

Modelling plant growth and architecture: Some recent advances and applications to agronomy and forestry

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Modelling plant structure and growth has undergone major changes in the last decades along two major lines: the integration of ecophysiological knowledge in process-based models which often lack a description of plant topology and geometry, and the generation of 3-D virtual plants using morphogenetic models which simulate the architectural development in a stable and homogeneous environment.

There is now a trend to merge these two approaches, that is to link plant architecture and functioning. This trend is based on the recognition that plant structure: (i) is the joint output of the physiological processes (water and carbon balance, etc.) and the morphogenetic programme of the plant, (ii) determines the external environment of the trees which itself regulates their functioning (competition for space, light attenuation, etc.), and (iii) directly conditions the physiological processes within the tree (hydraulic structure, self-shading, allocation of photosynthates, etc.). Such models can be used in agronomy and forestry in various ways: to investigate the effects, local and global, immediate and delayed, of the biophysical environment on plant morphogenesis and yield; to study light attenuation through the canopy, to analyse the transport of water and the allocation of photosynthates within the plant; to analyse the competitive interactions among different plants in the same stand; to calibrate remote sensing techniques and to visualize large landscapes.

BESIDES the improvement of classical empirical growth and yield models, elaborated from classical agronomic and forestry field experiments and permanent plots (see ref. 1 for an example of such models in forestry), most recent developments in plant growth modelling rely on either an ecophysiological or a morphogenetic approach.

The ecophysiological approach is usually based on a simple description of the plant in a few broad compartments (leaves and branches, flowers, fruits, stem, roots), and aims at predicting the dry matter production as the result of the functioning of the plant (transpiration, photosynthesis, photosynthate allocation, nutrient cycling, etc.), and of its regulations by environmental factors (light, temperature, water and nutrient availability, etc.).

Most of these process-based models focus on the water balance and on the carbon balance and partitioning (e.g. see refs 2, 3). The main drawback of these models is that they often omit the structural properties of the plants which may be crucial for their functioning (e.g. the hydraulic structure of a tree) or even for their yield (e.g. the quality of softwood timber is highly dependent on the distribution of the annual growth rings and knots).

As an alternative approach, morphogenetic models were developed and mainly progressed along two lines: (i) theoretical models based on formal grammars initially developed for studying the development of multicellular organisms⁴; (ii) stochastic models initially based on the qualitative botanical descriptions of plant architecture and their classification in 'tree architectural models'⁵ (see also refs 6, 37 for ecological applications of the 'architectural models' to forest succession and dynamics in India). The first quantitative morphogenetic models aimed at generating 3-D virtual plants which grew in a homogeneous and stable biophysical environment and were faithful to botany⁷: these models simulated the architectural development of the plant according to its morphogenetic programme. Thus, they provided important features such as the position of fruit-bearing areas in a plant or the size, status and position of knots in a tree stem, but they were not able to predict the effect of changing growing conditions, for example the influence of a water stress or the influence of agronomic and silvicultural treatments such as fertilization, irrigation, thinning or pruning.

A recent trend consists in combining the ecophysiological and architectural approaches, that is in linking the structure and functioning of the plants^{4,8-10}. The underlying assumptions are indeed that, at a given point of time, plant structure (i) is the joint and cumulative output of the morphogenetic programme and the earlier physiological growth processes, (ii) determines the external environment of the plant which itself regulates the functioning of the plant, and (iii) directly conditions the subsequent physiological processes.

The aim of this paper is to review and illustrate different ways of generating 3-D virtual plants, and how such models can be applied to various agronomic and

forestry contexts. The paper is organized in three sections which correspond to three broad types of plant models:

- Static and numerical 3-D plant models which are directly derived from field measurements and can be used to investigate specific ecophysiological processes;
- Morphogenetic models which describe the average architectural development of the plants in a stable and homogeneous environment;
- Models which link the architecture and the ecophysiological functioning of the plant.

The paper is centered on the methods developed by AMAP (Atelier de Modélisation de l'Architecture des Plantes) Laboratory at CIRAD (Centre de Coopération Internationale en Recherche Agronomique pour le Développement). As suggested in this introduction, there are however several other teams and approaches in this field (for a recent reference, see ref. 11).

Static 3-D plant models and their utilization

Static 3-D plant models

Static 3-D models of plants do not aim at describing how a plant functions and grows but at visualizing its architecture, as it is, at a given date. They are thus pure numeric descriptive models which can be obtained using various field and laboratory methods¹²: reconstruction of tree architecture using coupled cameras and a pair of stereoscopic photographs¹³, non-destructive digitizing techniques based on mechanical, ultrasound or magnetic devices¹⁴, manual measurement and coding of botanical entities¹⁵. A coffee tree digitized using a mechanical system is visualized in Figure 1.

Use of static 3-D plant models

Such static numerical plant models can be used for various purposes: for visually exploring the qualitative and quantitative morphological variability of a species (see next section), as well as for investigating various ecophysiological or biophysical processes, which depend on plant structure, and for elaborating, calibrating or validating process-based models.

For example, it is possible to model the hydraulic structure of a digitized plant and simulate its transpiration according to ecophysiological knowledge and parameters: such simulations can then be tested by comparing the local information (e.g. sap flow, leaf temperature) predicted on the virtual 3-D plant, to the observations made on the corresponding standing plant (Figure 1)¹⁶.

A similar application can be done for the interception and transmission of light through the canopy. Virtual 3-D stands composed either of digitized plants or of

plants generated by morphogenetic rules (L-systems or reference axis: see below) can be simulated and linked to various physical light attenuation models: ray-tracing, radiosity, etc.¹⁷. In that case, the comparison between simulations and observations concerns the quantity of light that is transmitted to the ground through the foliage (Figure 2)¹⁸.

