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Two Geometrical Models of Branching of Botanical Trees

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ABSTRACT

A botanical tree may be regarded as a system of axes which develop by repeated bifurcation. A complicated tree can be described by a few parameters of bifurcation which determine the geometry of the bifurcation process. A bifurcation model (*H*-model) has previously been proposed and shown to be useful for comparison with trees which have branch complexes which approach a horizontal plane (e.g. *Terminalia*). Another bifurcation model (*P*-model) is now proposed which is appropriate to branching systems in which successive branch planes are perpendicular to each other (e.g. *Cameraria* and *Tabernaemontana* of the Apocynaceae). By modification of the *P*-model to take into account a geotropic effect, a more realistic branching model for one kind of tree species is produced. The relationship among these geometrical models of branching is discussed and illustrated with computer simulations.

Key words: computer simulations, tree crown geometry, branching patterns, bifurcation models, *Terminalia*, *Cameraria latifolia*, *Tabernaemontana*. sp.

INTRODUCTION

In 1971, a geometrical model of branching was proposed which enabled the shape of botanical trees with a few branching parameters to be simulated by a digital electronic computer (Honda, 1971). The model has been improved on the basis of the actual observation of a tropical tree, *Terminalia* (Fisher and Honda, 1977), and has been used to investigate the functional significance of branching patterns (Honda and Fisher, 1978, 1979; Fisher and Honda, 1979*a, b*; Honda, Tomlinson and Fisher, 1981). The model is especially useful for plagiotropic branch complexes, i.e. those flattened dorsiventrally, and may be applicable to many botanical trees. However, we have encountered trees (e.g. *Cameraria* and *Tabernaemontana*, both in the Apocynaceae) in which the plane of bifurcation of a branch unit is perpendicular to the plane of bifurcation of its mother branch unit so that the branch complex becomes extended in three dimensions. The original branching model cannot be applied to such trees.

On the basis of measurements obtained from *Cameraria* and *Tabernaemontana*, we have now made another geometrical model of branching in which planes of successive bifurcations are perpendicular to each other. In this paper the new branching model is described in detail and compared with the first branching model.

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MATERIALS AND METHODS

Observation, measurement and photography of *Cameraria latifolia* L. and *Tabernaemontana* sp. were performed at Fairchild Tropical Garden (Miami). Branching angles and ratios of branch lengths were measured directly on trees. Angles of branches and branch planes with respect to gravity were measured using a weighted circular protractor.

Calculations were carried out by IBM system 370 at the Harvard University Office of Information Technology. Simulations were drawn by an electronic digital microcomputer with a disc memory (P652 and DAS 604, Olivetti) and an XY plotter (WX 535, Watanabe-sokuki, Tokyo) at the Kanebo Institute for Cancer Research, Kobe, Japan. Drawings for a stereoscopic view were made with an XY plotter by rotating the angle of view by 3°.

MODELS AND RESULTS

The two branching models

Here we will regard a tree as a system of axes which develop by a process of repeated bifurcation. Bifurcation takes place synchronously throughout the tree at each discrete time interval, N (see Table 1). We will consider generally a unit operation for bifurcations. By repetition of such a unit operation, we can generate a branch complex or a total tree.

TABLE 1. Symbols of branching parameters used in the present paper

N	Discrete time in a computer simulation, or order of branching
R_1	Ratio of length of a more vigorous branch unit to its mother unit
R_2	Ratio of length of a less or equally vigorous branch unit to its mother unit
θ_1 and θ_2	Branch angles (in degree) of a more and less vigorous branch unit, respectively; their signs are opposite
β	Angles (in degrees) between a branch unit and the direction of gravity
β_0	Value of the first branch unit in a lateral branch complex

A branch unit $P_A P_B$ is fixed arbitrarily in three-dimensional space [Fig. 1 (a), (b)]. When a bifurcation takes place at P_B , we will determine two daughter branch units $P_A P_i$ ($i = 1$ and 2) geometrically by the following principles.

(1) The three branch units $P_A P_B$, $P_B P_1$ and $P_B P_2$ are assumed to be contained in the same plane (a *branch plane*).

(2) Since $P_A P_B$ is fixed, the plane ($P_A P_B P_1 P_2$) could be rotated around $P_A P_B$ as an axis. We can consider two possibilities. In the first possibility the direction of gravity has been considered. The branch plane ($P_A P_B P_1 P_2$) is fixed so as to be the closest to a horizontal plane, that is, it has the least possible slope [Fig. 1(a)]. So, $P_A P_B$ is the steepest gradient line on the initial branch plane with respect to gravity. The new branch plane ($P_B P_1 P_{11} P_{12}$) is fixed in the same manner as shown in Fig. 1(a). We can call this the *horizontal plane model* (*H-model*), which was described previously in Honda (1971).

