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THE GROWTH PROCESS OF TROPICAL TREES: A SIMULATION WITH GRAPHIC OUTPUT

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Abstract. Simulation is becoming an important tool of researchers studying the structure and adaptability of various botanical species. One goal of scientists is this field is the creation of models to explain global tree attributes, such as canopy shape, in terms of local growth behavior (the branching pattern). The validation and "tuning" of these models would be quite difficult without performing simulations based on the models constructed and then displaying the results of the simulation graphically. Models describing the structure and branching pattern of a species have incorporated both genetic factors and environmental influences on the species being analyzed. Simulation programs implementing models for three species of architecturally similar tropical canopy trees (Terminalia, Cameraria, and Tabernaemontana) have been created. These programs produce graphic output, as well as tabular information on the status of the tree at fixed time intervals. Examples are presented of a preliminary study of the effect of limiting branching density on tree structure.

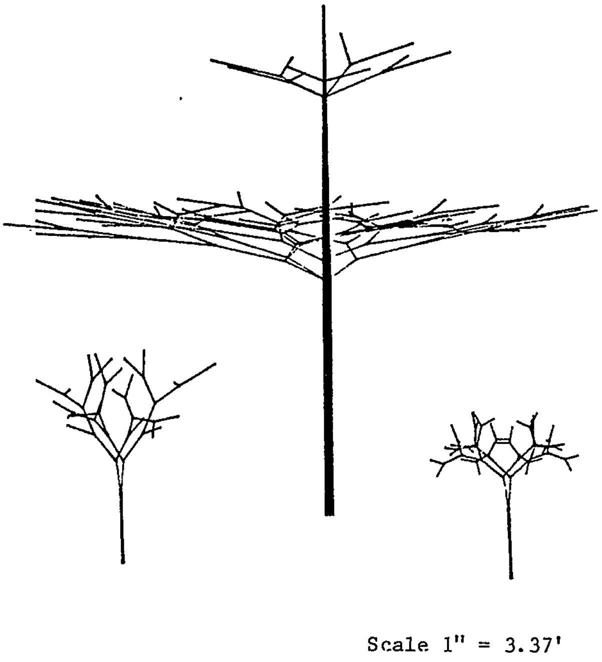

Figure 1. Simulated representative specimens of Tabernaemontana, Terminalia, and Cameraria latifolia after two years of growth

1. INTRODUCTION

The use of computer graphics to facilitate the communication of computer output to the user, and specifically the use of graphics to accompany simulation, is not a new idea. However, despite its long history, it has been slow, for a number of reasons, in gaining prominence among the variety of users who might benefit from its use. In particular, there has been an interest among botanists, in recent years, to simulate the growth of certain species of plants in order to answer a wide range of questions concerning their growth and environment. Simulations have been written to describe the growth of cotton plants (McKinion, et. al., [19]), rhizomes (Bell, [1,2]), conifer tree crowns (Smith and Scoullar, [24]), soybeans (Curry, et. al., [5]), and tropical canopy trees (Honda and Fisher, [6,9, 13-17]). Some of these researchers have employed simplistic graphics to illustrate their simulations. A computer produced picture of a species is much more easily compared with its natural counterpart, for validating a simulation or studying a species, than are reams of printed data.

A computer simulation of plant growth is based on a structural model of the species. To formulate this model the botanist must first define a small number of parameters which, considered together, describe the architecture of the species. These parameters may be thought of as a combination of genetically determined attributes and environmental influences. Secondly, algorithms must be formulated using those parameters which describe the growth and branching patterns of the species. The validity of the model, obviously, lies in the closeness of the relationship between the output of the simulation and the form of the actual species. According to Bell [3], the system may be approached in an empirical manner in which the parameters are based on actual measurements of the species taken in the field. The simulation may then provide a prediction of the range of architecture possible for the given species. Other systems may be approached intuitively, adjusting conjectured parameters until a graphical representation of the simulation output closely resembles for form of an actual plant.

