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CONTROL OF DEVELOPMENT IN THE BIFURCATING BRANCH SYSTEM OF TABEBUIA ROSEA: A COMPUTER SIMULATION[1]

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A computer model, simulating geometry and development of the branch system of *Tabebuia rosea* DC., was constructed. Early in development there is a transition from symmetric bifurcation and exponential increase in branch number to asymmetric branching, manifest in the morphological differentiation into leaders and lateral shoots and in the progressive reduction of increase in branch numbers. This reduction is an inherent geometric property of botanical trees and similar, branched systems. It results from the discrepancy between the increase in crown surface with the second power of branch order and the exponential increase in branches supplying the surface. In symmetric branching, mother and daughter branches are arranged in the same plane; in asymmetric branching, branch planes of leaders and laterals are inclined against each other. Development was assumed to be controlled by flux distribution within the tree: (1) Flux supplied to a terminal branch determines its vigor and branching potential. (2) Asymmetric branching results from asymmetric flux distribution. (3) Feedback interaction between main and lateral branches causes "apical control," i.e., enhanced growth of leaders as compared with lateral branches. (4) Growth of the branch system as a whole is limited by the sigmoid increase with time in flux to the tree. Reiteration of the set of geometric and developmental rules simulates time-dependent changes during normal development and regeneration of the branch system, which are strikingly similar to those observed in growing *Tabebuia* trees, suggesting that simulated controls are similar to those operating in real trees.

Introduction

Understanding of trees, the largest and most complex plants, has advanced significantly during the past decade (TOMLINSON 1983). (1) The principles of construction underlying the enormous variety in tree architecture, as observed particularly in tropical trees, has been analyzed (HALLÉ et al. 1978). (2) Increasing use of computers has enabled progressively more precise quantification and simulation of branch systems of trees (LÜCK and LÜCK 1982). (3) The interrelation between tree structure and water relations, i.e., the hydraulic architecture of trees, has been studied experimentally (ZIMMERMANN 1978; EWERS and ZIMMERMANN 1984). (4) The mechanical design of trees has been analyzed in detail (MCMAHON 1975*a*; WILSON and ARCHER 1979).

Mathematical models analyze trees at various levels. In the simplest case, the elements of a branched system are described and quantified (LÜCK and LÜCK 1982). The geometry of small, treelike systems was first modeled by HONDA (1971), based on relatively few parameters such as branch angle, branch unit length, and ratio between lengths of consecutive units. This geometric branch model was then used to simulate the regular, bidimensional, plagiotropic branch system of *Terminalia catappa* (FISHER and HONDA 1977) and to show that this branch system is optimized for maximum light interception (HONDA and FISHER 1978). Simple geometric considerations reveal that the branch number in such a branch system must be progressively restricted at higher branch orders, i.e., that bifurcation ratios must decline with increasing size of a tree (BORCHERT and SLADE 1981). Mechanisms to achieve this reduction in branch numbers through branch interaction were explored by HONDA et al. (1981).

In studies of the hydraulic architecture of trees, ZIMMERMANN (1978) observed that water flow to lateral tree branches is restricted relative to flow in the main trunk, presumably resulting in enhanced growth potential and, hence, "apical control" by the leader.

To gain a better understanding of the control of development in trees as complex branched systems, we combined mathematical rules determining the specific branch geometry with postulated developmental controls, based on the hydraulic architecture of trees, in a simulation of the relatively simple, bifurcating branch system of *Tabebuia rosea*, a tropical tree.

Material and methods

The morphology of shoot growth and branching in *Tabebuia rosea* DC. (Bignoniaceae), as observed in San José, Costa Rica, was described in detail (BORCHERT and TOMLINSON 1984).

The program for simulating the development of

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[1] In memory of MARTIN H. ZIMMERMANN, Charles Bullard Professor of Forestry at Harvard University and director of the Harvard Forest, Petersham, Massachusetts, who died on March 7, 1984.

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the branch system of *Tabebuia* was written in FORTRAN and executed on the University of Kansas Honeywell System. Output was printed on a DECWRITER IV or plotted on a Hewlett-Packard HP21 Plotter.

Simulation of the tridimensional branch system of *Tabebuia* was based on the geometric branching model of HONDA (1971), modified as described below. As many important structural and functional properties of branched systems reveal themselves only at higher orders of branching, up to 15 orders of branching were calculated. A branched system of 15 orders contains $2^{15} = 32{,}768$ potential links (= branch points). To minimize the problems resulting from the complexity of such a system, the simulation program was aimed at attaining the following goals: (1) generating a variety of outputs that facilitate analysis of the dynamics of branching and its control in entire trees or single branches; (2) minimizing computing time and memory requirements; and (3) maintaining adaptability of the program to the modeling of branch systems of different architecture.

MAIN CHARACTERISTICS OF THE PROGRAM

1. As each link (P_i) gives rise to two daughter links (P_{2i} and P_{2i+1}), the branch system is ordered and numbered as a binary tree (fig. 1). Where branching is unequal (asymmetric), the daughter link on the main branch (leader) is even numbered (P_{2i}), and the lateral is odd numbered (P_{2i+1}). Implicitly, all links of order N are numbered between 2^N and $(2^{N+1} - 1)$; numbers of all links on main branches are multiples of 2; and numbers of laterals are multiples by 2 of an odd number, which indicates the site of insertion of the lateral on the leader (fig. 1).

2. At higher branch orders, only a small fraction of potential branches actually exists in a botanical tree. To reduce memory requirements by ca. 90%, only information for the first three orders of links ($2^3 = 8$) was stored entirely. At higher orders, links for 12 orders (orders 4–15) of only one tree quadrant were considered. An array corresponding to the set of all potential links in this quadrant contains references to a table that stores the following information for each actual link: number; order; x, y, and z coordinates; branching angle; flux; branching potential; number of descendant links.