In the second possibility [Fig. 1(b)] before the branch plane ($P_A P_B P_1 P_2$) is fixed, we consider the previously determined branch plane which contains $P_A P_B$, its sister branch $P_A P_C$ and its mother branch $P_0 P_A$. The branch plane ($P_A P_B P_1 P_2$) is fixed so as to be perpendicular to branch plane ($P_0 P_A P_B P_C$). Next, the new branch plane ($P_B P_1 P_{11} P_{12}$) is fixed so as to be perpendicular to branch plane ($P_A P_B P_1 P_2$). We can call this the *perpendicular plane model* (*P-model*).

(3) After establishing the initial branch plane, we can determine a daughter branch $P_B P_i$ with the branch length ratio R_i ($= P_B P_i / P_A P_B$) and the branch angle θ_i between

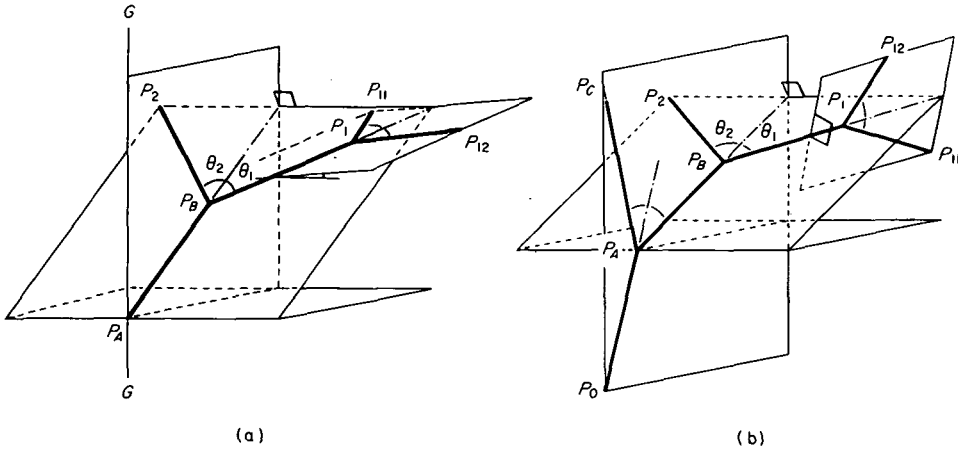


FIG. 1. Branching geometry of the two models. A mother branch unit $P_A P_B$, and two daughter branch units $P_B P_1$ and $P_B P_2$, belong to a branch plane $P_A P_B P_1 P_2$. θ_1 and θ_2 are branching angles. Branch length ratio is $R_i = P_B P_i / P_A P_B$ ($i = 1, 2$). A higher order branch is also shown in which branch unit $P_B P_1$ bifurcates into $P_1 P_{11}$ and $P_1 P_{12}$. (a) *H*-model where plane $P_A P_B P_1 P_2$ is perpendicular to plane $G P_A P_B$ (GG , the direction of gravity). (b) *P*-model where plane $P_A P_B P_1 P_2$ is perpendicular to previous plane $P_0 P_A P_B P_C$ and the subsequent plane $P_B P_1 P_{11} P_{12}$.

$P_A P_B$ and $P_B P_i$. $P_i(x_i, y_i, z_i)$ is represented with $P_0(x_0, y_0, z_0)$, $P_A(x_A, y_A, z_A)$ and $P_B(x_B, y_B, z_B)$ as follows:

Horizontal plane model (*H*-model)

$$\begin{aligned} x_i &= x_B + R_i(u \cos \theta_i - Lv \sin \theta_i / \sqrt{u^2 + v^2}), \\ y_i &= y_B + R_i(v \cos \theta_i + Lu \sin \theta_i / \sqrt{u^2 + v^2}), \\ z_i &= z_B + R_i w \cos \theta_i, \end{aligned}$$

where $u = x_B - x_A$, $v = y_B - y_A$, $w = z_B - z_A$, $u_0 = x_A - x_0$, $v_0 = y_A - y_0$, $w_0 = z_A - z_0$, and $L = \sqrt{u^2 + v^2 + w^2}$.

Perpendicular plane model (*P*-model)

$$\begin{aligned} x_i &= x_B + R_i[u \cos \theta_i + L(v_0 w - v w_0) \sin \theta_i / 1], \\ y_i &= y_B + R_i[v \cos \theta_i + L(w_0 u - w u_0) \sin \theta_i / 1], \\ z_i &= z_B + R_i[w \cos \theta_i + L(u_0 v - u v_0) \sin \theta_i / 1], \end{aligned}$$

where $1 = \sqrt{(u_0 v - u v_0)^2 + (v_0 w - v w_0)^2 + (w_0 u - w u_0)^2}$.