Such applications are very important, not only for testing the biophysical and ecophysiological models of plants and stands but also for more direct agronomic or silvicultural purposes such as predicting the quantity of light available for crops or tree understorey species which grow under the canopy of higher plants¹⁹.

Morphogenetic plant growth models

The morphogenetic modelling approach aims at generating 3-D virtual plants which are faithful to botany. It results in growth simulators which describe the architectural development according to the genetic programme of the plant, in a given biophysical environment (stand density, site quality, etc.). This approach articulates two complementary parts: (i) the elaboration of mathematical models based on botanical knowledge and experimental measurements, (ii) the computer simulation of plant development based on these mathematical models.

Measuring, coding and modelling plant architecture

There are several approaches to empirically model plant morphology from field measurements. In the case of trees, for example, empirical allometric models have

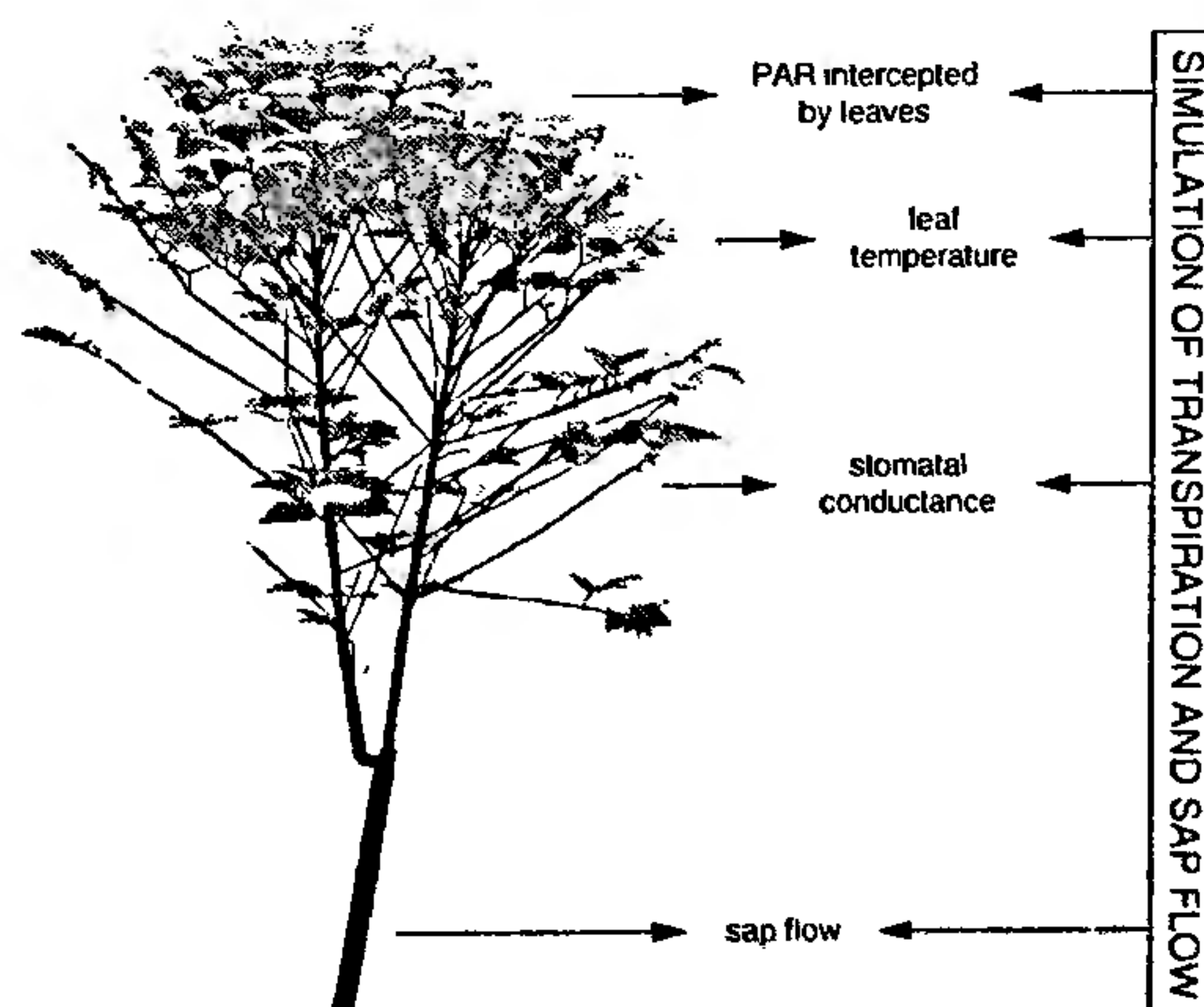


Figure 1. Visualization of a digitized coffee tree (*Coffea arabica* var. *caturra*) in Costa Rica. The tree was digitized by a non-destructive mechanical device. This plant model was used to model transpiration¹⁶ (Figure provided by J. Dauzat, CIRAD, Montpellier).

been developed to describe the relationship between branch growth (in length) and stem annual growth²⁰, or to predict the vertical variation of branch diameter from usual tree characteristics: tree age, height and diameter at breast height²¹.

The comprehensive approach developed in AMAPmod software is based (i) on a botanical hierarchical and multi-scale description of the tree, and (ii) on stochastic growth and branching models. AMAPmod thus aims at representing, analysing and modelling the architecture of a (set of) plant(s) measured in the field²². AMAPmod consists of a plant-oriented database management system and a set of tools and methods which operate on plant databases (Figure 3). The databases and tools are available through a functional language called Amap Modelling Language (AML).

AMAPmod relies on a standardized way of describing and coding the topological (relationships between botanical entities: e.g. leaves, internodes, annual growth units, branches, etc.), geometrical (e.g. 3-D orientation of a branch) and dimensional (e.g. length and diameter of a growth unit) structure of the tree. The computer representation of the trees (there may be several trees simultaneously described) uses the formalism of Multi-scale Tree Graphs (MTG).