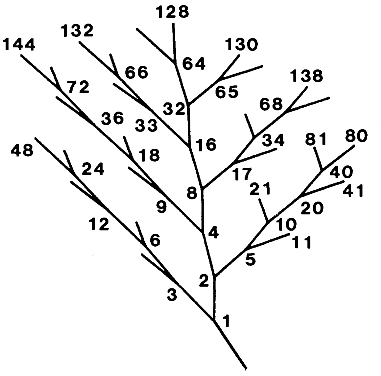

FIG. 1.—System of branch numbering used in computer simulation of *Tabebuia* branching. Branch numbers of minor lateral branches were omitted.

3. Coordinates of links in quadrants 2–4 are calculated by rotating quadrant 1 one to three times around the z-axis by 90° (divergence angle α of HONDA [1971]). This mode of calculation confers a radial symmetry to the tree model, which is more similar to the radial symmetry of botanical trees than the bilateral symmetry around the x- and y-axes, which results if the absolute values of x and y coordinates of corresponding links in all four quadrants are kept equal but changed in sign in the various quadrants.

4. Bidimensional projections of any quadrant or of the entire tree (x-y, x-z, or y-z projection, with or without perspective) can be drawn by plotter (figs. 2, 3); numbers (fig. 1), fluxes, or branch angles of all links can be printed or drawn by the plotter. Symbols and definitions of branching and control parameters are in table 1.

Results

GEOMETRY AND CONTROL OF BRANCHING: OBSERVATIONS AND ASSUMPTIONS

BRANCHING GEOMETRY.—*Tabebuia* represents the architectural model of Leeuwenberg as described

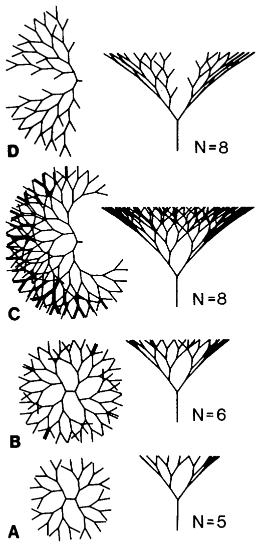

FIG. 2.—Projections (x-y on left, y-z on right [to avoid excessive density, projection of two quadrants only]) of a symmetrically branched tree without perspective. *A*–*C*, Order $N = 5$ to $N = 8$ without reduction in branch number at higher order. $\theta_1 = \theta_2 = 21°$; $R_1 = R_2 = 1$; $R_f = 0.5$; $F_1 = 30$. *D*, Branch reduction at order $N = 8$ resulting from use of $R_f = 0.7$ and $F_1 = 17$.

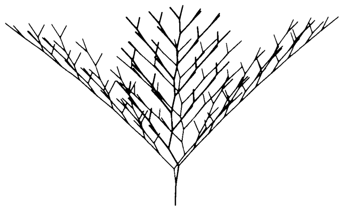

FIG. 3.—Simulation of the branch system of *Tabebuia* for 11 orders using the default parameters listed in table 1. Projection (y-z) of all four quadrants of the tree with perspective.

in HALLÉ et al. (1978). As in most trees of the Bignoniaceae, leaves are decussate. Initially, saplings form a straight, unbranched stem. Growth of the terminal bud is then arrested, and shoot growth continues by the symmetric outgrowth of two opposite, lateral buds. The plane of each bifurcation is perpendicular to that of the previous one. Branching remains limited to terminal branch units, giving rise to an apparently dichotomous branch system (fig. 4). During symmetric branching in the young branch system, each daughter segment forms an angle of 21° with the parent axis (θ_B); consecutive branch units are of about equal length; and both daughter branches appear equally vigorous (fig. 4).

Beginning at order 4 or 5, branching becomes increasingly asymmetric: the outermost daughter branch increases in vigor, and its branch angle decreases; in its less vigorous sister branch, the branch angle increases, and branch unit length becomes less than that of the mother branch (figs. 4, 5). The result of this asymmetric branching is a clear morphological differentiation into relatively straight and thick main branches (leaders) and weaker branches (laterals), which alternate along the leader and have branch angles at least twice those of the leader (figs. 5, 6). In older trees, additional branch systems, identical with that described above, may originate at the level of the first bifurcation of the older tree (reiteration; HALLÉ et al. 1978), eventually giving rise to an erect tree consisting of a set of superimposed, cup-shaped crowns (BORCHERT and TOMLINSON 1984).

Symmetric branching of *Tabebuia* at orders 1–4 can be simulated by the "horizontal plane model" (H-model, figs. 2, 7; HONDA et al. 1982). In the

TABLE 1

SYMBOLS OF BRANCHING AND CONTROL PARAMETERS AND DEFAULT VALUES USED IN SIMULATIONS OF TABEBUIA BRANCHING

Symbol	Definition	Value
Branching geometry		
B	Total number of branches in tree	
B_f	Number of actual branches as fraction of potential branches	
N	Branching order of tree quadrant[a] ($N = N_T - 2$) or discrete time in computer simulation	
N_s	Number of reiterations for which nonbranching terminal branch survives	3
N_T	Branching order of whole tree	
$P_i = P_B$	Branch point	
P_{2i}	Daughter branch point on vigorous (main) branch	
P_{2i+1}	Daughter branch point on less vigorous (lateral) branch	
R_1, R_2	Ratio of length of main or lateral branch unit to length of its mother unit	1, .85
T	Number of terminal branches on tree	
T_{ar}	Number of arrested terminal branches on tree	
T_m	Number of terminal branches supplied by branch point P_{2i}	
T_{lat}	Number of terminal branches supplied by branch point P_{2i+1}	
δ	Angle of inclination in branching plane in degrees	25
θ_B	Branch angle (in degrees) in symmetric branching	21
θ_1, θ_2	Branch angles of main and lateral branches (in degrees); branch angles are opposite in sign, and signs alternate in consecutive orders	10, 32
Flux distribution		
F_i	Flux to branch point P_i	
F_{2i}, F_{2i+1}	Fluxes to daughter branch points	
F_1	Flux to P_1 of tree quadrant	17
F_M	Flux gradient in leader with branch interaction	
F_m	Flux gradient in leader without branch interaction	
F_{min}	Minimum flux needed for branching	
F_N	Flux to tree quadrant at order N	
F_T	Flux to terminal branch unit of leader of tree quadrant	
R_f	Flux ratio determining the fraction of F_i going to F_{2i}	.7
R_{red}	Factor reducing exponential increase in F_N with increasing N	.895

[a] As explained in Material and methods, branch simulation is done for one quadrant of the tree only, beginning with branch points of order 3.