(4) By using these formulae, we can calculate the position of daughter branches at successive bifurcations. At each bifurcation two kinds of branches are produced. Generally these two branches differ from each other (e.g. Fisher, 1978). Branch unit 1 is a more vigorous one and branch unit 2 is either a less or an equally vigorous one. $P_B P_i$ is determined by using R_i and θ_i ($i = 1$ and 2 , specifying each kind of branch unit) as noted in Table 1. Usually the signs of θ_1 and θ_2 are opposite. In the *H*-model, the signs of the branch angles change at every branch order along a main axis, so that a zigzag main axis of unit 1's with alternating direction is formed (rule 3 of Fisher and Honda, 1977). In the *P*-model the signs of the branch angles are chosen so that branch unit 2 is always uppermost; therefore a main axis is established as the lower side of a branch complex.

Simulations

We will continue to explain the two branching models by using the results of some computer simulations. The trees simulated in Figs 2(a), (b) show a vertical branch unit, a trunk, which is parallel with the z -axis [= GG or gravity in Fig. 1(a)]. The first bifurcation takes place in the x - z plane. The results after three bifurcations ($N = 3$) are shown in Fig. 2(a) (H -model) and Fig. 2(b) (P -model). The patterns for the two models are exactly the same at $N = 1$ and 2. However, the third and subsequent bifurcations ($N \geq 3$) produce remarkable differences between the H - and P -models [cf. Figs. 2(a), (b)].

The essential difference between the two models is the effect of gravity. In the H -model, branches detect the direction of gravity and so influence the direction of new branch planes which contain their daughter branches. In contrast with the H -model, the direction of gravity does not effect patterns in the P -model other than determining that

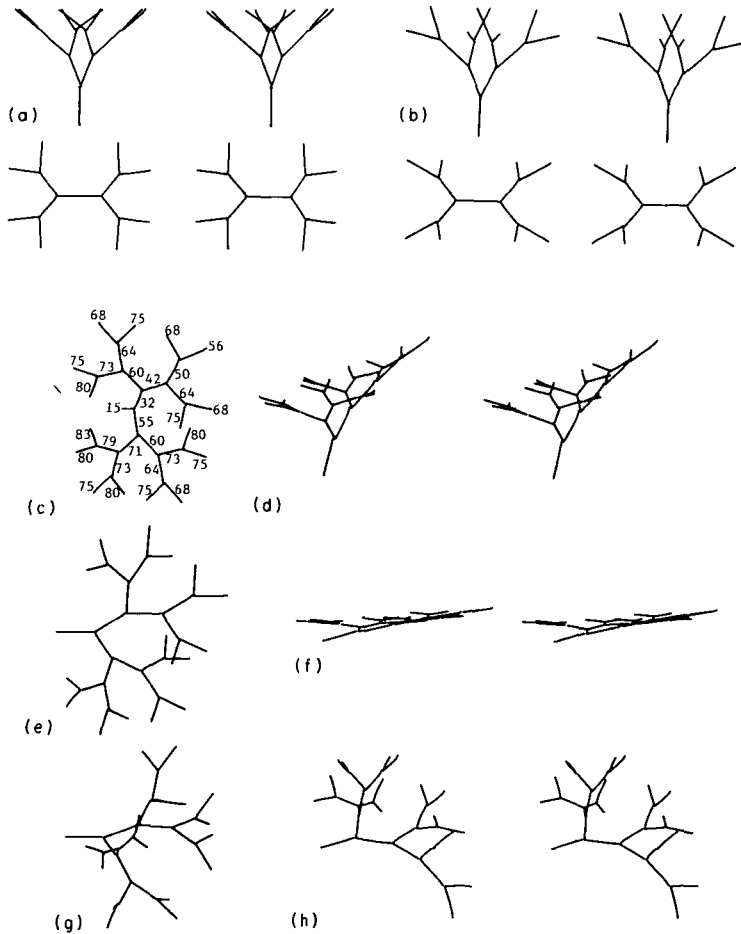


FIG. 2. Simulations of branching patterns. $\theta_1 = -\theta_2 = 35^\circ$ and $R_1 = R_2 = 1.0$ for (a) and (b) $\theta_1 = 29^\circ$, $\theta_2 = -54^\circ$, $R_1 = 0.99$ and $R_2 = 0.85$ for (c)–(h). (a) Stereoscopic side view and top view according to the H -model. (b) Stereoscopic side view and top view according to the P -model. (c), (d) Top view and stereoscopic side views, respectively, of a branch complex with $\beta_0 = 15^\circ$ according to the H -model. (e), (f) the same, but with $\beta = 75^\circ$. (g), (h) The same views of complex with $\beta = 75^\circ$, but according to the P -model. Numerals in (c) indicate the β values of the respective branch unit.

unit 2 is always uppermost. In fact, when bifurcation is symmetrical, that is, units 1 and 2 have the same length and branch angle, gravity is without influence on the P -model.

