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. Modeling of the functioning of meristems based on stochastic processes has been carried out in the Laboratoire de Modelisation of CIRAD (1980 1990) 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.

Key words. Plant growth; architecture; computer graphics; modeling; simulation; stochastic processes.

1.   Introduction

Much progress has been made in understanding tree growth and architecture over the past 20 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 Kunii 1984), graftals (Smith 1984), paracladial systems (Lindenmayer 1976; Prusinkicwicz 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 for their graphic results, they lack thorough botanical bases 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

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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 Modeling 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.

2.   Botanical basis of plant architecture

Halle 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. This concept does not correspond to the
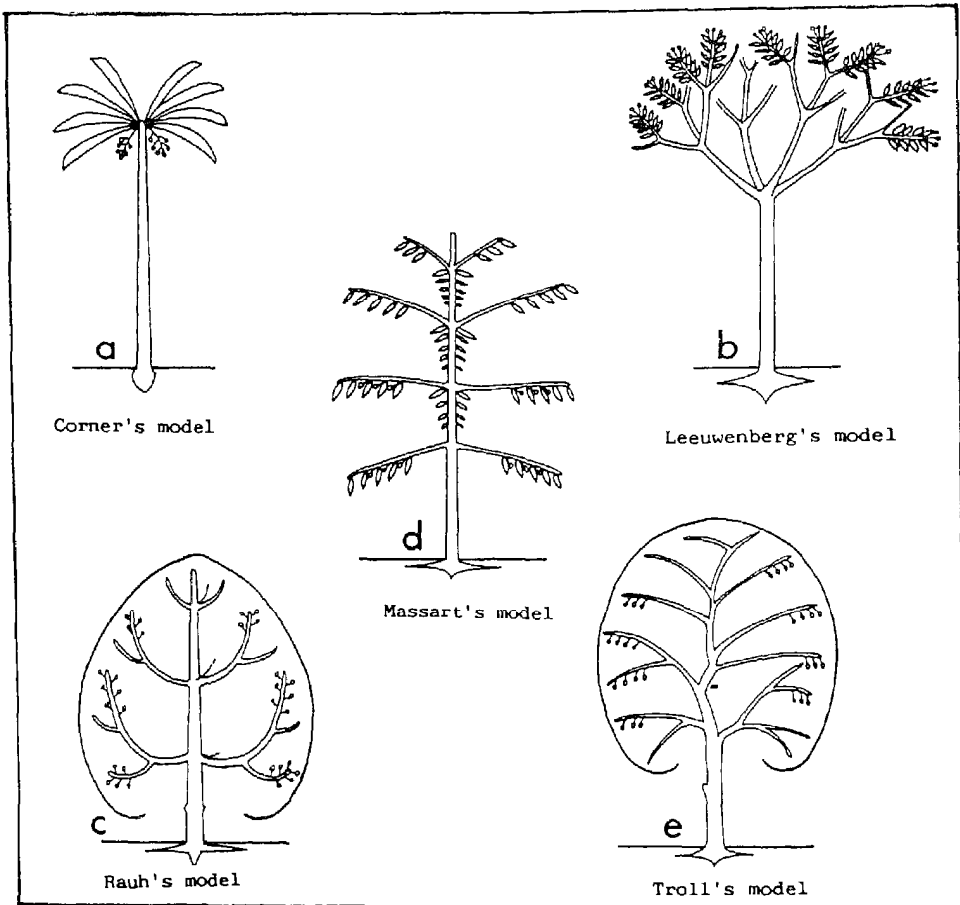

Figure 1.   Architectural models.