By either approach, simulation is a powerful tool by which to measure the essential elements that govern the form and shape of any species. It can be used to demonstrate architectural response to an alteration of the physical or genetic factors which are inherent to the species ([3]). Simulated architectural changes which result from varying a parameter value have been found to parallel those changes exhibited by an actual tree.

2. THE FISHER HONDA MODEL

One of the most extensive studies of architecture and branching patterns of botanical species has been made by Hisao Honda, a bio-physicist with the Kanebo Institute for Cancer Research, Kobe, Japan, and Jack B. Fisher, a botanist with Fairchild Tropical Garden, Miami, Florida [6-9, 13-17]. They have constructed models and limited simulations which depict the growth of three architecturally related species of tropical trees. These mathematical models form the basis of the current simulation. Honda and Fisher began their work with Terminalia, an erect tree whose branch pattern consists of regularly repeating, discrete units, making the species ideal for simulation. The species grows by bifurcation, a process in which each branch endpoint produces two daughter branches. The tree grows exclusively from the branch endpoints; existing branch units do not themselves continue to grow. More recently, Honda and Fisher have expanded their research to include two structurally similar species, Cameraria latifolia and Tabernaemontana. These are also discrete, bifurcating trees. Therefore, the original mathematical model could be expanded to encompass all three species by effecting elementary changes in parameter values and the growth equations.

The Fisher Honda model incorporates not only the genetically determined parameters (the essential branch angles and growth lengths of the bifurcation process) but also environmental factors which describe variances in nutrient flow, shading, and possible physical obstruction.

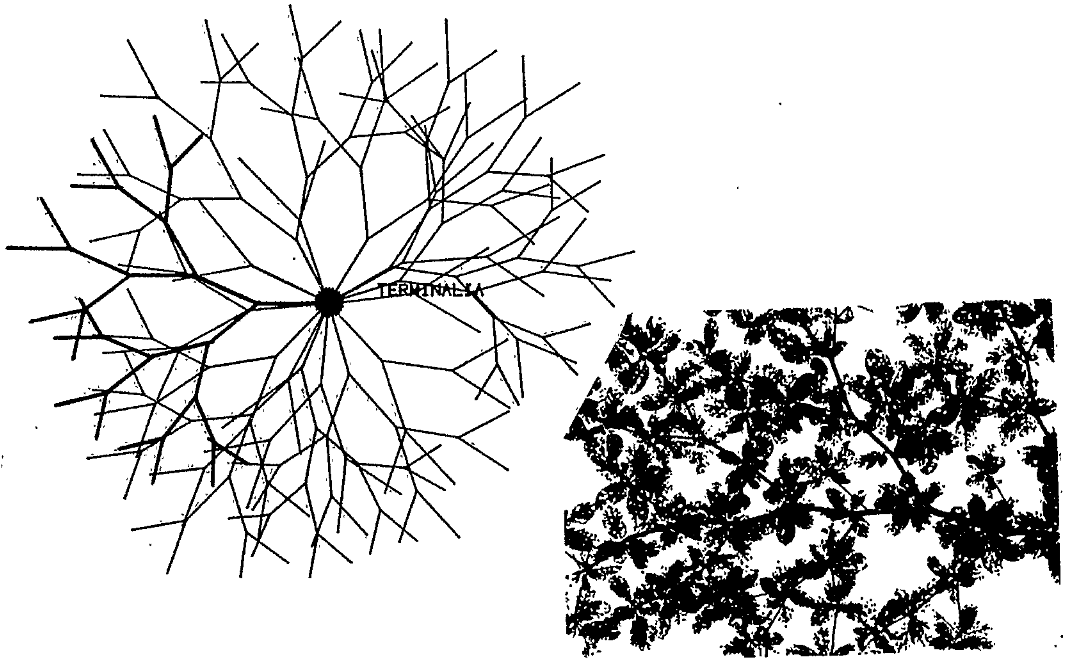

Figure 2. Simulated Terminalia sp. crown compared with an actual branch

3. THE GROWTH PROCESS

Bell [3] describes the growth of any botanical species as the growth of one apical meristem (the trunk) which bears further meristems which themselves may or may not grow. A meristem's growth may be governed by one of three cases:

1. it may grow into a branch;
2. it may abort; or
3. it may become dormant and may or may not grow at some stage in the future.