The effect of the direction of gravity on the H -model is represented in Figs 2(c)–(f). In Fig. 2(c), the β values (see Table 1) are represented for each axis. The β value of the first branch unit, β_0 , is 15° . In the more distal branch units, the β value becomes progressively closer to 90° , i.e. the branch unit becomes horizontal asymptotically, as can be seen in side view shown in Fig. 2(d). Figures 2(e), (f) are examples when β_0 , is 75° . In this example, the branch complex becomes dorsiventrally flattened. Figs 2(g), (h) are examples of the P -model in which the parameter values (β_0 , R_i , θ_i) are those used in Figs 2(e), (f).

First example. The shape of two tree species developed according to the P -model can now be investigated. The first example is *Cameraria latifolia*, which consists of many thin

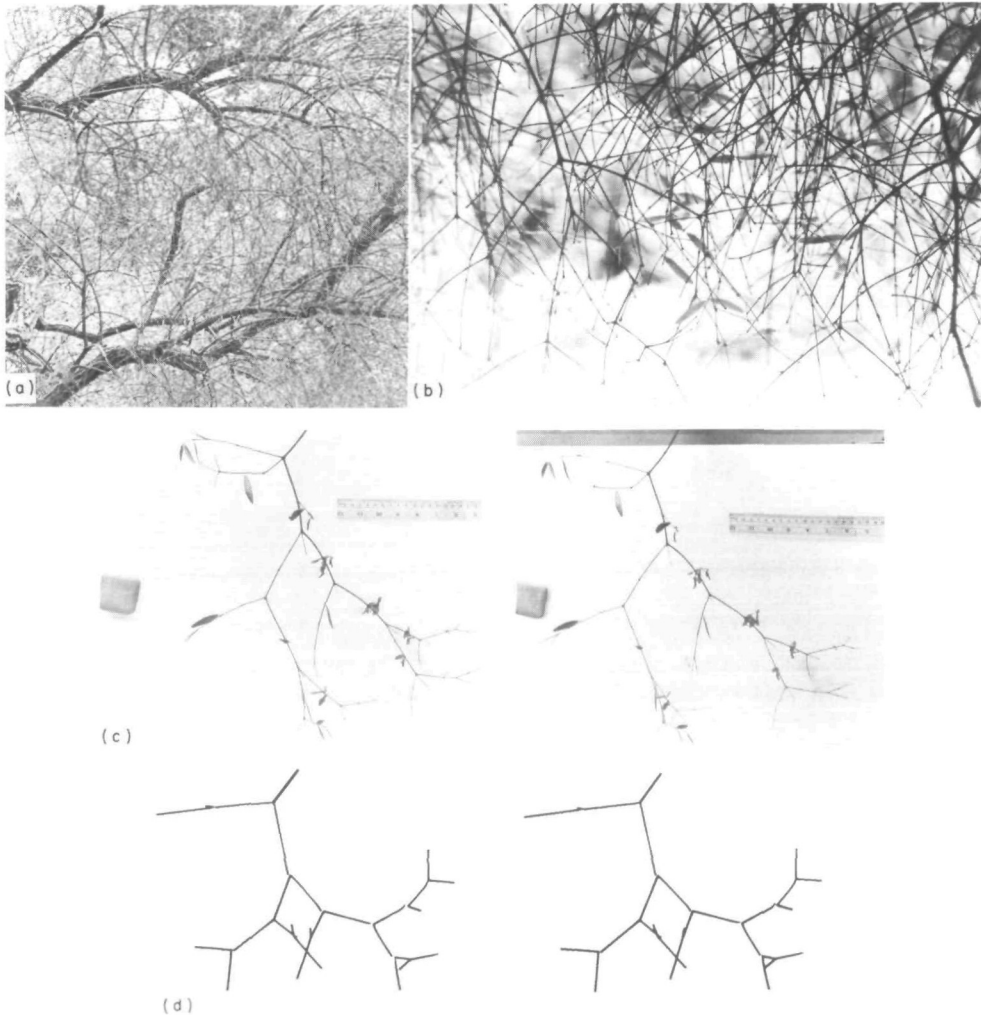


FIG. 3. *Cameraria latifolia*. (a), (b) Photographs of branching pattern in the tree crown. (c) Stereoscopic photographs of a real branch complex taken from two positions which were 33 cm apart horizontally from each other. (d) Stereoscopic computer simulations of a branch complex using the P -model with $\theta_1 = -\theta_2 = 48.2^\circ$ and $R_1 = R_2 = 0.834$. Branching was artificially limited according to the actual branching pattern in (c).

twigs [Figs. 3(a), (b)]. Its precise morphology is somewhat more complex than the model since it branches into three and not two axes at each articulation. The third branch unit which lies between two continuing daughter units is very thin and short and represents either a flowering shoot or an aborted axis [Figs 3(c) and 4(a)] which does not continue branching. We can neglect the third branch unit and regard branching of *C. latifolia* as a simple bifurcation. Another consideration in the real tree is the presence of leafy short shoots. As shown in Fig. 4(a), branching which adds permanent long shoots takes place at node 2, while further successive decussate branchings take place at nodes 3 and 4. These leafy short shoots do not branch further. Branching at node 5 adds two permanent long shoot branches which repeat the branching process.