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 I 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.
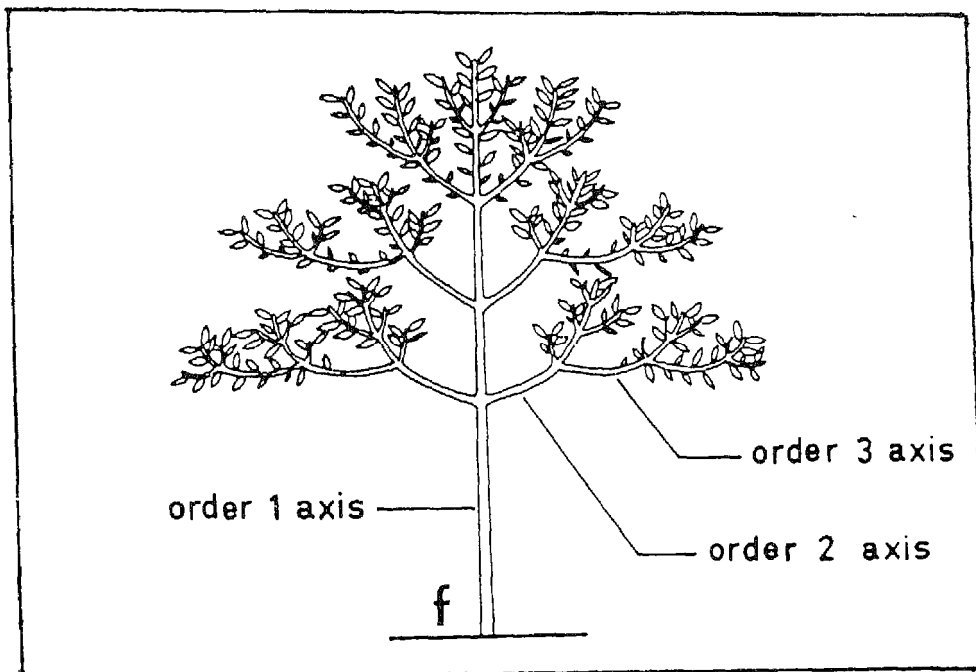

Figure 2. The concept of branching order.

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.

3. Stochastic processes for modeling the functional features of meristems

3.1 *Qualitative description of meristem structures and functional features*

Quantitative modeling can only be based on numbers characterizing measurable events. Qualitative analysis, as described earlier, enables grouping of tree axes into homogeneous populations, and provides an essential starting point.
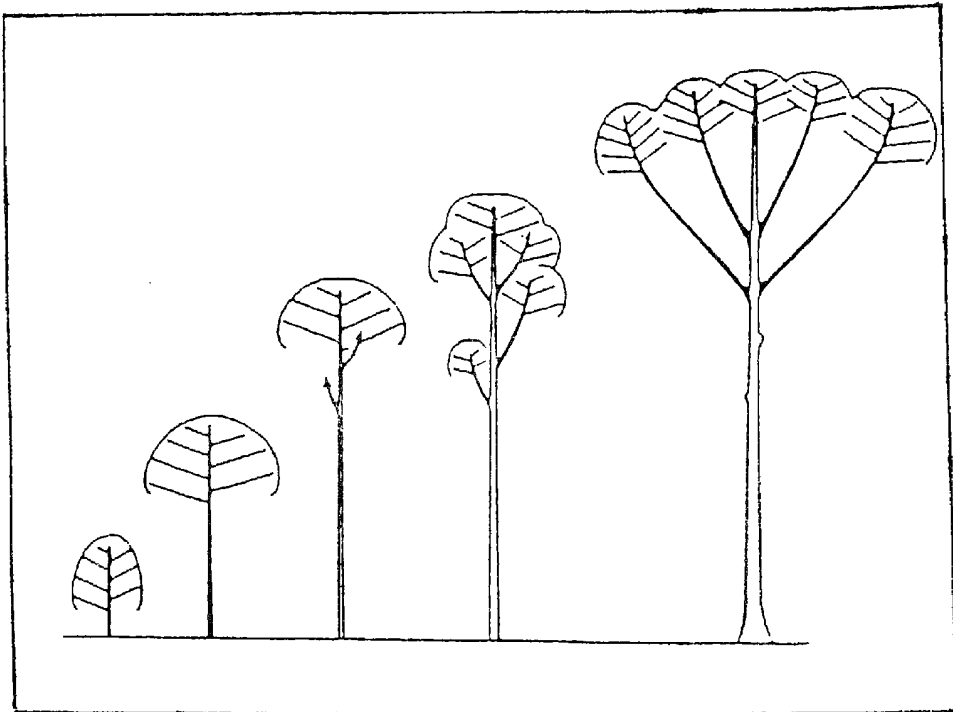
Figure 3. Growth and reiteration.

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 characterizes 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 synchronized. The portion of axis that separates two growth cessations of the meristem is referred to as a growth unit (GU).