FIGS. 4–6.—Fig. 4 (upper left), A young tree of *Tabebuia* showing five branch orders and transition from symmetric to asymmetric branching. Terminal branches growing toward the center of the tree crown (center of photograph) did not branch during the last growth period and thus did not produce branch order 5. Four outer terminal branches will develop into leaders. Fig. 5 (upper right), Asymmetric branching pattern in *Tabebuia*. A vigorous, relatively straight leader bears alternating lateral branches of less vigorous growth (viewed from below branch). Fig. 6 (bottom), Branch system of *Tabebuia* showing open, cup-shaped crown composed of several leaders with lateral branches (viewed at an angle from ground level).

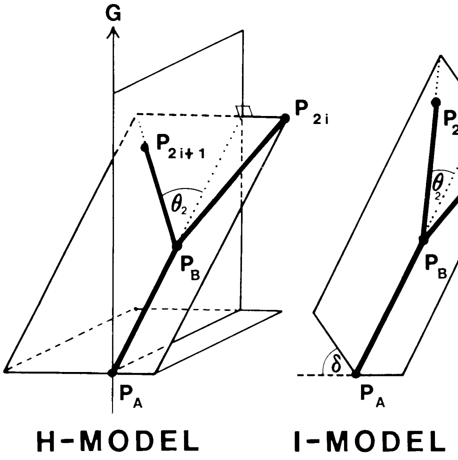

FIG. 7.—Branching geometry in the horizontal plane (*H*-model) and inclined plane (*I*-model) models. In the *H*-model the mother branch unit P_AP_B and the daughter branch units P_BP_{2i} and P_BP_{2i-1} are in the same branch plane. θ_1 (not labeled) and θ_2 are the branch angles. In the asymmetric branching shown, $\theta_1 < \theta_2$. Branch length ratios are $R_1 = P_BP_{2i}/P_AP_B = 1$ and $R_2 = P_BP_{2i-1}/P_AP_B = 0.85$. In the *I*-model, branch plane $P_AP_BP_{2i-1}$, containing the lateral branch and angle θ_2, is inclined by angle δ against plane $P_AP_BP_{2i}$, containing the main branch with small θ_1 and $R_1 = 1$.

simulation, branch angle θ_B was chosen to make x and y coordinates of links in order 4 equal and to obtain a slope equal to that of the main branches of the tree. This is necessary because the position of simulated branches remains unchanged while the position of branches in real trees is usually adjusted through the formation of reaction wood (WILSON and ARCHER 1979). In *Tabebuia*, such an adjustment is reflected in the upward curvature of main branches (fig. 6, right). Asymmetric branching at higher orders does not conform to the basic assumption of HONDA's model that mother and daughter branch units are contained in the same plane. Instead, the plane containing the less vigorous (lateral) daughter branch is inclined by angle δ against the plane containing the main branch; i.e., the two sister branches form a dihedral with the angle (180 − δ) between them (inclined plane model = *I*-model; planes $P_AP_BP_{2i}$ vs. $P_AP_BP_{2i+1}$ in fig. 7; compare fig. 6). Calculations to obtain coordinates of the links of the tree in the *H*- and *I*-models are in the Appendix.

Analogous to the initial asymmetric branching in *Tabebuia* (fig. 4), transition from symmetric to asymmetric branching was simulated at order 4 by assigning branching parameters of main branches (leaders, $\theta_1 = 10$, $R_f = 1$) to the "outer" daughter branch with greater distance from the z-axis (fig. 7), and branching parameters of lateral branches ($\theta_2 = 32$, $R_f = 0.8$) to the "inner" daughter branch. The sum of branching angles used for asymmetric branching ($\theta_1 + \theta_2 = 42°$) is within the range of measured values (40°–43°). In descendants of a main branch, asymmetry was maintained, and the observed alternation of laterals along the leader was achieved by alternating the signs of θ_1 and θ_2 at consecutive bifurcations (fig. 1: branches 1–2–3, 2–4–5, 4–8–9, etc.). In descendants of laterals the outer daughter branch again became the new main branch (fig. 1: branches 2–5–10–20, 4–9–18–36, etc.).

CONTROL OF BRANCHING.—In contrast to mathematical, binary trees, the branch system of *Tabebuia* does not constitute a geometric series in which every terminal branch unit gives rise to two daughter branches. At branch orders greater than 5 or 6, continued symmetric bifurcation of all terminal branches would produce very dense trees (fig. 2*C*), in which the surface area available for the display of leaves borne by terminal branches decreases to unrealistic, very small values (BORCHERT and SLADE 1981). In *Tabebuia*, as in most botanical trees, lateral branches cease branching at rather low orders (fig. 6). In the branch system of *Rhus typhina*, the increase in the number of terminal branches follows a sigmoid rather than an exponential curve (data of J. WHITE discussed in BORCHERT and SLADE [1981]).

HONDA et al. (1981) explored two theoretical constraints on branching of terminals: (1) exogenous or environmental control, where branch interaction such as shading causes the number of permanent branches to fall with increasing tree age through abortion or inhibition of bifurcation, and (2) endogenous control, in which the different growth potential of sister branches is the result of different flow rates to sister branches.

The open and very regular branching pattern of *Tabebuia* is the consequence of limited growth and branching of the lateral branches inserted along the few leading branches of the cup-shaped crown (fig. 6). Branching occurs exclusively in terminal branch units on the crown surface (fig. 6), and cessation of branching in the less vigorous terminal branches cannot be the result of shading or a similar exogenous mechanism of branch interaction but must be controlled within the branch system. In this study, we assumed that asymmetric branching results from asymmetric distribution of fluxes supplying apical meristems with materials needed for growth. Differences in flow rates between main and lateral shoots are suggested by differences in branch diameters (figs. 5, 6). Unequal flux of water in branch pairs with asymmetric bifurcation has been experimentally demonstrated in diffuse-porous hardwoods and in conifers and was attributed to vascular constrictions in lateral branches (ZIMMERMANN 1978; EWERS and ZIMMERMANN 1984).

