tree contains all the information necessary for the representation of tree organs: transformation matrix, age of organs, symbol number, etc. It can be manipulated on a high level. It enables conventional sorting and geometrical operations.

The tree can be visualised by linking the line tree and a 3-D base of organs (leaves, internodes) on the display (figure 7).

TREES: FROM THE FIELD TO THE COMPUTER

In practice, the simulation is carried out in several successive stages.

- Botanical field observations provide accurate qualitative data concerning the architecture of a plant and its growth pattern.
- The plant is then numerically measured. The secondary axes are identified and described from the top downward according to their location along the main axes. Plant follow-ups are carried out. Distribution of the number of internodes/GU is recorded, as well as the location of the branches and meristem mortality. Geometrical measurements complete the data (length, angles of insertion, diameter, etc.). A database may then be created and interrogated to obtain statistics for events corresponding to a physiological age determined by the meristems.
- The third phase is the creation of a reference axis which is based on the different laws obtained from the trees and on their architectural evolution.
- The last phase is tree simulation on a graphic workstation. If the tree has been analysed correctly, the simulations should be very similar to the trees studied. A parameter file is then established which can accurately reproduce how this tree will develop in its environment.

SCIENTIFIC FIELD OF APPLICATION

Several sectors are concerned with applications of plant modelling: training, agronomy, landscape architecture and computer graphics. Development and architecture could be made attractive and educational if animated films were used to illustrate how a tree occupies space.

Films of this type are produced at the CIRAD Modelling Unit using stop-motion films of plant growth simulations of coffee, wild cherry, Japanese elm, litchi and other trees. The visualisation of the concepts defined by Hallé (architectural models, reiteration) helps to understand them.

The quantitative aspect of this modelling makes it particularly easy for applications. The plant is expressed locally by statistical distributions which characterise the random functions of actual events (formation of internodes, branches, etc.). These random functions express the interaction between the plant and its environment (figure 8). If, for example, the environment is modified (by controlled irrigation density agronomical experiments), its impact on the plant development can be directly and accurately visualised. Different controlled situations can be interpolated to obtain optimum cropping conditions.

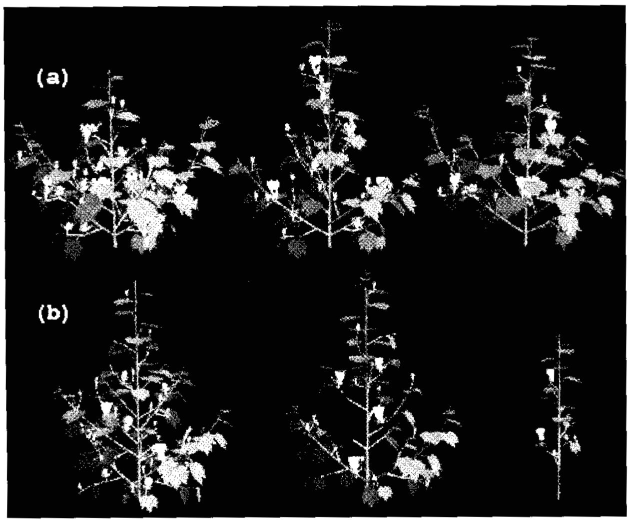


Figure 8.
(a) Three random simulations of cotton tree. (b) Simulation of density variation of the cotton tree.

Other types of applications are also possible: identification of yield factors (number of flowers produced, leaf area, wood volume), study of the genetic variability for the architecture of a species, and light interception by leaves.

The CIRAD Modelling Unit has studied industrial tropical and temperate crops.

Simulations by AMAP (Atelier de Modélisation pour l'Architecture des Plantes) software produced by the Unit are shown in the following figures:

Figure 9a. Textured details of an horsechestnut reiteration.