3.2 *Random characteristics of meristem activity*

This morphological description of terminal meristems corresponds to queueing 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.
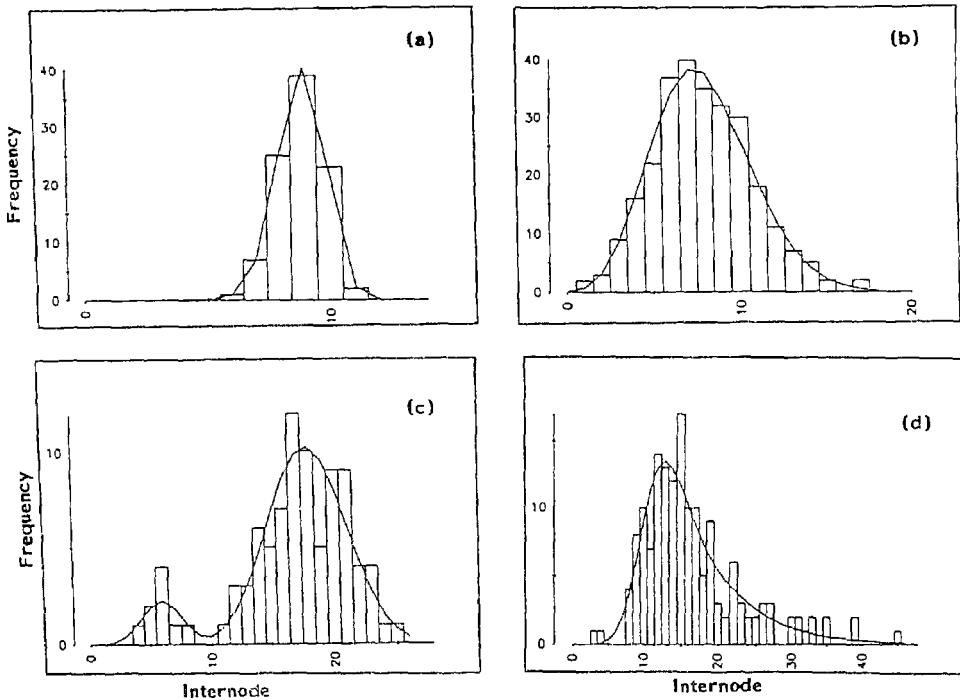

Figure 4. Statistic evolution of number of internodes/GU. (**a**) Young cocoa tree. (**b**) Litchi tree. (**c**) Wild cherry tree. (**d**) Apricot tree. (□), Frequency; (–), internode.

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 optimize these conditions.

4.   Mathematical model and its validation

4.1   *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.

   The time interval between two successive leaves is generally said to be distributed according to a random function, the first two moments of which are μ and σ.

   If the function is an exponential law, the law of occurrence at time t is a Poisson distribution. Feller (1950) showed that by using the central limit theorem, the law of occurrence converges to a normal distribution where:

> the average is $m = t/\mu$
>
> and the variance is $V = t\sigma^2/\mu^3$.

For longer time intervals between successive leaves with $V < m$, convergence to a normal distribution and the integer value of the number of internodes ensure good convergence towards a binomial distribution (N, b). Therefore

$$Nb \simeq t/\mu \ \text{and} \ Nb(1-b) = t\sigma^2/\mu^3$$

are good approximations. N corresponds to the number of artificial growth tests of the meristem called the "dimension". The associated probability b is called "meristem activity" and $1-b$, "rest probability".

   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 he approached by the binomial distribution).

4.2   *Interacction 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.

   The final distribution has a probability

$$P(X = i) = \sum_{n=i}^{s} P(N = n) \, C_n^i \, b^i (1-b)^{n-i}.$$

4.3   *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 arc 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* 1991 b). 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).

4.3a   *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 characterizes 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 characterizes its functional pattern.

4.3b   *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.