In unequal flux distribution, main branches receive more than half of the flux from the mother branch, i.e., flux ratio $R_f > 0.5$. Fluxes to daughter branches are then

$$F_{2i} = F_i R_f \tag{1}$$

$$F_{2i+1} = F_i (1 - R_f). \tag{2}$$

Flux to a branch is a function not only of supply by the root system and geometry of the conducting elements but also of the driving force generated in the leaves by transpiration and, hence, of the leaf area supplied by a branch. Assuming that each terminal branch bears the same leaf area, flux distribution between any two sister branches below the terminal branches will then be a function of the ratio between the number of terminal branches supplied by main and lateral branch (T_m, T_{lat}) in addition to the flux ratio:

$$F_{2i+1} = F_i (1 - R_f) T_{\text{lat}}/T_m, \tag{3}$$

$$F_{2i} = F_i - F_{2i+1}. \tag{4}$$

With increasing size (maximum branch order N) of a tree, the size of its root system increases. As the capacity of the root system to expand is limited by the physical constraints of the soil and competition with other trees (BORCHERT 1978), the size-dependent increase of flux into the tree trunk and the number of leaf-bearing branches will eventually level off.

In the model, slowdown of exponential increase in flux with increasing order was achieved by exponentiation with a factor R_{red}, whose value is reduced with increasing N:

$$a = (N - 1) R_{\text{red}}^{N}, \quad \text{where } R_{\text{red}} < 1. \tag{5}$$

Flux into the tree quadrant is then for each order

$$F_N = F_1 2^a. \tag{6}$$

Because of the size-dependent increase of flux into the tree, flux distribution to each link within the entire tree must be recalculated after each increase in order, according to equations (3)–(6). As N represents both the number of orders in the branch system and the number of discrete time units in branch simulation, equation (6) constitutes a difference equation describing the time course of the driving variable "flux."

Each terminal branch in *Tabebuia* has three developmental options: shoot growth with branching, shoot growth without branching, and cessation of shoot growth. Flux was assumed to determine branch vigor and, hence, branch development as follows: (1) Terminal branches receiving $F_i > F_{\text{min}}$ continue to branch; (2) terminals receiving $F_i < F_{\text{min}}$ survive for N_s additional increments during which their flux remains constant; then they die, and their flux becomes zero. The default value for the survival time N_s of nonbranching terminals was chosen arbitrarily, as there are no observations.

SIMULATION OF BRANCH DEVELOPMENT

BRANCH GEOMETRY.—A comparison (figs. 2*C*, 3, 6) shows the improvement of geometric similarity between the real and simulated branch systems of *Tabebuia* resulting from the introduction of improved rules for simulating branch geometry and reduction in branch number. The effect of tilting the branching plane (*I*-model, Appendix) and of reducing branch unit length is illustrated in figure 8. As a consequence of the control mechanism discussed below, in the simulated branch system (fig. 8*C*, *D*) as in the real tree (fig. 6), all laterals along a leader grow to about the same length, causing progressively larger gaps between the tree sectors at higher orders of branching (figs. 6, 8*D*), i.e., a decline in crown density.

The reduction of crown density caused by the assumed endogenous control mechanism is reflected in the following quantitative changes during development of the simulated branch system (fig. 9): (1) During symmetric branching, up to branch order 5, the numbers of total branches (B)

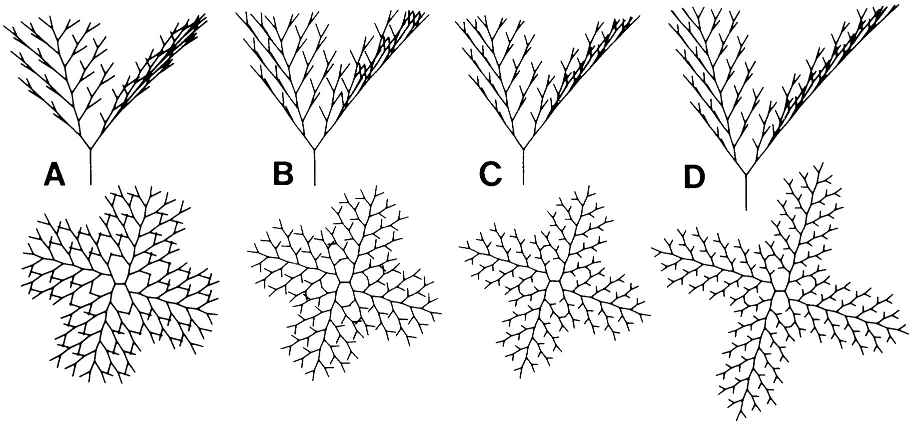

FIG. 8.—Effect of inclined branching plane, branching ratio, and order on the geometry of the simulated branch system. *A*, Branch system calculated according to the *H*-model with $\delta = 0$, $R_1 = R_2 = 1$; *B*, according to the *I*-model with $\delta = 25°$; *C*, reduction of branch unit length in lateral branches by $R_2 = 0.85$. In *A*–*C*, order $N_T = 12$. *D*, Parameters as *C*, but $N_T = 15$.