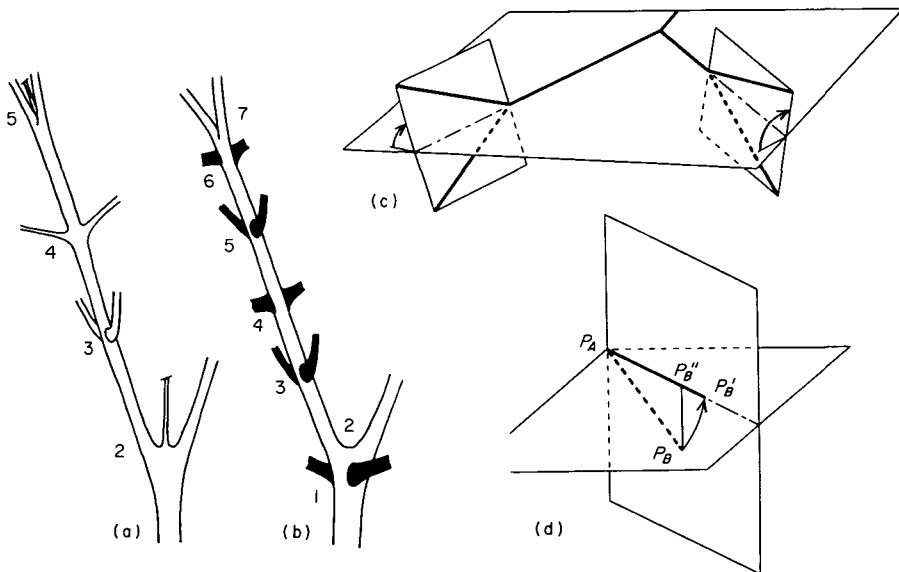


FIG. 4. (a) Schematic illustration of branch unit of *C. latifolia*. (b) Similar illustration of *Tabernaemontana* sp. Branch planes at nodes 2 and 5 in (a) or at nodes 2 and 7 in (b) are perpendicular to each other. Shoots from nodes 3 and 4 in (a) are short and leafy. Petioles (solid black) are at nodes 1, 3, 4, 5 and 6 in (b). (c) Diagram explaining the measurement of the angle (arrows) between two successive branch planes in the *P*-model. (d) Diagram explaining the geotropic approximation. When a branch unit $P_A P_B$ is downward, the branch unit is rotated upward into $P_A P_B'$ in three-dimensional space. $P_A P_B'$ is horizontal and its length is the same as $P_A P_B$ and its direction is the same as $P_A P_B''$ which is the projection of $P_A P_B$ on a horizontal plane.

Since the phyllotaxis is decussate and permanent branches are produced at odd intervals [usually separated by two nodes as in Fig. 4(a)], successive branch planes are perpendicular to each other as in the *P*-model of branching. For quantitative information, we measured the angle between two branch planes as shown by arrows in Fig. 4(c) in a branch complex [Fig. 3(c)] of *C. latifolia*. The average value was 86.4° (sample size, 36) corresponding closely to the *P*-model in which an angle of 90° is assumed. A computer simulation of a branch complex using the *P*-model and the observed parameter values of *C. latifolia* [$\theta_1 = -\theta_2 = 48.2^\circ$ (sample size, 30) and $R_1 = R_2 = 0.834$ (14)], resulted in Fig. 3(d), which was compared with the photograph of an actual branch [Fig. 3(c)]. Branching was artificially limited to the same number of branch orders as in the actual branching pattern observed in Fig. 3(c).

Another computer simulation of the branching pattern of *C. latifolia* in which branching takes place to a high order without limitation is shown in Fig. 5(a). The pattern

is complicated but resembles Fig. 3(b), although we have not made a statistical analysis to measure the precise degree of similarity.

Second example. The second example using the *P*-model is *Tabernaemontana* sp., the morphology of which has been previously described by Prévost (1972). The basic branching pattern of *Tabernaemontana* is shown in Fig. 4(b). The phyllotaxis is decussate, with permanent branches added at intervals separated by four nodes [nodes 3–6 in Fig. 4(b)]. Consequently, successive branch planes are at right angles to each other as in the *P*-model. In Fig. 4(b) this is shown as a pair of branches at nodes 2 and 7 which are almost perpendicular to each other. The measured average angle between two branch planes in a small tree of *Tabernaemontana* sp. as shown in Fig. 4(c) (arrows) was 89.3° (sample size, 28). The result of a computer simulation of a sapling of *Tabernaemontana* sp. is shown in Fig. 2(b).