For the three species in question, each year's growth cycle consists of a new tier of branches being produced (containing from three to five main branches), a spike being formed above the tier (which will become the next section of trunk), and each branch endpoint in the tree bifurcating or not as the conditions indicate

In the first case, as mentioned above, as a branch node bifurcates, it produces exactly two daughter branches. One of these is considered to be the dominant branch, and will in general, grow to a greater length than its sister. The angles of bifurcation and the daughter-to-mother length ratio are determined by the user at the initiation of the simulation. In the species studied, the signs of the respective bifurcation angles alternate, so that the dominant branches on a main axis form a regular zig-zag pattern. Terminalis bifurcation occurs in a single plane which lies horizontal with angle of the main branch as it emerges from the trunk. In contrast, both C. latifolia and Tabernaemontana exhibit branching in alternating horizontal and vertical planes.

There are basically two reasons for which a branch node might not bifurcate. First of these is lack of available space. If a spherically shaped volume around each branch endpoint contain any other branch endpoints, the subdominant branches will cease to bifurcate (case 2 above). The radius of these spheres, called the radius of interaction, is determined by the user. Abortion of the branching process in this manner closely approximates the natural phenomena of shading, where branches in close proximity are in competition for sunlight, and of bud damage caused by physical contact.

A branch endpoint which passes the test for available space must also have sufficient accumulated flow in order to bifurcate. If the accumulated flow is low (in the simulation, less than a species determined value), then the branch becomes dormant (case 3 above). A branch may remain dormant for any length of time and will resume bifurcation once its accumulated flow increases to a sufficient level. The increase in accumulated flow is modeled by an equation which is species dependent. If the accumulated flow is sufficient, the branch bifurcates, and new daughter branches are created. For _Terminalia_ and _C. latifolia_ the flow rate and accumulated flow are constant; thus, there may be aborted branches caused by close proximity, but there are no dormant branches. _Tabernaemontana_ has two growth phases. Phase two is initiated when the branch angle, measured from a horizontal plane upward to a branch, becomes greater than the threshold angle, an input parameter specifically for this species. During phase one growth, flow rate and accumulated flow are constant as in the other species. During phase two, the parameter means for branch lengths and angles of bifurcation are changed and flow rate and accumulated flow become decreasing functions. This allows the formation of dormant branches. During the dormant period, however, accumulated flow again increases, so that the bifurcation process may resume at some future time. After several iterations, the branches of the tree _Tabernaemontana_ begin to droop.

4. THE PROGRAM

This simulation has been written using a hierarchical structure [28]. This type of design was chosen not only to facilitate the implementation and maintenance of the program but primarily to allow its expansion at some time in the future as the research of botanical models progresses. The top level modules in the design are described below.

INPUT--The mean and standard deviation of each of the exogenous parameters is entered by the user within the framework of an interactive user interface. Each parameter is described briefly, including a format description of its values, and the user is prompted to enter its mean and standard deviation. It is recognized that some species require special input parameters to describe chracteristics which are peculiar to that species; such is the case with Tabernaemontana. In such instances those values are entered by the user in a separate but similar user interface which remains invisible when simulating the other species. It was felt that the interactive input approach would provide the user with great flexibility to test the architectural response to variations in particular parmeters.

INITIALIZATION--The simulation requires the initialization of certain arrays and markers to handle dormant branches and the conversion of all angles from degrees (which is convenient for the user) to radians (which is necessary for the simulation equations). The graphic display requires the establishment of the axes scales as well as the location and orientation of the viewer with respect to the axis system.

TRUNK--This component produces the coordinate output as well as the graphic construction of a slender, cylindrical trunk from the ground to the first tier of branches.

BRANCH TIER--A new tier of branches is produced with a new section of trunk above it.