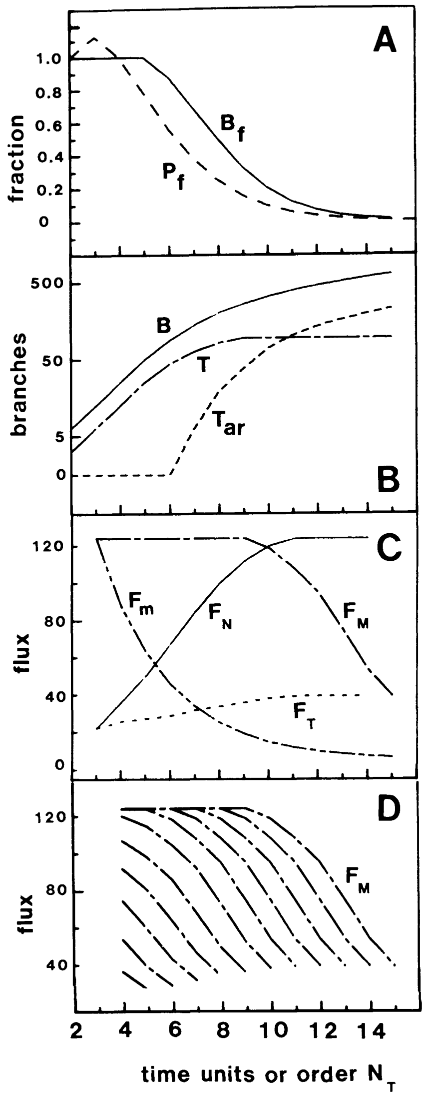

FIG. 9.—Quantitative changes within a simulated tree (see fig. 3) with increasing order. *A*, Decline in the fraction of actual branches relative to potential branches as obtained from branch simulation (B_f) and as predicted by the function $N^2/2^N$ (P_f). *B*, Changes in the number of total branches (B), active (T) and inactive terminal branches (T_{ar}). *C*, Increase in flux to the trunk of the tree (F_N) with increasing order, flux gradient within a main branch of 15 orders calculated with (F_M) and without (F_m) branch interaction, and flux to terminal branch unit of main branch (F_T) as a function of increasing order N_T. *D*, Changes in flux gradient in main branch (F_M) with increasing order N_T as a result of branch interaction causing apical control.

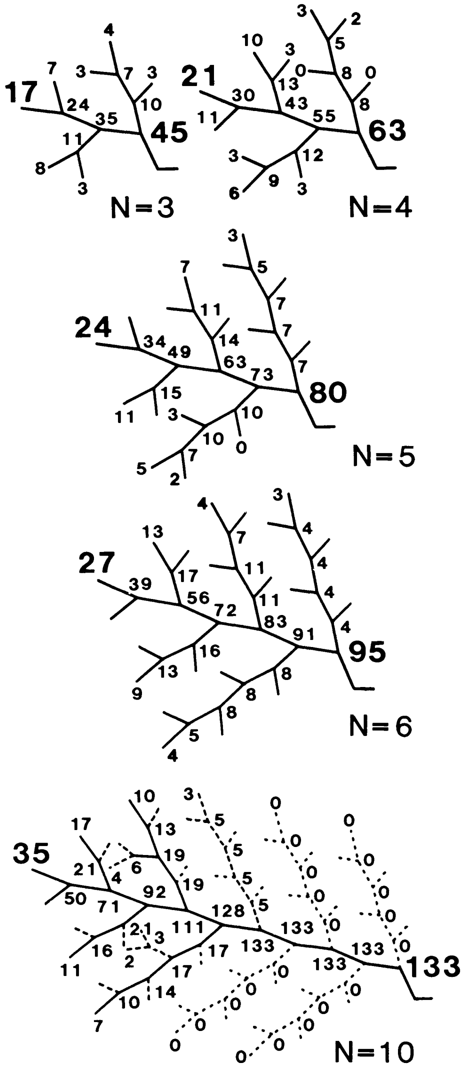

FIG. 10.—Flux distribution in branch systems of 3–6 and 10 orders. Fluxes entering each branch (on right) and flux to terminal branch of leader (left) characterized by large numbers. Fluxes calculated with $F_1 = 17$, $R_f = 0.7$, $R_{red} = 0.895$. Dotted branches at order $N = 10$ have ceased growing because $F_t < F_{min}$.

and of terminal branches (T) increase exponentially (fig. 9*B*), constituting a geometric series in which the numbers of total and terminal branches are 2^{N+1} and 2^N, respectively. (2) At branch order 5, asymmetric branching begins, and constraints on branching start taking effect; the number of branch units increases at a less than exponential rate (fig. 9*B*), and the number of actual branches as a fraction of potential branches begins to decline (B_f in fig. 9*A*). (3) At order 6 the number of inactive terminal branches (T_{ar}), i.e., arrested branches which in a real tree would eventually die, begins to rise rapidly and then approaches the number of active terminal branches (fig. 9*B*).

The rapid decline in the fraction of actual branch units (B_f) with increasing branch order (fig. 9*A*) resulted from empirically selecting a set of branch control parameters for optimum geometric similarity with real trees (table 1). A similar decline in the fraction of actual branches can be predicted on the basis of the following geometric considerations: Assume that in the crown of a tree such as *Tabebuia* all branch units are of the same length L, and all terminal branches and the leaf rosette they bear are arranged in a hemisphere forming a monolayer of leaves. The radius of this hemisphere will be at each order

$$R_L = L\,N, \quad \text{where } N \text{ is order number}, \tag{7}$$

and the surface of the hemisphere (crown surface) will be

$$S_N = 0.5 \cdot 4\,\pi\,R_L{}^2 = 2\,\pi\,(L\,N)^2 = k_1\,N^2. \tag{8}$$

With symmetric branching, the number of potential terminal branches would be

$$B_p(N) = 2^N. \tag{9}$$

In a botanical tree forming a monolayer of leaves on the crown surface, the leaves on each terminal branch will occupy leaf area LA, and the number of terminal leaf rosettes that can be displayed on the crown surface is

$$B_a(N) = S_N/LA = k_1\,N^2/LA = k_2\,N^2. \tag{10}$$

The number of actual terminal branches as a fraction of potential terminal branches will then be

$$P_f(N) = B_a(N)/B_p(N) = k_2\,N^2/2^N. \tag{11}$$

At $k_2 = 1$, P_f (4) has the value of 1 ($4^2/2^4 = 1$). At higher orders, P_f declines rapidly (fig. 9*A*), providing a measure of branch reduction and increasing asymmetry of the branch system. In symmetric branching, the same function describes the reduction in crown surface area available to each terminal leaf rosette (Borchert and Slade 1981).