The question can be asked if a lateral branch complex of *Tabernaemontana* sp. [Figs 6(a)–(c)], instead of a main branch, is adapted to the *P*-model? It is clearly not the *H*-model because it is not dorsiventrally flattened. Using parameter values derived from lateral

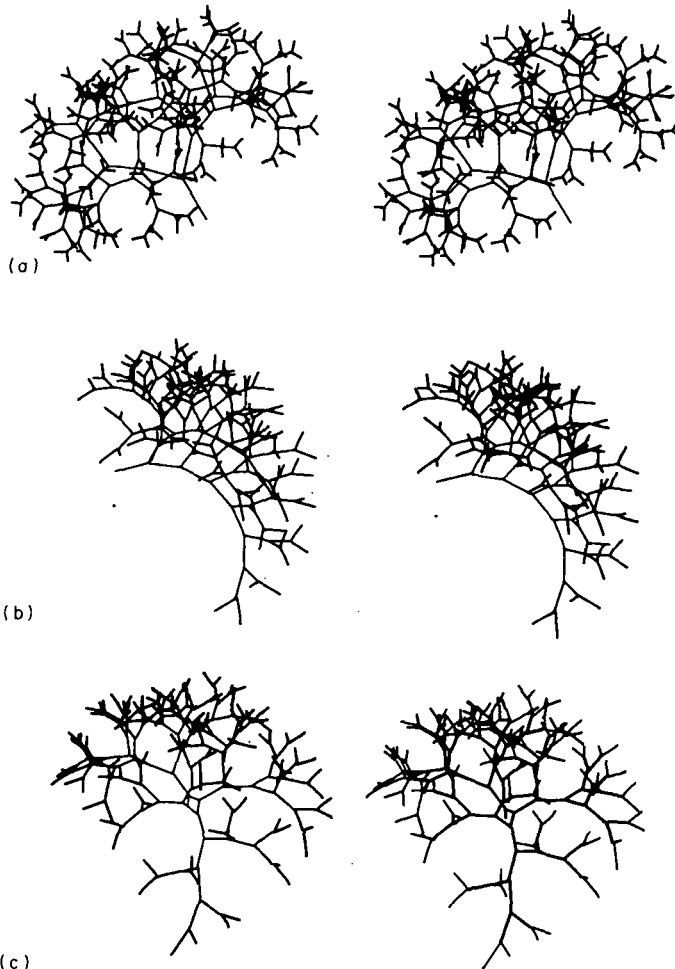


FIG. 5. Stereoscopic simulations of branching patterns. (a) Branch complex of *C. latifolia* using the *P*-model at $N = 8$ with $\theta_1 = -\theta_2 = 48.2^\circ$ and $R_1 = R_2 = 0.834$. (b), (c) Views from two sides of a complex of *Tabernaemontana* using the *P*-model with $\theta_1 = 29^\circ$, $\theta_2 = -54^\circ$, $R_1 = 0.99$ and $R_2 = 0.85$ (from Honda *et al.*, 1981) without limitation of bifurcation.

branches of *Tabernaemontana* sp., the results of computer simulation with the *P*-model are shown in Figs 5(b), (c) and 7(a). Comparing real and simulated complexes, branching is considerably limited in an actual branch complex [cf. Figs 5(b) and 6(a)]. We have developed an appropriate simulation program on limitation of branching (Honda *et al.*, 1981), and when branching is limited according to this program, the resulting simulation appears as Fig. 7(b). The great difference between an actual branch [Fig. 6(a)] and a theoretical one [Fig. 7(b)] is the orientation of the main axis of the lateral branch. Figure 6(a) shows that a branch unit belonging to a main axis grows downward at first but curves gradually upward and bifurcates at the next branch order. This curvature of the branch unit is an example of geotropism. The bending is probably caused by a changing primary growth response in the new branch unit, although a later effect of reaction wood might also be a contributing factor (Fisher and Stevenson, 1981). A curved branch unit is replaced by a horizontal straight one as an approximation in our simulations. Geometrically this is formulated as in Fig. 4(d). When a branch unit $P_A P_B$ is extended downward, it is rotated in three-dimensional space upward to $P_A P'_B$ in a horizontal plane, where the length of $P_A P'_B$ is equal to that of $P_A P_B$ and is the length used in the program. The direction of $P_A P'_B$ is the same as the direction of $P_A P''_B$ which is the image of $P_A P_B$ projected orthogonally on to a horizontal plane. We will call this procedure the *geotropic approximation*.