AMAPmod can be used to explore the organization of the plant by selecting and visualizing different types of data: values (e.g. the average number of internodes per growth unit), sequences of values (e.g. the sequence of flower-bearing and non flower-bearing internodes along a growth unit), tree-structured values, sets of values (e.g. the number of internodes per annual growth unit according to the position of the growth unit in the tree), sets of sequences of values, etc.

AMAPmod can further be used to model the growth

and branching processes from the different types of data described above. AMAPmod integrates several types of models²³: discrete distributions and combination of discrete distributions (e.g. for modelling the number of internodes per annual growth unit), renewal processes (e.g. for analysing time-marked sequences of events such as the dates of leaf appearance), discrete Markovian processes (e.g. for modelling the sequence of branched and unbranched internodes along an annual growth unit).

A major perspective in this domain consists in utilizing AMAPmod for exploring the variability of plant architecture of a given species: across genotypes, ecological conditions and/or agronomic and silvicultural treatments.

Simulating the architectural development of plants

The simulation of the architectural development of a plant may be realized using several techniques: (i) pure morphological algorithms which aim at generating plant-like models (e.g. fractals²⁴), (ii) formal grammars (L-systems) which represent plant growth by morphogenetical rules^{4,25}, (iii) the 'reference axis' technique which has been implemented in AMAPsim software²⁶ (see below). The two latter techniques rely on a description of the morphogenetic processes and can thus be linked to field observations.

The 'reference axis' in AMAPsim may be considered as a graph which describes and links the different architectural states of the growth units within the same plant. The graph is indeed associated to an automaton which simulates the changes in the 'physiological age' of the growth units²⁷ along the various tree axes, as they appear and grow. For example: the change in the physiological age may either be progressive (e.g. to describe the drift along a given axis); it may also be



Figure 2. Simulated map of transmitted PAR (Photosynthetic Active Radiation) under a 20-year-old coconut plantation¹⁸ (Figure provided by J. Dautat, CIRAD, Montpellier).

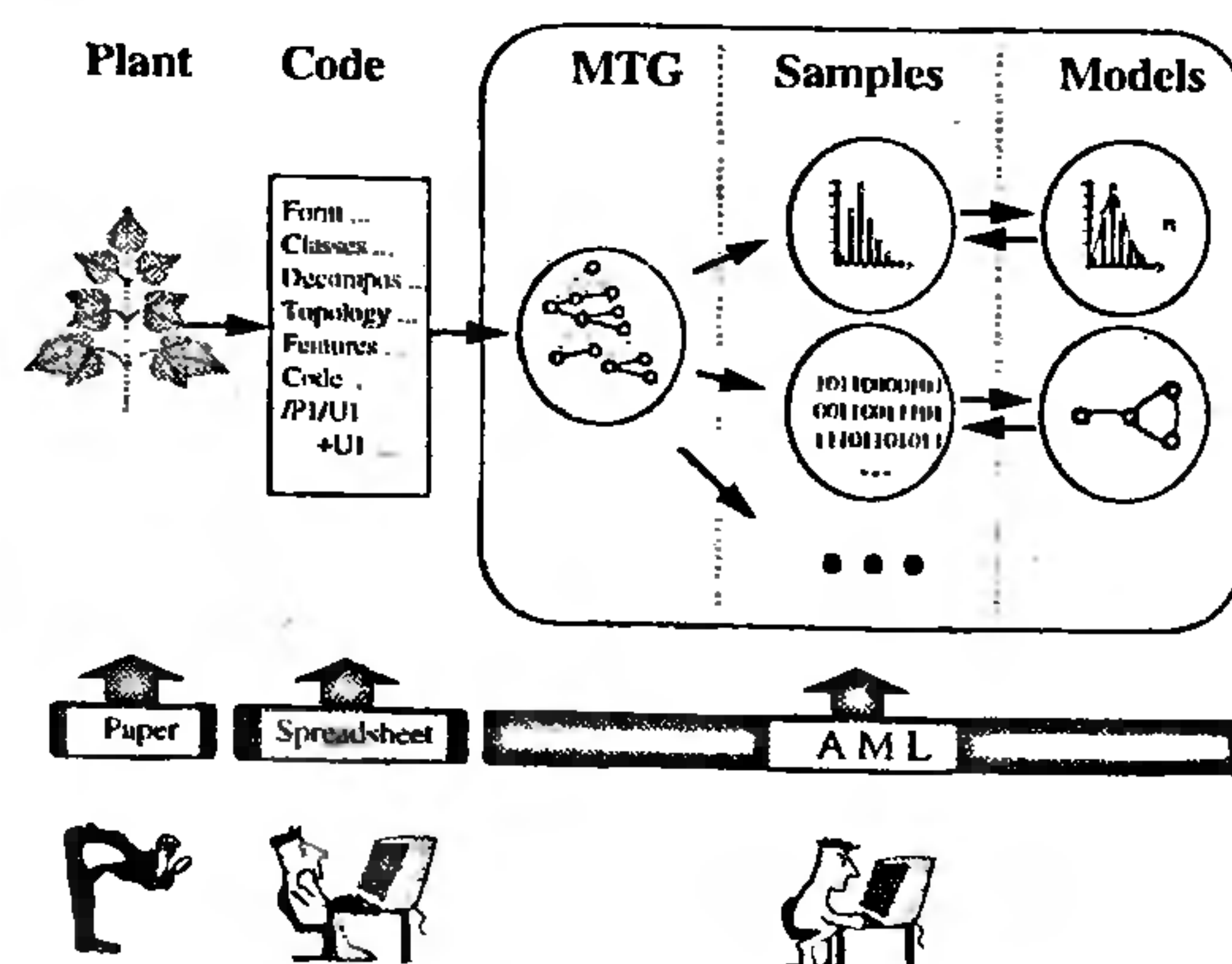


Figure 3. The AMAPmod software: from field observations to plant models (Figure provided by C. Godin and Y. Guedon, CIRAD, Montpellier).

brutal (e.g. loss of vigour between a carrying branch and the carried branchlet). To a given physiological age, AMAPsim associates stochastic models and their parameters (models and parameters can be identified and estimated from field observations using AMAPmod software, see above). If, for a given physiological age, no information is available, AMAPsim can interpolate between the physiological ages for which the parameters are known.