CONTROL OF BRANCHING BY ASYMMETRIC FLUX DISTRIBUTION.—Flux distribution in branch systems of orders $N = 3$–6 (fig. 10) illustrates the operation of the simulated control of branching by flux and represents the functional state of the branch system at consecutive developmental stages: (1) At each branch point, flux is divided asymmetrically between main and lateral branch. (2) At $R_f = 0.7$, the laterals receive only 30% of flux from the mother branch, and flux attenuation is more rapid in lateral than in main branches. (3) Increasing fluxes to the stems of consecutive orders reflect the size-dependent increase of flux into a tree. (4) The developmental potential of each terminal branch is determined by its flux: branches with flux >5 (F_{min}) bifurcate during the next reiteration; branches with flux <5 do not branch, and their flux remains the same until they cease growing after three (N_s) reiterations (example: branch 45–35–11–3 at $N = 3$; 63–55–12–3 at $N = 4$; and 80–73–10–0 at $N = 5$. (5) In spite of the manifold increase of flux into the tree between orders 3 and 6, flux to the terminal branch unit of each quadrant leader increases only moderately: 17–21–24–27 at orders 3–6, 35 at order 10 (compare F_T in fig. 9*C*).

Beginning at order $N = 4$, flux to the terminal units of lower lateral branches declines below F_{min}, arresting their further development (fig. 10). This trend has become very pronounced by order 10 and is accompanied by a marked delay of flux attenuation in the lower segments of the main branch (fig. 10, F_M in 9*C*). As size and order of the branch system increase, flux attenuation in the main branch occurs at progressively higher orders, while flux to the main branch terminal unit changes little (fig. 9*D*).

The two main driving variables, R_{red} and R_f, affect the development of simulated trees to varying degrees (table 2). Because of its use at the Nth power (eqq. [5], [6]), small changes in R_{red} strongly affect total flux to the tree (F_{10}) and, hence, the density of the entire branch system (total branch number B) and the ratio between active and inactive terminal branches (T, T_{ar}, rows 1–5 in table 2). Reduction of the flux ratio R_f from 0.7 to 0.63 (flux to lateral branches 42%–59% of flux to main branches) affects density and branching potential (B, T, T_{ar}) only little but significantly reduces the vigor of the leader's terminal shoot (F_T) and implicitly the flux gradient in the leader and the degree of apical control (rows 5–8 in table 2). Similar effects of variation in flux ratio on branch geometry were found by Honda et al. (1981; their figs. 9–11): an R_f value of 0.67, virtually identical with our value of 0.7, generated a branch system most similar to that of the tropical tree *Tabernaemontana* sp., which has an architecture similar to that of *Tabebuia*.

As predictable from the data in rows 5–9 in table 2, moderate random variations in flux ratio produced only minor variation in branching patterns as compared with patterns generated with constant flux ratio (data not shown).

REGENERATION.—If the leader of a simulated branch system is removed, subsequent growth displays the regeneration pattern observed in real trees: initially several lateral branches below the cut increase in vigor, but ultimately the uppermost lateral establishes apical control and repeats the

TABLE 2

EFFECT OF VARIATION IN SIZE-DEPENDENT FLUX INCREASE (R_{red}) OR FLUX RATIO (R_f) ON SELECTED PROPERTIES OF SIMULATED TREES AT $N_T = 10$ AND $F_1 = 17$

	R_f	R_{red}	F_{10}	F_T	T	T_{ar}	T_{ar}/T	B
1	.7	.94	327	64	116	32	.28	296
2	.7	.93	257	56	100	36	.36	272
3	.7	.92	205	50	80	40	.50	240
4	.7	.91	166	46	64	44	.69	216
5	.7	.9	137	39	60	44	.73	208
6	.69	.9	137	36	64	44	.69	216
7	.67	.9	137	33	64	44	.69	216
8	.65	.9	137	28	72	40	.56	224
9	.63	.9	137	24	76	44	.58	240

NOTE.—Variable names as defined in table 1.

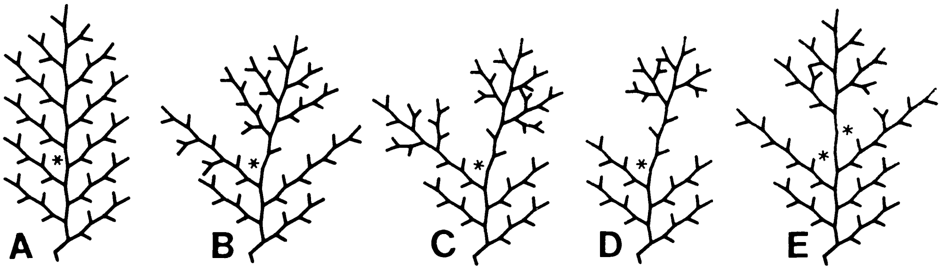

FIG. 11.—Regeneration of branch system after pruning. *A*, Nonpruned branch of 12 orders (compare fig. 9*D*). *B–D*, Leader was pruned at the same point (*) at times 7, 8, and 9, respectively, and then simulation was continued until time 12. The uppermost remaining lateral branch replaces the lost leader, but lower laterals may also temporarily increase in vigor. Branch angle of new leader was reduced during regeneration. *E*, Pruning of two lateral branches at time 7 and 8 (*) causes increased vigor of leader and lower laterals.

branching pattern of a young tree (fig. 11) (reiteration; HALLÉ et al. [1978]). Pruning of laterals enhances the vigor of the leader and of laterals above the cut lateral in accordance with the flux previously supplied to the pruned lateral.

Discussion

GEOMETRY OF BRANCHING

The geometric branching model of HONDA (1971) was used to generate branching patterns of individual branches or branch tiers of several tree species (FISHER and HONDA 1977; HONDA et al. 1981, 1982) and has been used here to simulate development of the tridimensional branch system of an entire young tree up to 15 orders of branching. HONDA's model has proved to be adaptable to trees of different geometric characteristics: the original horizontal plane model gave rise later to the perpendicular plane (*P*-model; HONDA et al. [1982]) and now to the inclined plane model (*I*-model).