4.4   *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
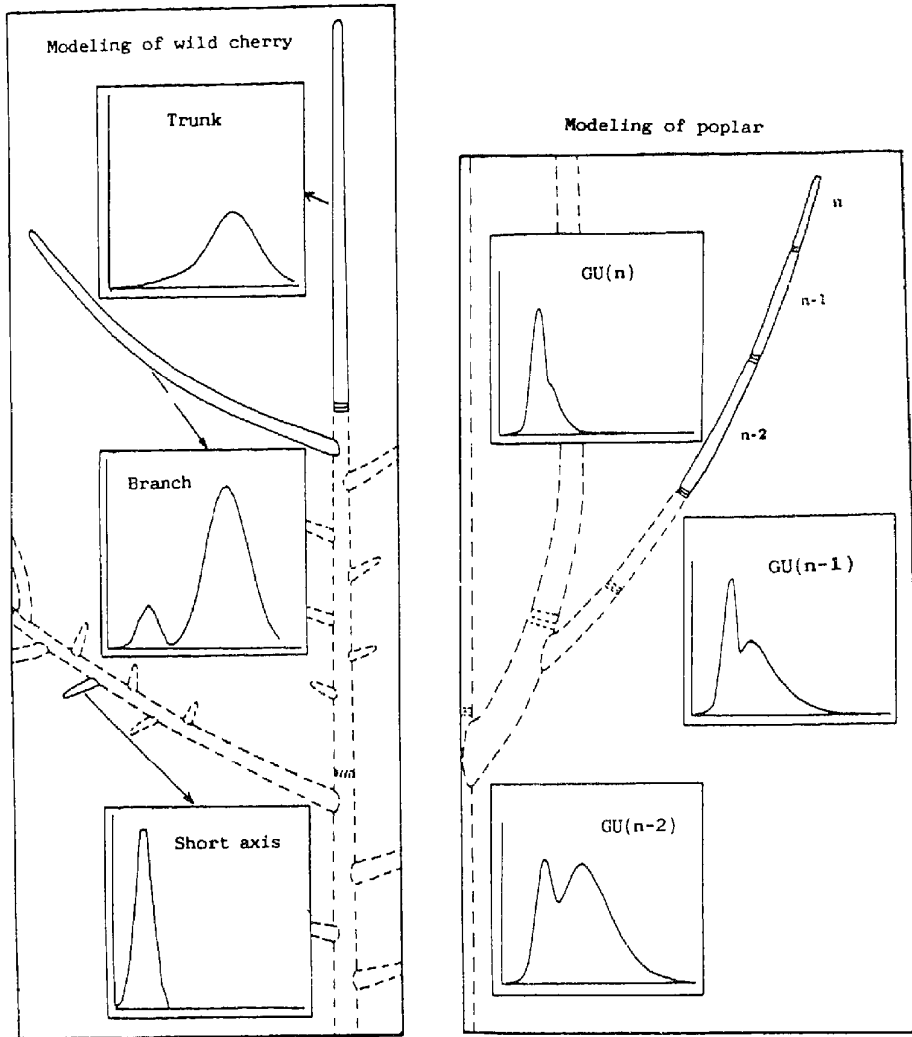
On the graphs
Abscissa : internodes number/GU
Ordinate : effectives

Figure 5.   Distribution at different branching orders.

successive branches. Sequences of branches can be analysed by Markoff chains, thus the branching process can be measured like growth and mortality processes.

5.   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).

The processes are thus described according to a unique, irreversibleaxis, 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 genérally 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).

5.1 *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.

Buds are processed in prefix order according to this simplified pseudocode:

> *While* there are buds to process, *do*
> > Bud viability test
> > *If* bud is still alive, *then*
> > > Bud growth test
> > > *If* bud is growing, *then*
> > > > Calculate bud geometry
> > > *End if*
> > > Bud branching test
> > > *If* bud is branching, *then*
> > > > Create a new bud
> > > > Process new bud
> > > *End if*
> > *End if*
> *End if*

In each test a random number is checked against the law governing the process at the current stage of the reference axis. Each test could produce a jump along the axis.
The geometry of each element formed from a bud is computed in two steps:

> > *If* element is the start of an axis, *then*
> > > Calculate axis orientation in relation to main axis
> > > Calculate effect of weight on new axis
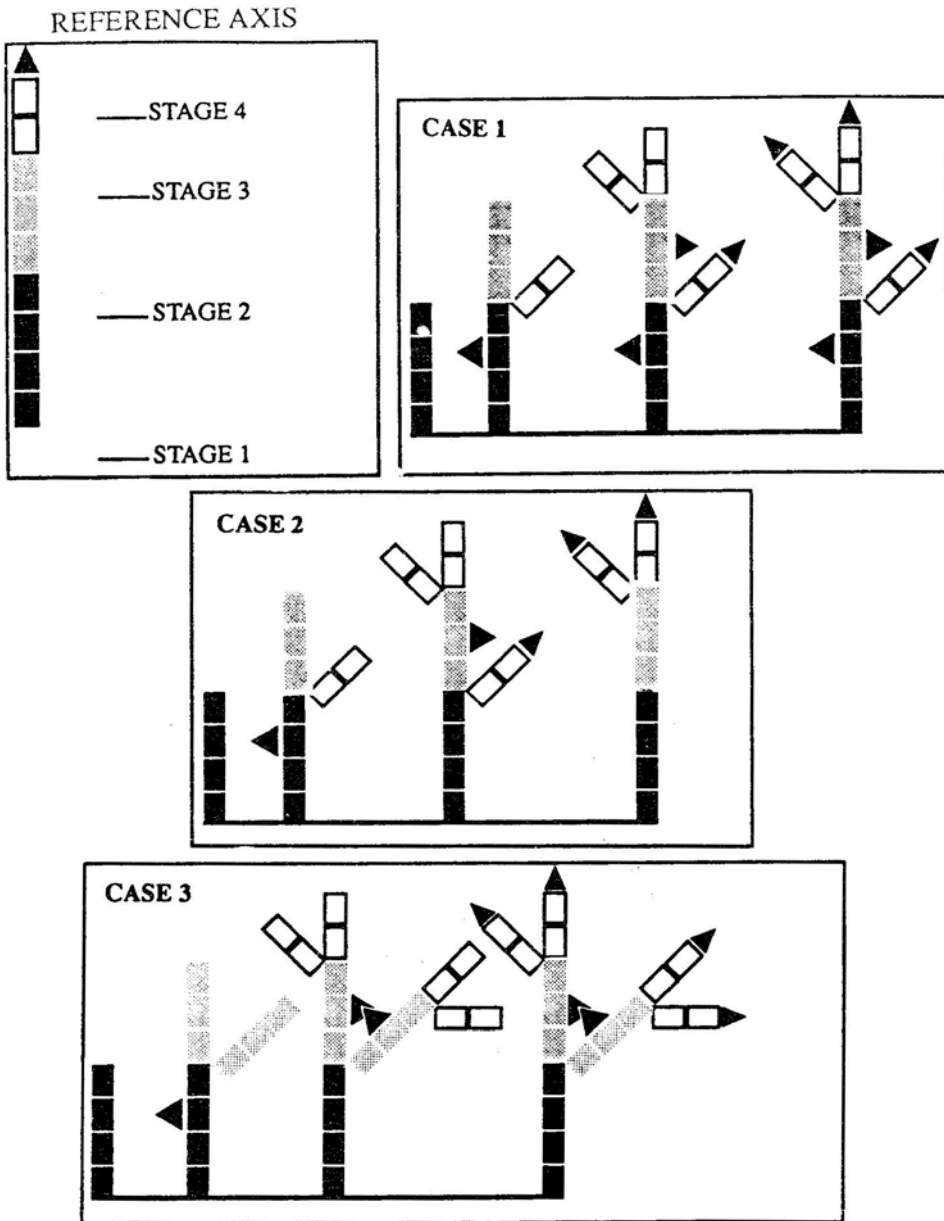> > *End* if
> > Calculate local deviation of element

Figure 6.   Growth principle expressed by means of a reference axis in the case of a theoretical plant showing 4 successive differentiation stages.

Case 1. Growth based on reference axis in the case of a plant presetting 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 every branching area the upper bud takes a jumpup to stage 4.
  When an axis reaches the last stage of the reference axis, plant stops growing.

Case . Same kind ofprocess as in case I, excep t 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.

Calculate scales (length, thickness)

Write result

The result of the simulation is a list of 4, 3 matrices describing the position and orientation of each simulated element. The simulation provides supplemental information such as the number of axes and flowers.

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.

5.2 *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 visualized by linking the line tree and a 3-D base of organs (leaves, internodes) on the display (figure 7).
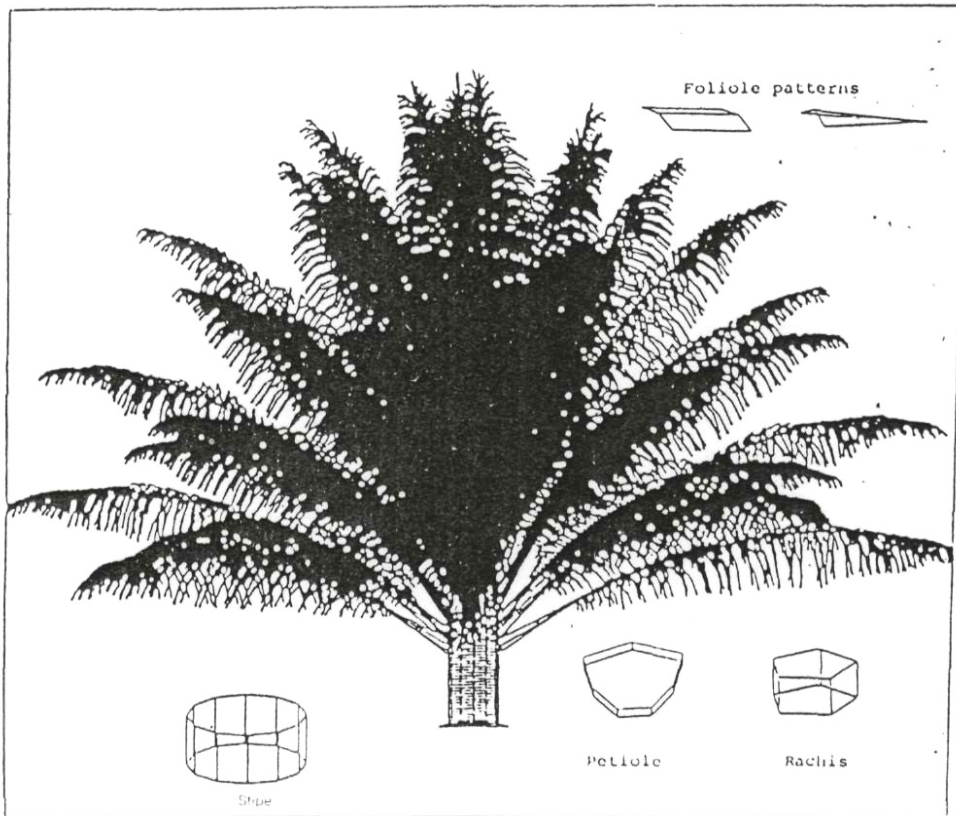