A crucial point is that AMAPsim is linked to AMAP-

mod and that the theory of graphs and automata makes it possible to estimate the transition probabilities among the states in the graph from experimental data (which is not the case for most simulation methods which



Figure 4. Simulated growth of a pine (*Pinus nigra*): 10-, 15- and 20-years old (unpublished figure provided by Y. Caraglio, CIRAD, Montpellier).



Figure 5. Simulated growth of a *Eucalyptus saligna* (clone 2-32): 18-, 42-months old²⁸ (Figure provided by T. Coudurier, CIRAD, Montpellier).

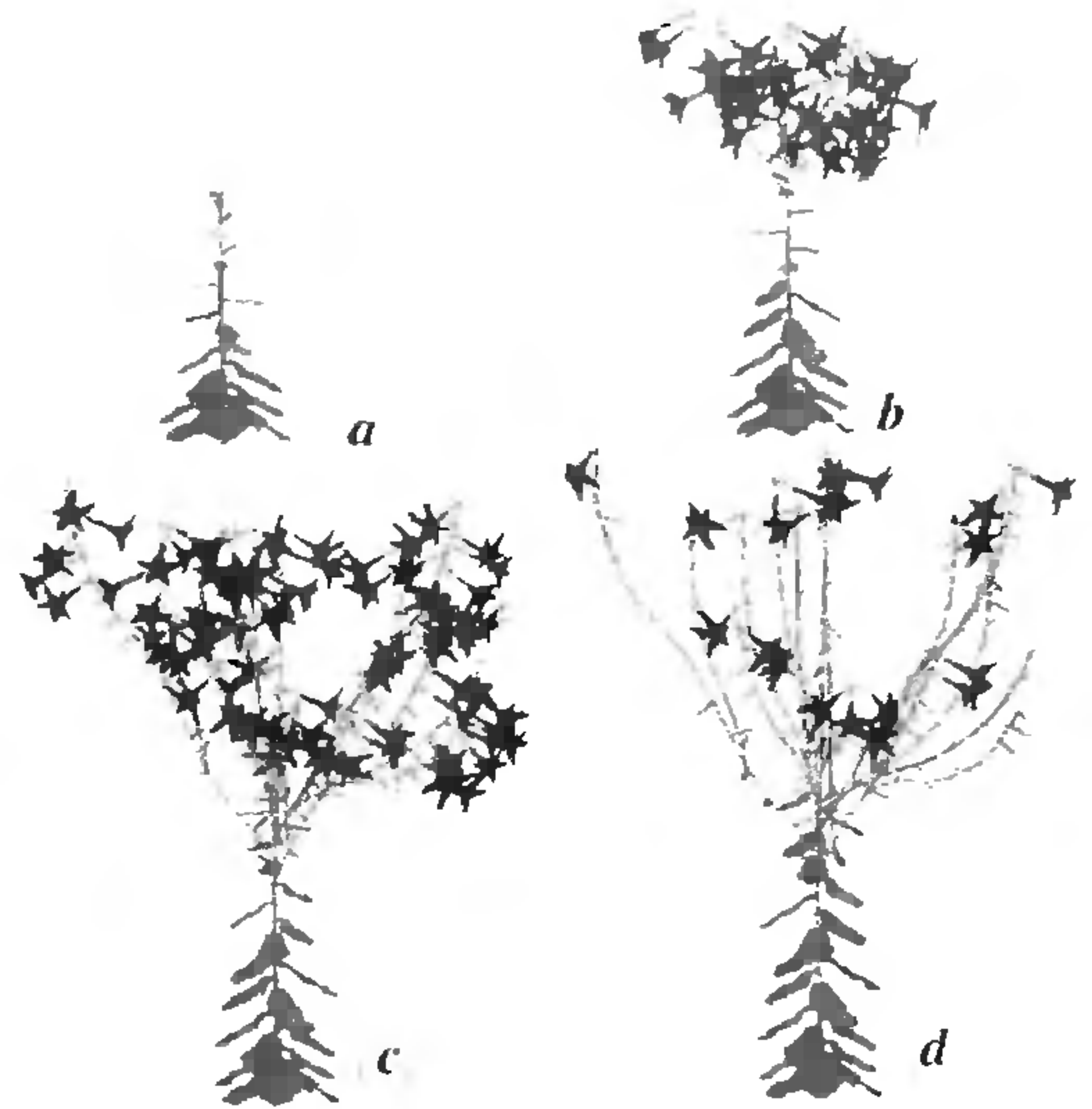


Figure 6. Visualization of four simulated 90 days-old tobacco plants grown under different light conditions: *a*, 10 Klux; *b*, 20 Klux, *c*, 30 Klux, *d*, 40 Klux (ref. 29) (Figure provided by H. Rey, CIRAD, Montpellier).



Figure 7. A simulated 11-year-old oil palm tree (*Eleaais guineensis*) in Ivory Coast. The architecture of the aerial and root systems was independently modelled (with AMAPmod) and simulated (with AMAPsim)³⁰ (Figure provided by C. Jourdan, CIRAD, Montpellier).

cannot be 'fed' by observations). There is thus a bridge between empirical observations of plant architecture and the morphogenetic simulations of AMAPsim, thus the possibility to adjust and validate the model.