BIFURCATION--All existing branch endpoints are tested for growth factors, accumulated flow and inhibition by more vigorous branches in close proximity. Each branch may bifurcate into two daughter branches according to the particular algorithm of its species; it may remain dormant for possible bifurcation at some time in the future; or it may discontinue bifurcation. Because the separation of species occurs at this level in the hierarchical structure, the addition of other species to the simulation should be a relatively uncomplicated procedure.

UPDATE--During each cycle of simulated growth the colors of the graphic image are altered to reflect the aging of the tree, and the diameter of each trunk segment is increased dependent upon the effective leaf area supported by the segment.

GRAPHIC MANIPULATION--Once the image of the completed tree has been simulated and graphed, the user may wish to alter his perspective in order to study one particular aspect of the tree. A second interactive user interface gives the user the option of rotating the tree on its vertical axis, moving the viewpoint in an arc from eye level upwards toward the tree crown, or zooming in on the image. The options may be implemented either individually or cumulatively. At any time the user may return to the original image and resume the perspective studies.

5. STORAGE AND DATA STRUCTURES

The formulation of data structures to support botanical simulation presents a considerable problem in that an extensive amount of storage is required. With each growth cycle of the tree the number of branch nodes and therefore the required storage approxiamtely doubles. Several status variables describing both growth factors and architectural attributes must be kept for each oranch endpoint in the system. In addition to these growth parameters, it is necessary to store the X, Y, and Z coordinates of each branch endpoint as well as the mother o each daughter branch. Furthermore, during certain stages of tree growth, a number of branches may be in a dormant phase, and the simulation must be able