Figure 7.   3-D organs for the oil palm.

6. Trees: From the field to the computer

In practice, the simulation is carried out in several successive stages:
 (i) Botanical field observations provide accurate qualitative data concerning the architecture of a plant and its growth pattern.
 (ii) 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 he created and interrogated to obtain statistics for events corresponding to a physiological age determined by the meristems.
 (iii) 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.
 (iv) 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.

7. Scientific field of application

Several sectors are concerned with applications of plant modeling: training, agronomy, landscape architecture and computer graphics. Development and architecture could be made attractive and educational if animated films were used
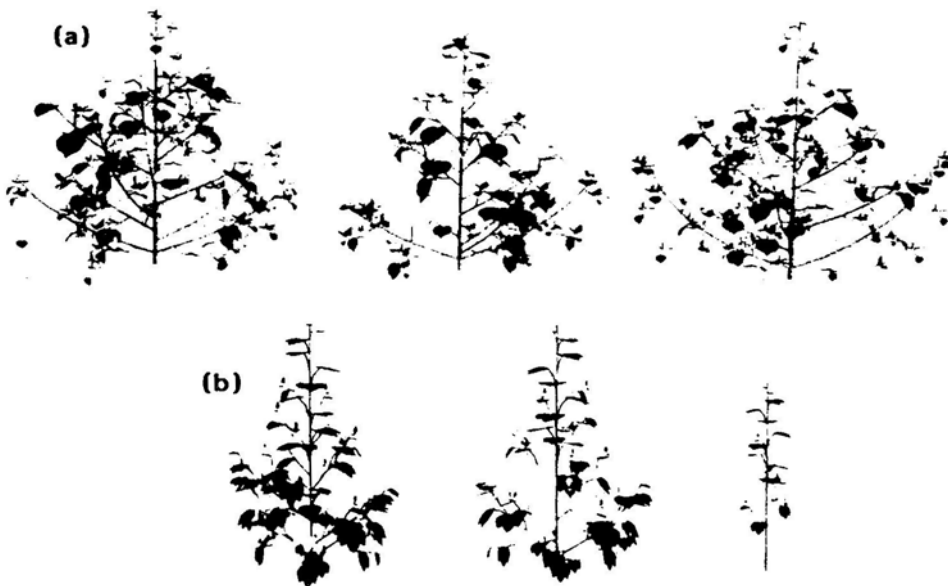

Figure 8.   (a) Three random simulations of cotton tree. (b) Simulation of density variation on the cotton tree.

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

The quantitative aspect of this modeling makes it particularly easy for applications. The plant is expressed locally by statistical distributions which characterize 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 visualized. Different controlled situations can be interpolated to obtain optimum cropping conditions.

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 Modeling Unit has studied industrial tropical and temperate crops.

Figure 9a. Begonia flower.

Simulations by AMAP (Atelier de Modelisation de 1'Architecture des Plantes) software produced by the Unit are shown in the following figures:
— oil palm (figure 7)
— begonia flower (figure 9a)
— growth of wild cherry (figure 9b)
— apricot (figure 9c)
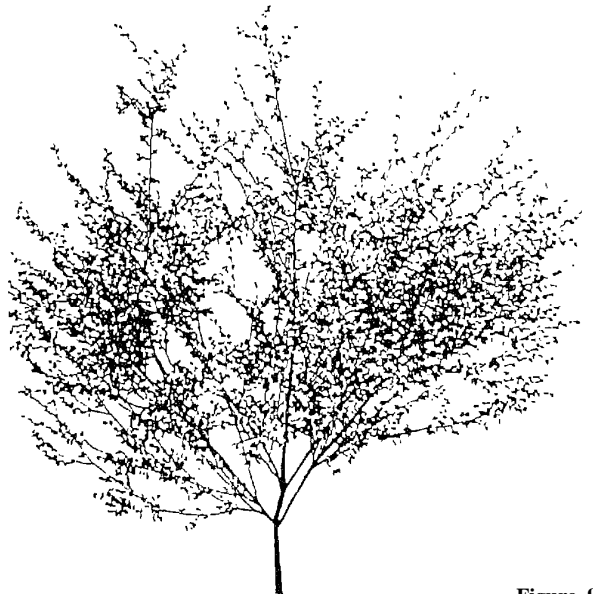

Figure 9b. Growth of wild cherry tree.