The functionalities of AMAPsim are illustrated in Figures 4 to 7. AMAPsim can be used to generate 3-D virtual plants for situations (i.e. species, site quality, stand density) which have been observed in the field (Figures 4 and 5), but also to interpolate between various situations where controlled experiments have been monitored (Figure 6). AMAPsim and the reference axis can also be used to represent and simulate the architecture of root systems (Figure 7). Besides applications already discussed (see above: radiative transfers, water conduction), these 3-D virtual plant models can be used for various purposes: to estimate the aerial biomass, to evaluate the volume of soil prospected by the roots, to simulate the retrodiffusion of the canopy for calibrating remote sensing techniques, to study the mechanical status of a standing tree, etc.

Combining ecophysiological and architectural models

The trend to combine process-based and architectural

models relies on the idea that plant functioning and structure are intimately intertwined, that the integration of ecophysiological knowledge is needed to simulate the reaction of the plants to changing environments and that structural information is important for many agronomic and silvicultural applications. The aim of such models is indeed to develop virtual experiments which, provided that the models are well calibrated and validated, may save a lot of time-consuming and expensive field experiments and provide a comprehensive understanding of the underlying processes. There are however different ways to represent these links: (i) plant and canopy structures can be considered as factors which condition the physiological processes (see above 'Use of static 3-D plant models'); (ii) plant architecture can also be seen as the output of ecophysiological processes (see below); (iii) the reciprocal influence of structure and functioning can be jointly integrated into a single model (see below).

Morphogenetic models driven by ecophysiological processes

Process-based models can be used to predict the global behaviour of the plant (e.g. biomass production of broad compartments, total number of fruits, etc.) and constrain

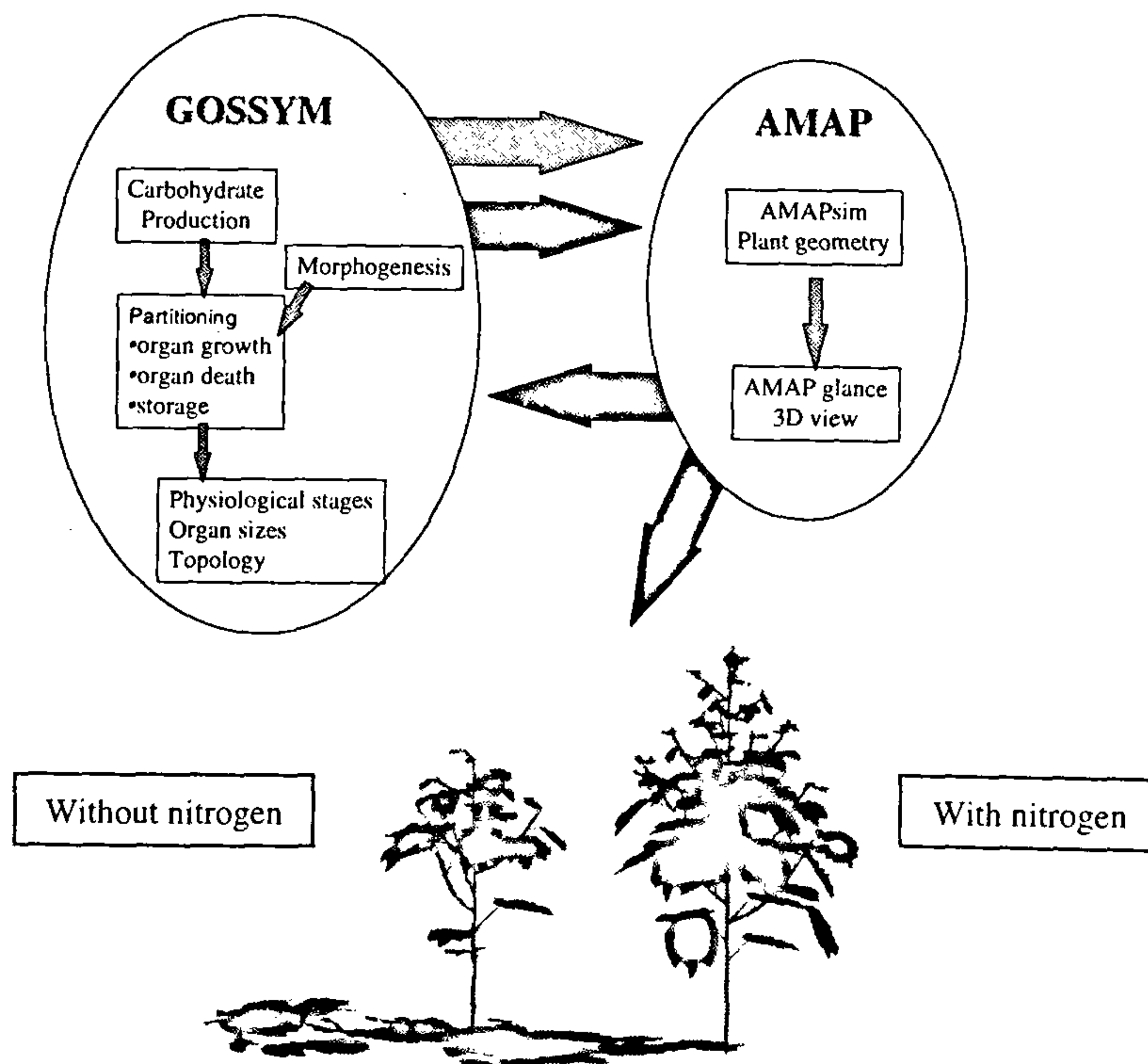


Figure 8. Influence of nitrogen availability on cotton growth and architecture (Software: Gossym and AMAPsim)³¹.