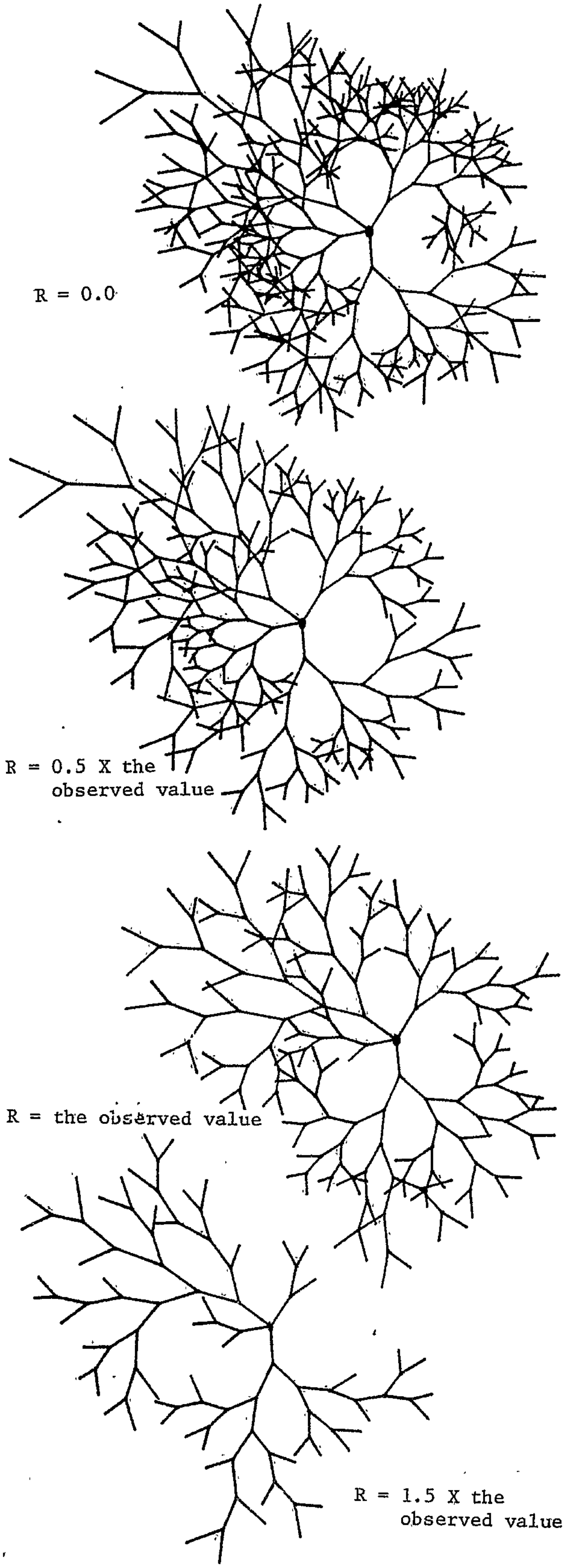

Figure 3. Response of Terminalia tree shape to varying values of the radius of interaction, R

to locate and access these branches and their associated parameter values.

The tiers of branches, for this simulation, are numbered from 1 to MXTIER (an input parameter), and within each tier the branch nodes are numbered from 1, designating the trunk section of that tier, consecutively for each daughter ranch produced. The growth parameters, the three coordinates, and the mother node for all branch nodes in a tree are each stored in separate two-dimensional arrays. Three of the growth parameters have been consolidated into the size of a single array by using the (UNIVAC) Fortran BITS function. This function allows the reduction of storage space while retaining the mode of access used for the other parameter arrays. All values associated with a particular branch can then be accessed from the arrays by the tier number and node number of the branch. Two markers, STRT and FIN, are necessary for each tier to distinguish the endpoint nodes which are about to bifurcate from nodes which have previously bifurcated. A separate linked list stores the tier and node numbers of all dormant branches so that their parameters values and coordinates can be accessed when they are ready to bifurcate.

6. GRAPHICS

The graphics routines which accompany the simulation are written in GCS, Graphic Compatibility Sytem [26,27], a Fortran-based graphics package developed by West Point Military Academy and be the U.S. Army Engineer Waterways Experiment Station. The routines are machine independent; this simulation has been used to produce four-color images on the Hewett Packard plotter or green on black images on the Imlac screen.

The simulation produces a series of graphic images showing the increasing age and growth of the tree. The first image is of a slender trunk with one tier of main and daughter branches in colors which designate new growth. Each successive loop of the simulation produces a new graphic image with updated colors to reflect tree age, an increased trunk diameter, and new main and daughter branches.

Main and daughter branches are represented graphically as lines. The tree trunk, however, is roughly cylindrical, with the radius of the cylinder at each branch tier being a function of the effective leaf area supported by the branches above that point.

The sequential design of the graphic output is facilitated by the use of graphic segmentation. Each of the components of the simulation, as described in the hierarchical structure, produces a named graphic segment. The segments can be accessed separately, updated, and redraw to parallel growth and aging of an actual