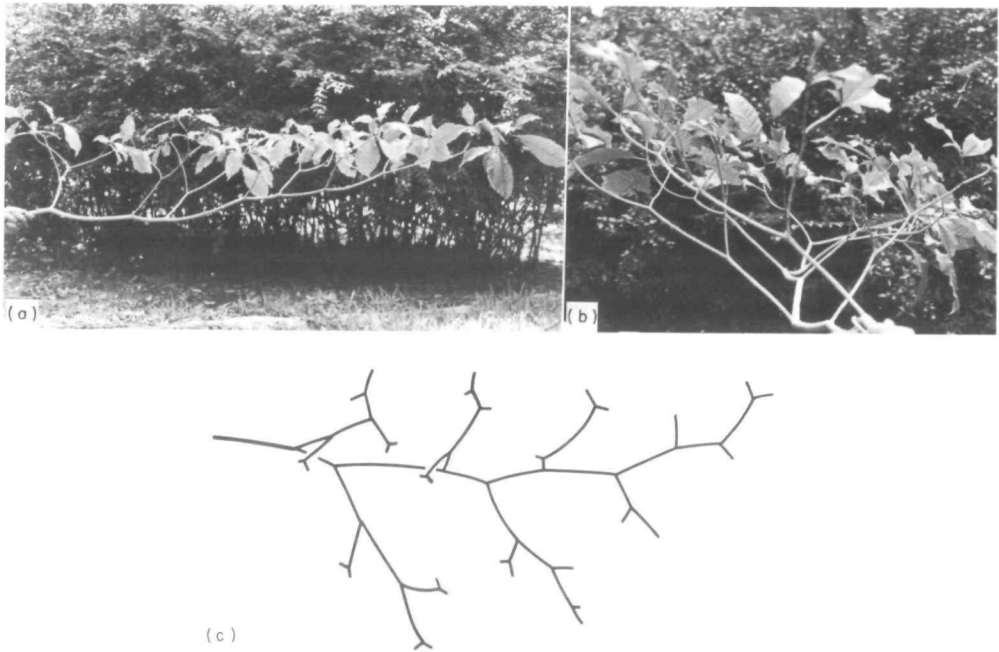


FIG. 6. *Tabernaemontana* sp. (a), (b) Photographs of a lateral branch complex in two side views, similar to Figs 7(j)–(k). (c) Drawing made from photograph of a branch complex viewed from below, similar to Fig. 7(i) (from Honda *et al.*, 1981).

Figure 7(c) shows the result of a computer simulation using the *P*-model, but now applying the geotropic approximation to the main branch units of a lateral branch complex shown in Fig. 7(b) in which the β_0 value is 35° . Figures 7(d), (e) show the result of simulations where the β_0 value is 55° and 75° . Figures 7(i)–(k) are all the same simulation as Fig. 7(e), but represented stereoscopically from three different views, and they may be compared with the real complexes, shown in Figs 6(a), (b), respectively.

Figures 7(f)–(h) are the results of a computer simulation with the same parameter values as in Figs 7(i)–(k) but using the *H*-model instead of the *P*-model; the resulting pronounced dorsiventrality is very clear.

We can consider a tree of *Tabernaemontana* sp. to consist of branch complexes belonging to two contrasted phases. The first is an initial phase in which a branch unit is orthotropic and bifurcates symmetrically. Measurement of a young specimen of *Tabernaemontana* sp. gave values $\theta_1 = -\theta_2 = 35^\circ$ and $R_1 = R_2 = 1.0$ (sample size, 5) for this phase. In computer simulation these produce the branching patterns shown in Fig. 2(b). In the second phase a lateral branch complex is represented by Figs 7a–c. Using values derived from a plagiotropic and asymmetric branch unit where $\theta_1 = 29^\circ$, $\theta_2 = -54^\circ$, $R_1 = 0.99$ and $R_2 = 0.85$ (Honda *et al.*, 1981), and simulating with the geotropic approximation, a branch complex in the second phase can be reproduced [Figs 7(c)–(e), (i)–(k)]. The actual mechanism whereby such a phase change is made by the tree may be related to an ontogenetic change in which the system becomes more sensitive to the influence of gravity as the horizontal plane is approached by the distal branches. On the other hand, the tree may have a switch mechanism with a critical gradient value, above which a branch unit is in the initial phase and below which it enters the second phase. Reiteration in a matured tree is the contrary case in which a change takes place from the second phase back to the first phase (Hallé, Oldeman and Tomlinson, 1978). However, this change may be very abrupt if it is initiated by a previously resting meristem.