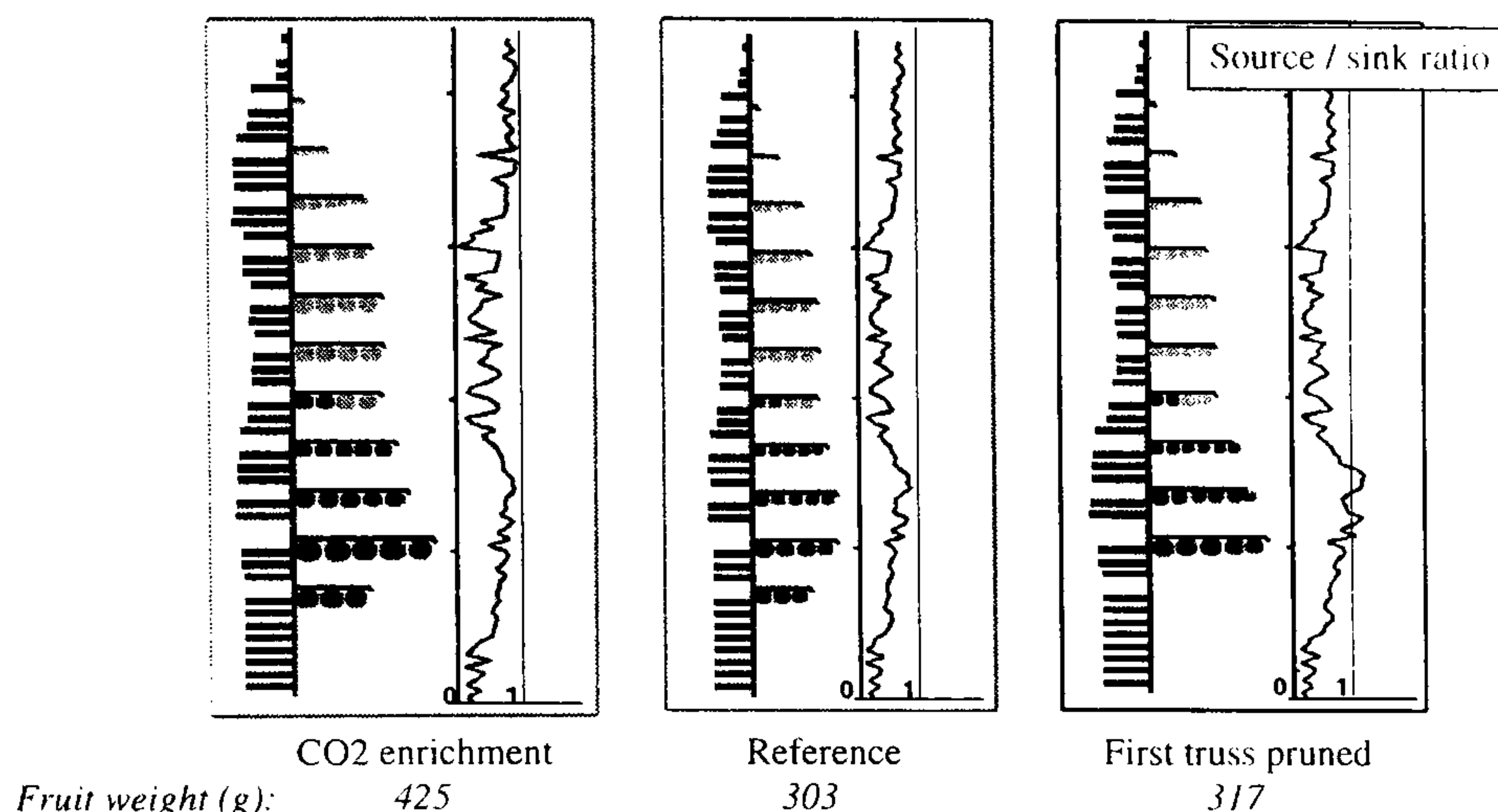


Figure 9. Simulated structure of a tomato plant grown under controlled conditions (Software: TOMGRO and AMAPsim)³².