- oil palm (figure 7),
- horsechestnut flowering (figure 9a),
- oil palm root studies (figure 9b),
- aleppo pine (figure 9c),
- Japanese elm (from 2 years to 100 years) (figure 9d),
- natural forest landscape (figure 9e).

Figure 9b. Oil palm roots.

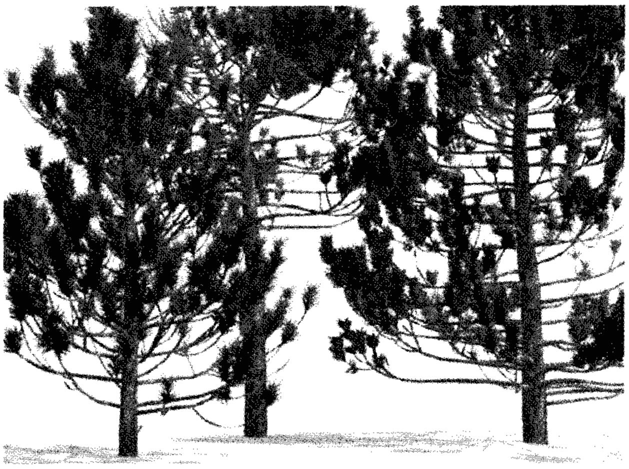


Figure 9c. Aleppo pine.

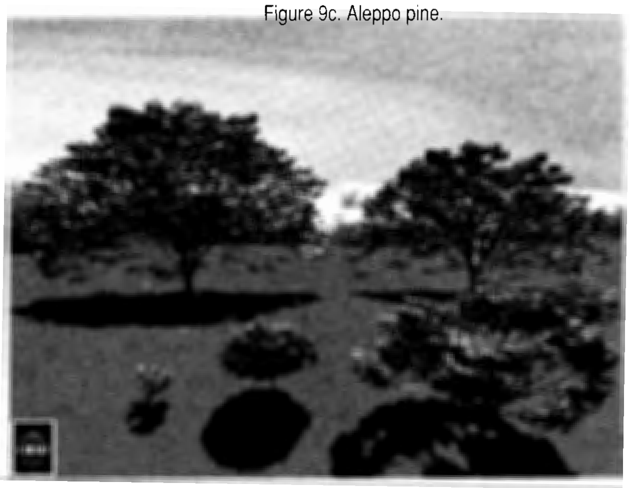


Figure 9d. Japanese elm tree.

Figure 9e. Chichibu forest (Japan), more than 50.000 trees.

With the AMAP program, plants can also be selected for landscape architects. Parks, gardens, and other open spaces in urban centre can be designed and their development predicted. This tool is quite helpful for landscaping because it allows professionals to find the best solutions and avoid mistakes. AMAP is also adapted to solve impact studies, such as road or railway layouts, as well as quarry projects with new vegetation planting (figure 10).

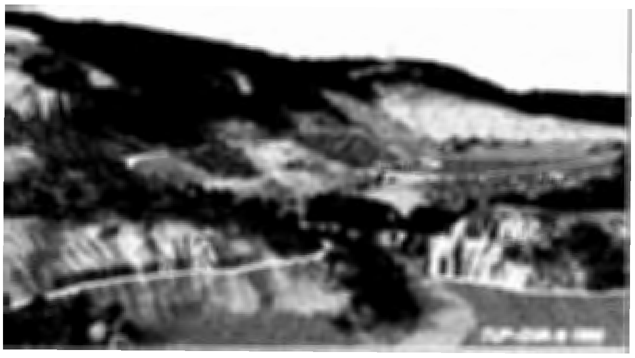


Figure 10. Quarry project supporting new vegetation.

The AMAP software is equipped with a regularly updated library of commonly used plants (trees, shrubs, flowers, grasses, etc.). It is easy to integrate in existing CAD programs.

AMAP has brought plants – real or imaginary – into the world of computer graphics. It offers live procedural objects for computer graphics, and contributes to the set of objects that modellers can use for scenario design.

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