The sigmoid increase in branch number (*B* in fig. 9*B*) and the corresponding exponential decline in the fraction of actual, relative to potential, links at higher branch orders (B_f in fig. 9*A*) have been observed in real trees and in the simulation of *Tabebuia* branching. We have shown here that the gradual reduction of terminal branches in trees optimized for display on the crown surface of a constant leaf area per terminal branch results from the basic geometric fact that terminal branches in a geometric series increase exponentially with order, while crown surface increases only with the second power of the crown radius. Increasing asymmetry of the branch system and reduction of branch number by the relation $N^2/2^N$ are thus inherent properties of botanical trees and any other branched system in which a surface or volume is supplied by a branched network of conducting elements. This rule is comparable to other rules derived from geometric properties of organisms, such as elastic similarity in trees, the power law functions of locomotion in animals, and the self-thinning rule ($^3/_2$ power law) in plant population biology (MCMAHON 1975*a*, 1975*b*; WHITE 1981).

SIMULATED FLUX DISTRIBUTION IN THE BRANCH SYSTEM

The simulated gradients in flux distributions (fig. 10) are remarkably similar to the gradients in leaf specific conductivity (flux/time/leaf area above branch point) measured in conifers and diffuse porous hardwood trees (fig. 12) (ZIMMERMANN 1978; EWERS and ZIMMERMANN 1984). Flux and, hence, vigor and branching potential decline slowly in main branches and rapidly in lateral branches. Simulated flux gradients and their change with increasing size of the branch system (figs. 9*D*, 10) result from the three assumptions expressed in equations (1)–(6).

1. Unequal flux distribution between main and lateral branches (eqq. [1] and [2], as modeled by HONDA et al. [1981]), successfully reduces flux to laterals and, hence, their branching potential, because flux is decreased exponentially as $F_N = F(1 - R_f)^N$. At $R_f = 0.7$, the lateral derivative of only

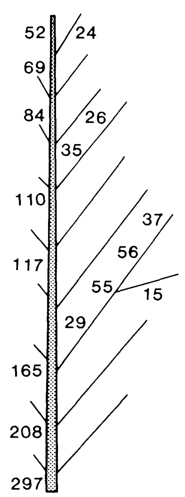

FIG. 12.—Gradients of leaf-specific conductivity for water (flux/time/leaf area above branch point) in *Tsuga* (from EWERS and ZIMMERMANN 1984).

three unequal bifurcations will receive 0.3^3 or 2.7% of the flux entering the first branch. The similar, low vigor of all laterals along a leader (figs. 3, 6) is thus the result of similar flux gradients in these branches resulting from a constant R_f. Flux ratios also cause a rapid—and unrealistic—decline of fluxes within the leader ($F_N = F\ R_f^N$; F_m in fig. 9*C*). Continued growth of the leader and of the whole branch system is then possible only if flux to the tree increases exponentially with branch order, an assumption which is also unrealistic (see explanation for eq. [5]). Such an exponential increase in flux to the tree was implicitly assumed in the use of relative, not absolute, fluxes by HONDA et al. (1981).

2. If flux to the tree is reduced with increasing order by a sigmoid growth function (eqq. [5] and [6]), then continued growth of the branch system is not possible without branch interaction favoring flux to the leader, because the exponential decline of flux in both leader and laterals causes flux to decline below the flux threshold $F_{\min}$, and branching will cease. For instance, because of multiple terminal ramification and absence of apical control, the density of the branch system of mistletoe (*Viscum album*) increases rapidly (cf. fig. 2*C*), and growth increments of all terminal branches start declining markedly at order 5 (LEGAY 1980).

3. Feedback interaction between main and lateral branches (introduced by ratio T_{lat}/T_m in eqq. [3] and [4]) enables continued growth of the branch system by establishing apical control, which manifests itself in the leader as slow flux attenuation and preservation of high vigor in the terminal branch (fig. 9*C*), in laterals as low vigor, arrested growth, and eventual death of lower lateral branches (fig. 10, dotted branches at $N = 10$).

VALIDATION OF THE MODEL

The number of criteria for judging the realism of tree simulation has been augmented substantially. Validation of earlier simulations was usually limited to evaluations of geometric similarity between real and simulated trees at a certain stage of development (HONDA et al. 1981, 1982; references in LÜCK and LÜCK [1982]). The present model permits assessment of the dynamics of growth and branching of each terminal branch and of the branch system as a whole. Not only the end result of simulation but also the development of simulated trees of progressively higher order can be compared with that of real trees. Physiological mechanisms implied in the assumed control of branching can also be judged for compatibility with current physiological knowledge.

Results of the simulation of *Tabebuia* branching meet the following criteria: (1) The geometry of simulated trees and changes in growth patterns observed with increasing size of the branch system are the result of manifold reiterations of the same developmental rules. (2) Within the limits of a deterministic model, simulated trees are geometrically similar to real trees (figs. 3, 6). (3) With increasing order, the branch system of simulated trees undergoes the same quantitative changes as real trees: the number of total and terminal branch units follows a sigmoid time course; reduction of exponential branching increases, and appearance of nonbranching terminals begins around order 5 (fig. 9*B*). (4) Simulated trees manifest strong apical control: growth of laterals is markedly less vigorous, i.e., branching is less frequent, than that of main branches (fig. 3). (5) Flux entering the tree changes with increasing order in a sigmoid manner (fig. 9*C*); yet (6) flux to the terminal unit of the main branch varies little with increasing order (fig. 9*C*). (7) Flux attenuation is slow in leaders, fast in lateral branches (fig. 10). (8) Regeneration of the simulated branch system in response to injury (pruning) is similar to that of real trees and reflects the potential response of the system to random destruction of individual branches, which constitutes an important stochastic element in the morphogenesis of most trees.