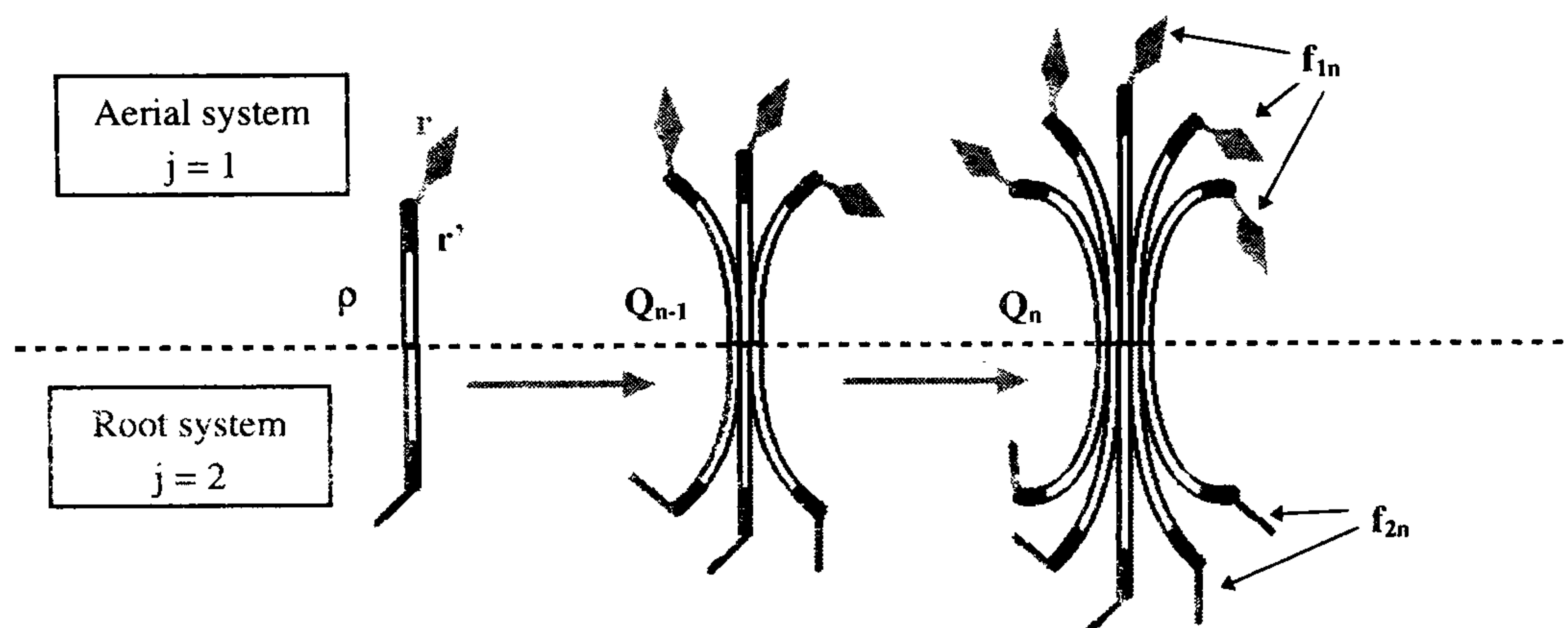


Figure 10. Theoretical modelling of tree growth as the joint result of morphogenetic programme and ecophysiological processes (software: AMAPpara). At date n (time step is one year), the cumulated transpiration of the tree is computed as the result of water potential ($\Delta\psi_n$ = difference between leaves and soil) and the hydraulic structure of the tree which depends on: the number of branch growth units which carry leaves and are photosynthetically active (f_{1n}); the number of root growth units which can absorb water (f_{2n}); the resistance of the various structural elements (r_j = resistance of leaves to transpiration and of absorbing roots to water absorption; r_j = resistance to sap conduction in terminal growth units; ρ_j = resistivity to sap conduction in sapwood annual growth rings; $j=1$ for the aerial system; $j=2$ for the root system). The annual dry matter yield (Q_n) is supposed to be proportional to the annual transpiration (k = water use efficiency). Dry matter is then partitioned among various 'sinks' to make, either immediately or with a 1-year delay, new elements according to their morphological constraints: annual growth rings around existing stem, branch and root growth units; new branch or root growth units; new leaves and water-absorbing root hairs.

For simple deterministic morphogenetical programmes, this model yields a simple recurrence formula which links tree growth (transpiration, carbon assimilation, dry matter partitioning, size of new elements) to its aerial and root architecture. This formula accounts for memory effects which are cumulatively inscribed into tree structure:

$$Q_n = \frac{k \cdot \Delta\psi_n}{\sum_{j=1,2} \left[r_j \cdot A_j + r_j \cdot B_j \cdot \left(\frac{Q_{n-1}}{f_{jn}} \right)^{1+\alpha} + \rho_j \cdot C_j \cdot \left(\sum_{i=1}^{n-1} \left(\frac{Q_{i-1}}{f_{ji}} \right)^{1+\frac{\alpha}{2}} \right)^2 \right]} \cdot Q_{n-1}$$

where α = allometric parameter which describes the morphology of the growth units; A_j, B_j, C_j = parameters which depend on the morphology of the various plant elements and on the rules of dry matter partitioning. For more realistic morphogenetical programmes, tree growth is simulated using AMAPpara software.