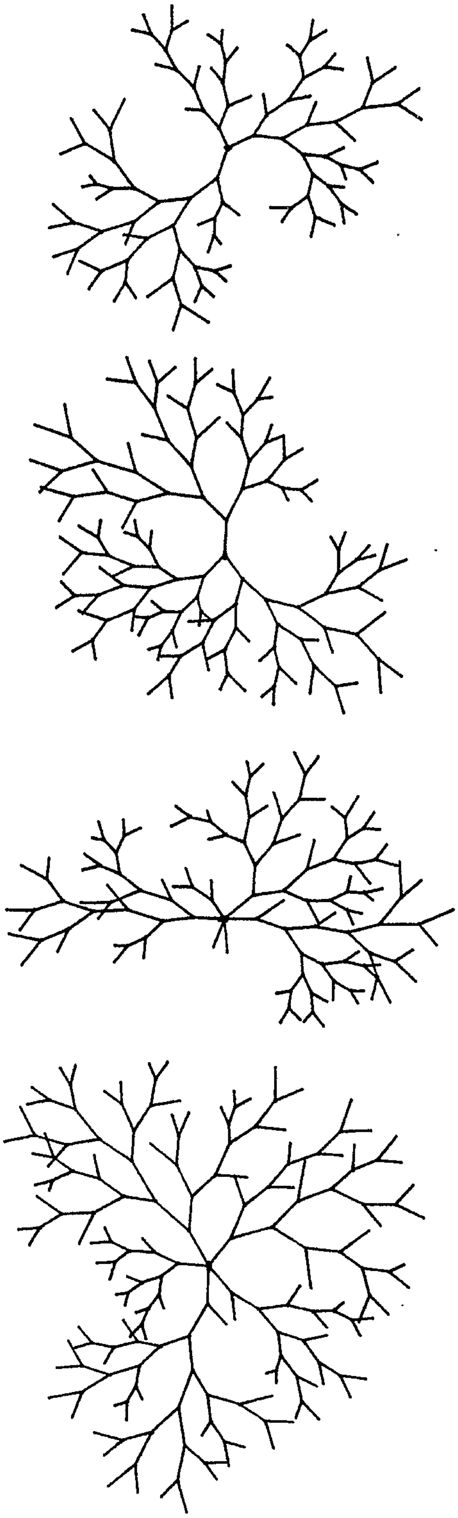

Figure 4. Tree crowns of Terminalia Catappa showing the wide range of architecture found within the species. These simulations were made using all variable means and standard deviations as observed in nature and varying only the seed to the random number generator.

together, comprises the whole tree which also may be accessed for graphic manipulation.

Once the simulation and graphic representation of the species is complete, the rotational and scaling facilities of G.C.S. are utilized allowing the user to view the tree from a variety of viewpoints and perspectives. The user may rotate the tree any number of degrees around its vertical axis and he may change his viewpoint to any point from ground level upward toward the tree crown. A combination of these two options should allow the user any perspective he desires. Once the desired perspective is obtained, the user may choose to enlarge the image, allowing closer scrutiny of any portion of the tree. At any time during these mainpulations, the user may return to the original image; otherwise the manipulations are cumulative in their effect.

7. PRELIMINARY RESULTS

While the validation of any simulation is difficult, special problems occur with a biological system because of the possibilities of extreme individual variation and environmental influences. Preliminary results in the validation process have been encouraging. For example, figure 2 shows an actual Terminalia branch, and a view of a (simulated) tree crown, with a highlighted branch. Figure 1 shows representative simulated Tabernaemontana, Terminalia, and Cameraria specimens, at approximately the same age (two years). While no photographs of equivalent age are immediately available, J. B. Fisher, of Fairchild Tropical Garden, has testified to the botanical reasonableness of the simulated structures.

To simulate the effects of a decrease in branch density (as might be caused by excessive shade), runs were made with successively increasing values for the radius of interaction. These are shown in figure 3, and show the expected modifications in tree structure.

To illustrate some of the graphics functions of the simulator, figures 5 and 6 show the effect of rotating the user's viewpoint horizontally and vertically. Note that the original graphs were drawn using colors to illustrate the age of branch segments; the monochrome reductions used here at least convey the feeling of the originals.

8. CONCLUSIONS

There are three basic purposes for simulating the morphology of a tree. Initially, the simulation provides a means by which a researcher can formulate, refine, and validate conjectures about explanations for those attributes of interest to the investigator. Once the model has been established and validated, the simulation may be used as a measure of the essential elements governing the form and shape of an individual tree. Simulation may be used to predict the range of architectures possible within a species by varying parameter values within their extreme ranges. Simulation may also be used to demonstrate the architectual response of a species to an alteration of its genetic or environmental factors, as indicated above.

In almost all living systems, from molecular to macroscopic scale, there is a strong relation between the (three dimensional) shape of the object being studied to its function in tis enviornment. A major goal for the simulation has been the generation of spatially accurate models; this goal has largely been realized. The use of simulation programs, especially with interactive graphics display, seems to be the only feasible means of investigating such models, especially the complex plant morphological models which are becoming increasingly important in the botanical sciences.