Figure 9c. Apricot tree.

– Japanese elm (at 2 years and 100 years) (figure 9d)
– Hevea (figure 9e)
For CAD applications AMAP is a useful tool for composing natural landscapes with seasonal changes. With the AMAP program, plants can also be selected for landscape architects. Parks, gardens, and other open spaces in urban centers can be
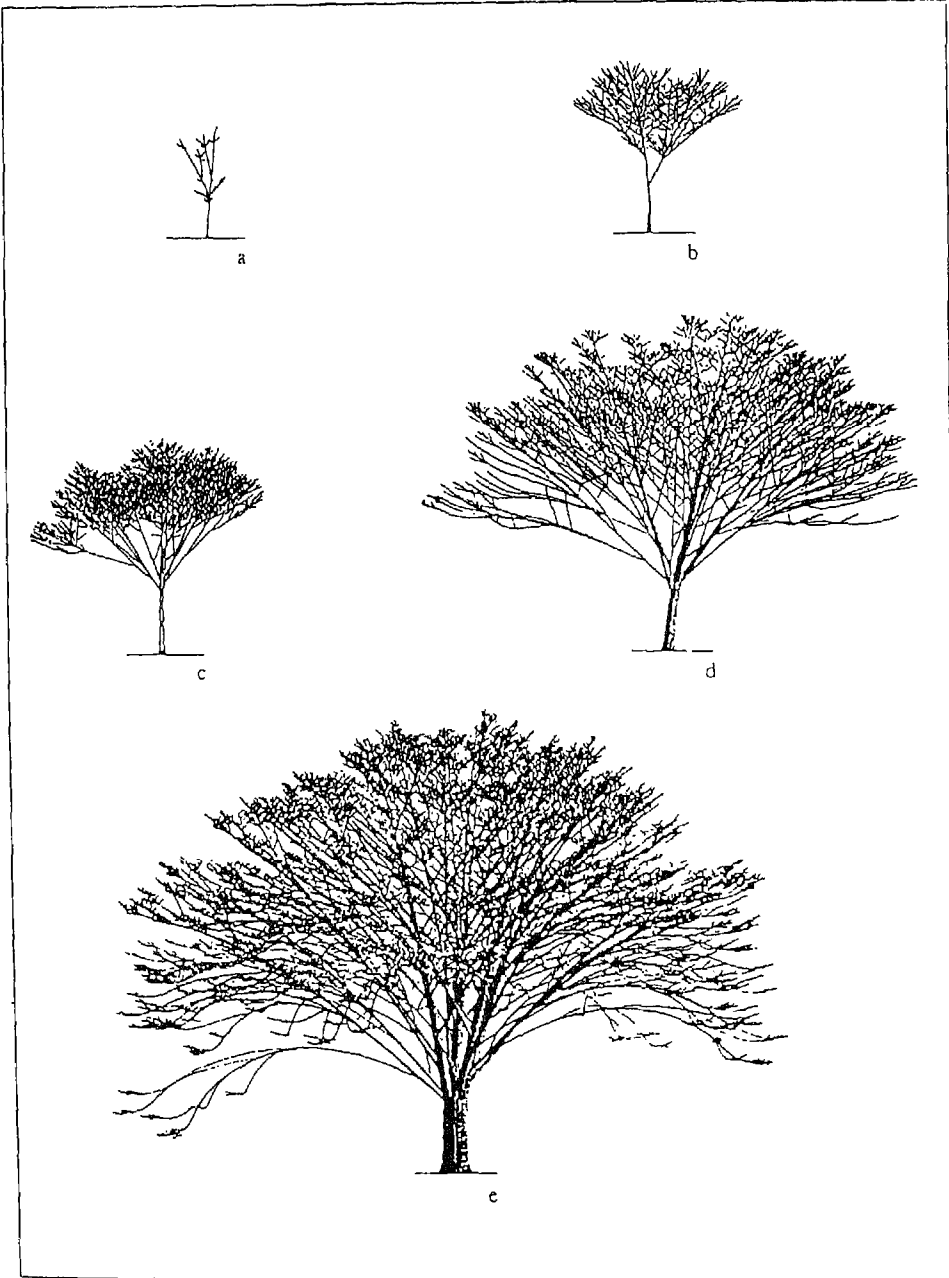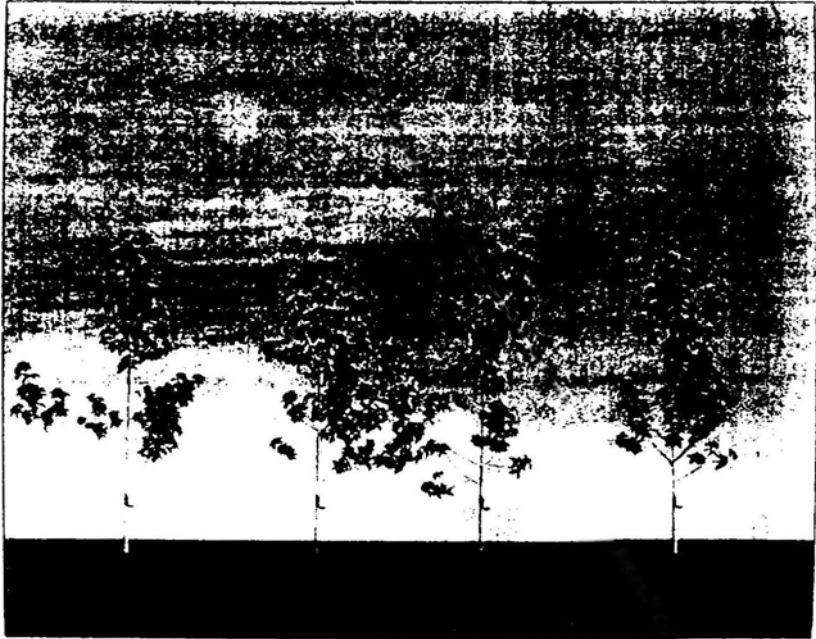