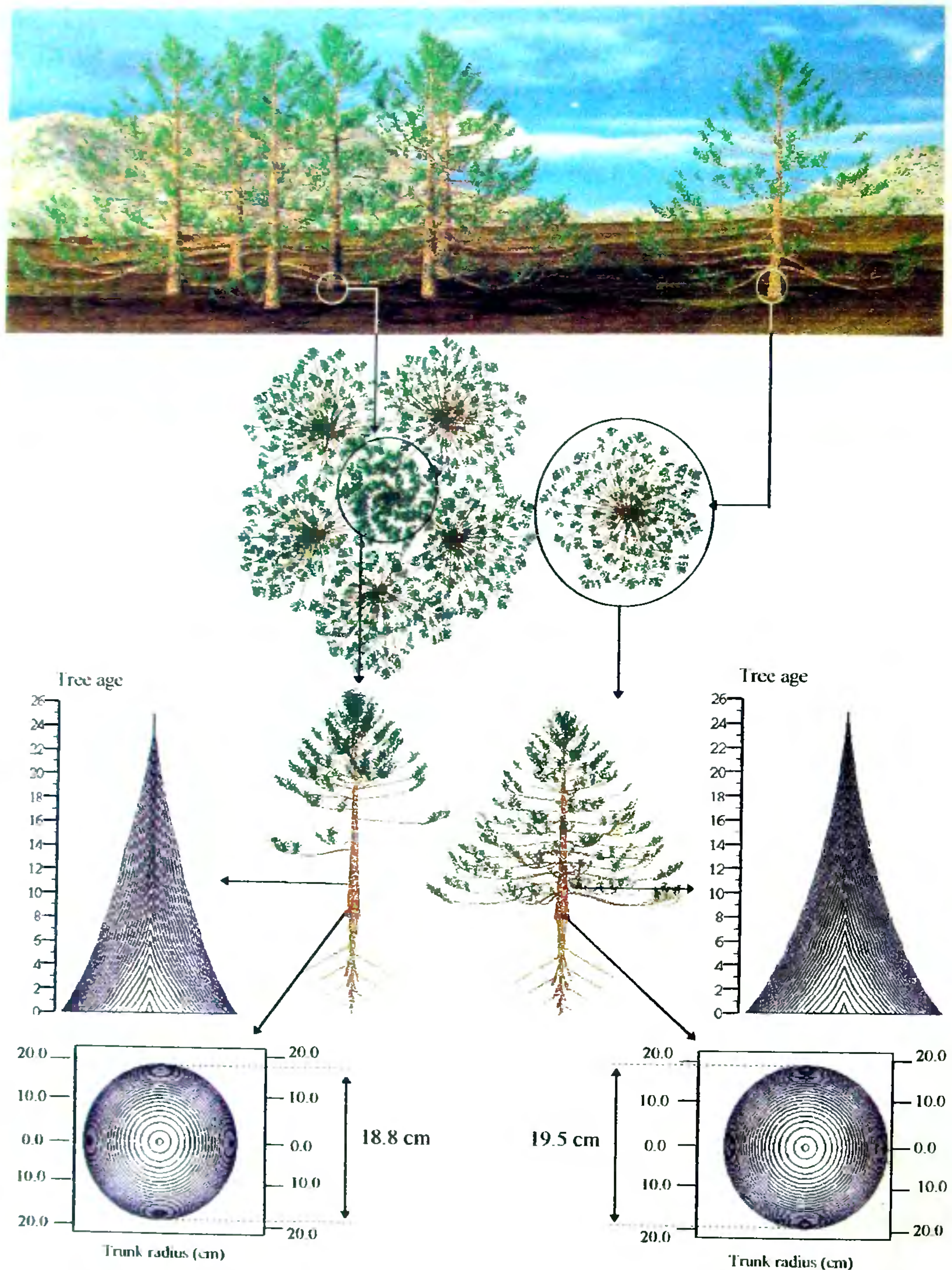


Figure 11. Simulation of pine growth in a grove as the result of tree architectural development regulated by competition for space (self-pruning) and internal resistance to sap conduction. Top: side view of tree architecture; Middle: view from above; Bottom middle: view of tree architecture of the open grown tree (right) and the central tree (left); Bottom right: longitudinal section and transversal section (at stump level) of the stem of the open grown tree; Bottom left: longitudinal section and transversal section (at stump level) of the stem of the central tree (Figure provided by F. Blaise, CIRAD, Montpellier).

its morphogenetic programme. This approach is being developed to simulate detailed growth of the cotton tree. This work consists of linking the AMAPsim software to the GOSSYM-COMAX system³¹, an ecophysiological model which was developed independently at USDA. The GOSSYM model simulates mass, number, size and type of organs, water and nitrogen stresses, carbohydrate production and partitioning, and the complete description of the cotton plant topology. GOSSYM could be made more useful by taking into account the plant geometry provided and visualized by AMAPsim. For example, GOSSYM and AMAP are jointly able to describe and predict the effects of fertilization on cotton growth and production (Figure 8).

Another example deals with the growth of tomato³²: the method again consists in coupling an ecophysiological model, Tomgro, and AMAPsim (Figure 9).

Process-based architectural models

In this case, the double regulation, of the ecophysiological processes by the structure of the plant and its neighbours, and of the morphogenetic programme by the availability of the internal and external resources produced or consumed by the physiological processes (e.g. photosynthates, water, light, space), is explicitly considered in the very same model. Such an approach is being implemented in AMAPpara which simulates the parallel functioning and growth of plants which interact with each other³³⁻³⁵.

AMAPpara includes an architectural description of aerial and root systems. Their morphogenetic programme is *a priori* parameterized according to the selected species (topology, geometry, allometric relationships for botanical elements such as leaves, maximum lifespan of leaves and roots). The actual architectural development of the plant is then regulated by physical constraints (competition for space and light³³) and physiological processes (water transpiration, carbon assimilation, allocation of photosynthates, etc.) which themselves depend on the structure and biophysical environment of the plant (internal hydraulic architecture, competition for space among neighbour trees, light interception including self-shading). An ecophysiological component of AMAPpara is illustrated in Figure 10 and a simulation of a small grove is provided in Figure 11.

Discussion

The approach reviewed in this paper aims at developing agronomic or silvicultural virtual experiments. It relies on the integration of diverse knowledge, ecophysiological and morphological, and of mathematical and computer techniques. Although 'virtual-oriented', this approach is

not purely theoretical: on the contrary, it is based on a good and detailed botanical description of the plants, and there is a strong need for experimental data to fit, calibrate and validate the various components described above; this approach is also helpful in suggesting future critical experiments (to test some of the underlying hypotheses).

Another important remark is that there is a need to simultaneously develop (i) mathematical models which are analytically tractable for simple plants and provide a qualitative understanding of plant behaviour (e.g. Figure 10), and (ii) modular simulation software which can be linked to each other and used for plants which have a complex architecture.

The applications of this approach are numerous, from higher education (it provides a good way to comprehensively integrate several pieces of knowledge) to the elaboration of agronomic and silvicultural guidelines, the calibration of remote sensing techniques and the visualization of large landscapes. As an example, a collaborative research project was recently designed by the French Institute, Pondicherry, with the long-term aim to study and simulate the dynamics of the moist evergreen forests of the Western Ghats^{36,37}.

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MEETINGS/SYMPOSIA/SEMINARS

International Seminar on GLP in Safety Evaluation of Pesticides

Scientists from Europe, Japan and national institutions will deliver guest lectures on GLP and GAP in pesticide safety studies.

Date: Second week of January 1998

Place: Chennai, India

Contact: Director
Fredrick Institute of Plant Protection and Toxicology (FIPPAT)
Padappai 601 301
Tel: 04111-44246/44266; Fax: 044-2367832/2368024
email: fippat@giasmd01.vsnl.net.in

Training Programme on Immunopathology in Pant University

Topics include: Immunodeficiency, hypersensitivity, autoimmune diseases, impact of environmental pollutants on immune system of body, immunomodulation, particularly the use of immunomodulators of herbal origin.

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