9. FUTURE RESEARCH

The most obvious area for future expansion is the addition of other species of trees to the simulation. Holle [11] categorized tree architectures into twenty three distinct models; the present species studies represent two of these; research will be initiated shortly to investigate a third. Since the project was specifically designed for ease of modification, it is believed that these additions can be made easily within the existing program structure. It is also likely that as research of tree architecture continues, additional exogenous parameters and growth factors may be incorporated into the simulation. Other consideration for future work include: the simulation and graphic representation of leaves and effective leaf area, dying branches and their removal from the data structure and from the graphic display, and the gradual drooping of the lower branches of the tree with age. The simulation presently displays only the trunk with thickness; the branches are represented by lines. This will also be remedied in a future avatar of the simulator.

The perplexing problem of storage to handle the enormous amount of data required for growth parameters and coordinates and the optimization of data structures still exists. It is believed that improvements will be found which will allow the simulation of "larger" trees.

Although simulation output has been graphed on a plotter and the Imlac vector graphics terminal, it has not been graphed on a raster type device. This would allow a much faster and smoother transition between cycles of tree growth, but it would also require the reworking of the data structures used for graphics processing. These changes are planned for the near future, so that the program output can be displayed on a Ramtec 9135 color terminal.

One final change that is contemplated is the production of line images in red/blue stereo. This would not be difficult, given the viewpoint modification capabilities already present in the graphics interface; its usefulness remains to be evaluated.

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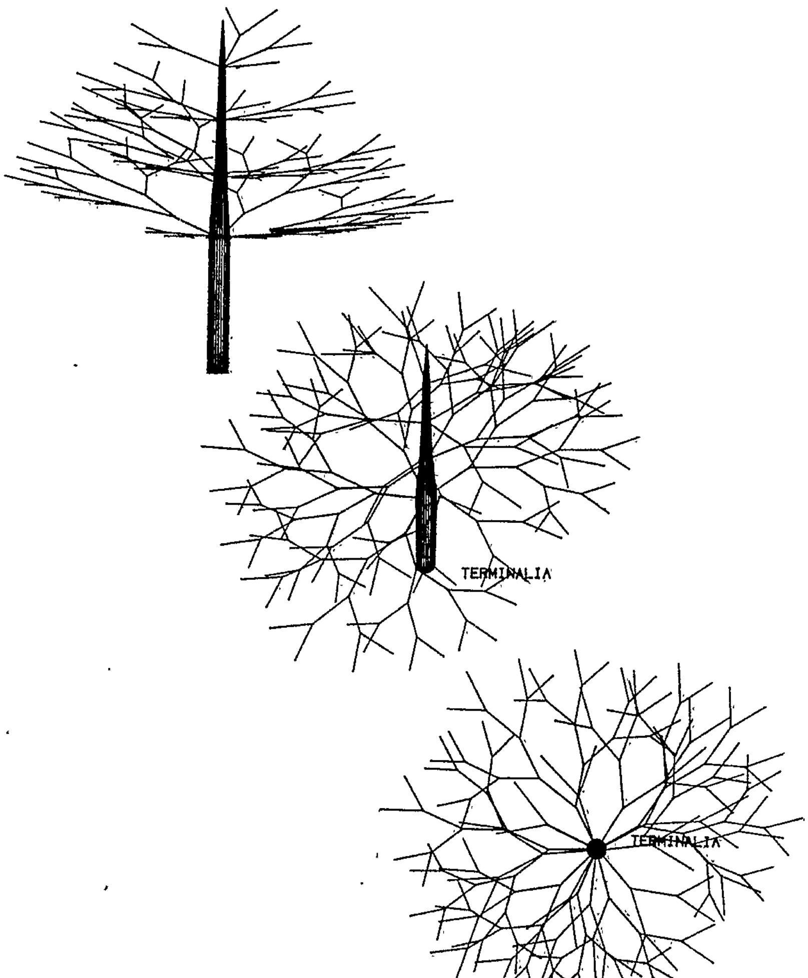

Figure 5.
Rotation of the user's vertical
viewpoint by 30, then 60 degrees

Figure 6. Rotation of the user's horizontal viewpoint in 90 degree increments

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