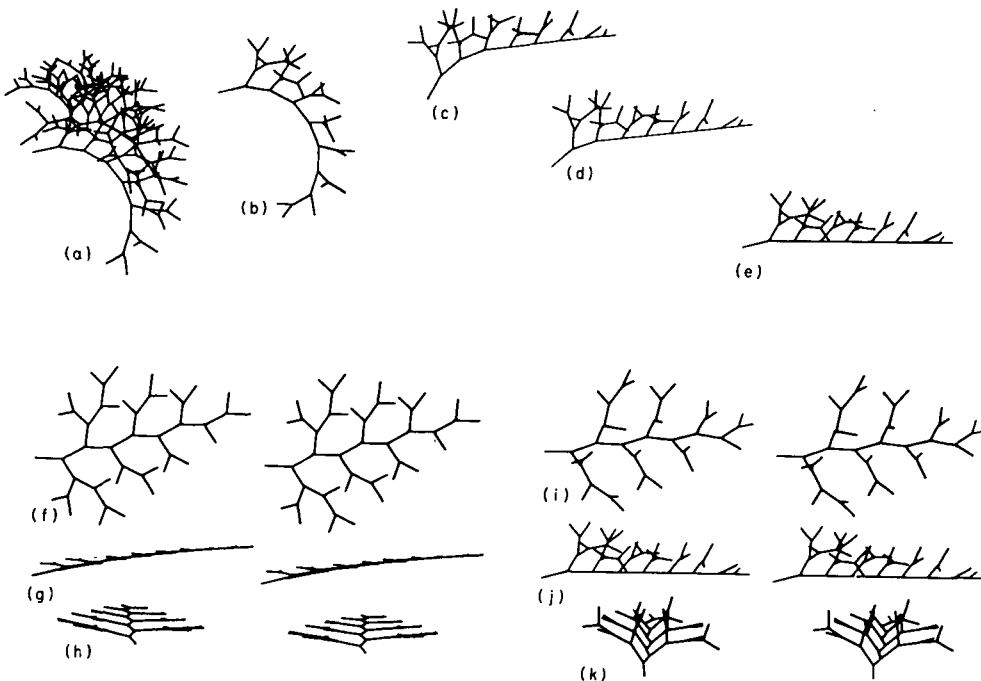


FIG. 7. Simulations of branching patterns in a lateral branch complex of *Tabernaemontana* with same parameters as Figs 5(b), (c). (a) The same pattern as Fig. 5(b). (b) The same pattern as (a) except that branching was limited according to the model with different flow rates ($f = 1/2$; Honda *et al.*, 1981). (c) The same as (b) except for application of the geotropic approximation and $\beta_0 = 35^\circ$. (d), (e) The same as (c) except that $\beta_0 = 55^\circ$ and 75° respectively. (f), (g), (h) Stereoscopic views from the top, sides, and end, respectively, of a complex using the *H*-model and same conditions as in (e). (i), (j), (k) Stereoscopic views from top, sides, and end, respectively, of a complex using the *P*-model and same conditions as in (f), (g) and (h).

DISCUSSION

The present paper is intended to describe a new branching model, the *P*-model, in comparison with a former model, the *H*-model. The *P*-model is a special case of the more general model in which successive branch planes rotate with a definite divergence angle related to spiral or opposite phyllotaxis. In the *P*-model, the divergence angle is 90°. The general model is still at a theoretical stage and needs more actual observations before it can be refined.

We have investigated branching models which are influenced by gravity in differing ways. The orientation of successive branch planes is unchanging and in a constant relationship to gravity in the *H*-model. Some change in orientation with respect to gravity occurs in the *P*-model which is modified by the process we have called geotropic approximation. Finally, the branch planes are perpendicular to one another without respect to the direction of gravity in the *P*-model proper. A tree may try to maintain its own original branching rule under the influence of gravity and establish an equilibrium point between its own rule and gravity. Such an equilibrium point is different among tree species, since some respond greatly to gravity while others do not.

Our purpose in developing these models was to make a tree-like body close to an actual tree and in so doing develop an appreciation of how many ecological and morphogenetic factors influence tree form. The *H*-model has been very useful in objectively establishing that branching angles, size of branch tiers, and branch length ratios observed in nature are those that maximize effective leaf area and its equitable distribution (Fisher and Honda, 1979*a*; Honda and Fisher, 1978, 1979). Simulations of two-dimensional branching patterns have also been useful in studying the growth and reproductive strategies of rhizomatous plants (Bell, Roberts and Smith, 1979). Additionally, simulation studies have shown that relatively simple controls or constraints on bifurcation are able to give rise to the highly complex patterns found in real trees (Honda *et al.*, 1981). Ultimately, the programs we have developed may contribute to forest ecology, in which a tree-like body is a basic component, since it may allow us to use an electronic computer facility for understanding an integrated system. In the present paper we have investigated geometrical models of branching in three-dimensional space. Frequency of branching, or limitation of bifurcation, has been investigated elsewhere (Honda *et al.*, 1981). By combining the geometrical branching model with one that limits bifurcation, a realistic and useful tree-like model can be created.

Some of the remaining parameters still to be investigated in order to produce a tree-like body close to an actual tree are the girth of a branch (or a trunk) and the variation and differentiation of branches as tree ages, such as the probabilistic change from the initial phase to the second phase of branching. The former subject has been investigated empirically and theoretically by Yamakoshi *et al.* (1976), Oohata and Shinozaki (1979) and McMahon and Kronauer (1976). The latter subject has been considered qualitatively by Hallé *et al.* (1978).

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