Figure 9d.   Japanese elm.

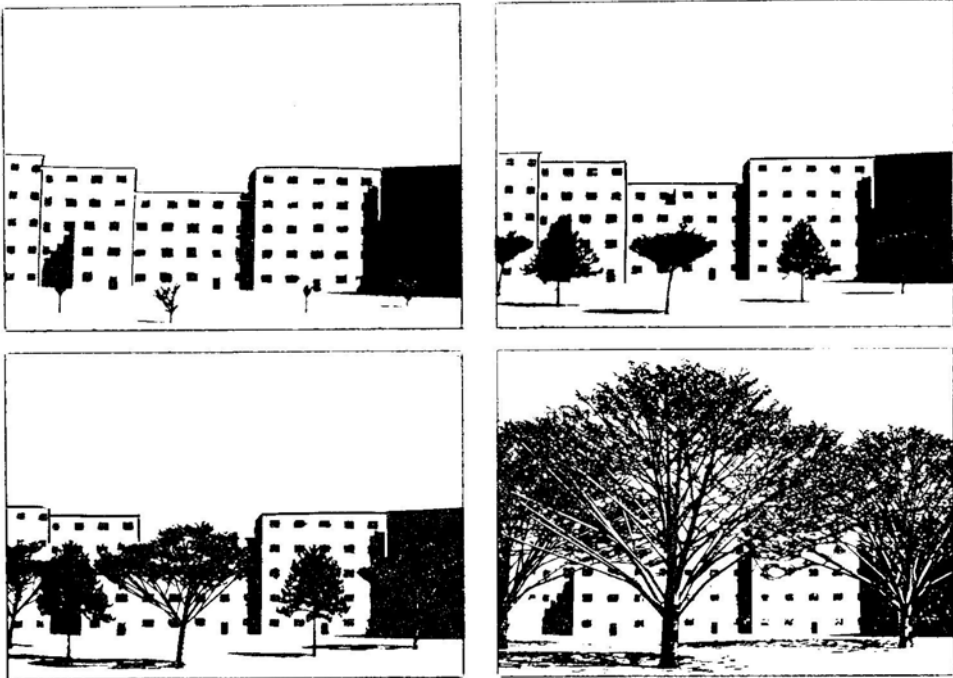**Figure 9e.**   Four simulations of hevea.

Figure 10.   Application to landscaping.
(Figures 1- 10 were designed by D Barthélémy, E Elguero, M Jaeger and M Gérenton of the CIRAD Modeling Unit).

designed and their development predicted. This tool is quite helpful for landscape architects because it allows them to find the best solutions and avoid mistakes (figure 10). The AMAP software is also 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 modelers can use for scenario design.

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