The developmental rules used in the branching model were based on observations of growth patterns of real trees or on acceptable physiological hypotheses, partially supported by experimental evidence. The probability of generating realistic branch systems by the manifold reiteration of logically inconsistent rules is minimal. Thus, in spite of the gross oversimplifications made in this model with respect to branch geometry and developmental control, we may conclude that developmental controls similar to those simulated are likely to operate in real trees.

IMPLICATIONS OF THE MODEL

The assumed regulation of branching by a specific pattern of flux distribution has several theoretical implications:

1. The simulated branch interaction consists in the competition of various branches for a limiting resource, namely, total flux entering the tree. The concept of "competition" constitutes a typical example of interaction between the individual members of a plant population. In the proposed model, competition is within a single organism between the individual branches of the branch population constituting the whole tree (WHITE 1979). Differential resource allocation to competing organs within whole plants, e.g., to growing apical meristems versus growing fruits, is usually discussed in plant physiology texts, but the term "competition" is not found in the indices of most textbooks of plant or tree physiology, suggesting a basic deficiency in the conceptual analysis of the developmental controls of plants as branched systems.

2. Leading shoots in trees exercise apical control—i.e., reduction in vigor of lower laterals—not apical dominance, i.e., suppression of the outgrowth of lateral buds below the apical bud (ZIMMERMANN and BROWN 1971). Apical control of the branch system is the result of a feedback mechanism favoring flux to the leader, as implied in equations (3) and (4).

3. The diminishing rate of flux increase with higher branching orders is a manifestation of the common decline of the root:shoot ratio in trees of increasing size (BORCHERT 1976, 1978). It reflects environmental control of development of the tree as a whole but not of its specific branching pattern. As flux levels off at higher orders, it limits the number of terminal branches vigorous enough to branch and, because of apical control, enhances the arrest of development and ultimately death and abscission of the lower branches.

4. The simulated branch system undergoes size- or age-dependent changes in overall structure, similar to those observed in botanical trees. These changes are the consequence of branch interaction within the tree (endogenous control) in conjunction with environmental limitations to growth imposed by the limited resources available to the root system (exogenous control).

Most branching models devised to date are either strictly descriptive or lack branch interaction (LÜCK and LÜCK 1982). In branching models without branch interaction, growth and branching of each element depend only on its own state or on the interaction between the terminal branches and their environment (e.g., MEINHARDT 1976). The theoretical analysis of developmental algorithms has shown that many types of branching cannot be produced by interaction-free lineage algorithms but must originate from interactive algorithms (LINDENMAYER 1982). In their evaluation of branching models in plants, LÜCK and LÜCK (1982) also stressed the need for interaction between two different levels of integration, those controlling branching (i.e., geometry or tree architecture) and growth potential, and recommended introduction of sigmoid growth functions to limit growth of the branch system as a whole. Control of growth by a hypothetical ascending gradient, analogous to the flux gradient of the present model, was modeled by FRIJTERS (1978).

Our results suggest that any realistic simulation of the development of the branch system in botanical trees requires at least four sets of rules addressing (1) geometry of the branch system, (2) reduction of branch numbers at higher orders through reduction of branching in lateral branches, (3) the establishment of apical control through branch interaction, and (4) control of growth of the branch system as a whole by a sigmoid growth function.

In essence, the model of *Tabebuia* branching represents a paradigm of the "open" or "continuous" development of plants. The same structural elements or modules, terminal leaf-bearing branches, are repeatedly added to the existing branch system and generate a characteristic spatial pattern, the architecture of *Tabebuia*. The method used to simulate the development of *Tabebuia* is identical with that of GREEN and POETHIG (1982): a set of rules determining tree architecture was obtained by "differentiation" from the actual sequence of developmental stages and combined with a differential equation describing the time course of flux as the driving variable of branch growth. Consecutive developmental stages were simulated by integration, i.e., by deriving the next developmental stage from the present state of the branch system while retaining the unaltered parts of the system. GREEN and POETHIG deduced this procedure from developmental sequences in cells, tissues, or individual organs. The procedure has been applied here to the development of the organ system in an entire plant, a branched tree.

While certain rules of the simulation reflect the genetically fixed determinants of *Tabebuia* architecture (e.g., the species-specific mode of sympodial branching, branch angles, greater vigor of outer branches), the repeated execution of the genetic program for the production of one branch module is unlikely to be under genetic control and has been postulated to result from the distribution of "metabolic flux," i.e., a biophysical parameter.

The observed and simulated size-dependent changes in the branching pattern of *Tabebuia* imply changes in the efficiency of the branch system for the display of leaves to light, i.e., changes in the adaptive geometry of the tree, and changes in the mechanical properties of branches (BORCHERT and TOMLINSON 1984). The dynamics of these processes in simulated branch systems will be analyzed in future studies.

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Appendix

CALCULATION OF COORDINATES OF LINKS

H-MODEL.—Coordinates of the daughter links P_{2i} and P_{2i+1} are calculated from branch angle θ_j and from coordinates of points $P_A(x_A\ y_A\ z_A)$ and $P_B(x_B\ y_B\ z_B)$ as follows (fig. 7, table 1) (HONDA et al. 1982):

$$x_j = x_B + R_k\,(u \cos \theta_j - L\, v \sin \theta_j/M)$$

$$y_j = y_B + R_k\,(v \cos \theta_j + L\, u \sin \theta_j/M)$$

$$z_j = z_B + R_k\, w \cos \theta_j,$$

where $u = x_B - x_A$, $v = y_B - y_A$, $w = z_B - z_A$, $L = \sqrt{u^2 + v^2 + w^2}$, $M = \sqrt{u^2 + v^2}$, $j = 2i, 2i + 1$, and $k = 1, 2$.

I-MODEL.—Coordinates for branch point P_{2i+1} are obtained as follows (fig. 7):

$$x_j = x_B + R_k \left[u \cos \theta_j - \left(\frac{L\, v \cos \delta + u\, w \sin \delta}{M} \right) \sin \theta_j \right]$$

$$y_j = y_B + R_k \left[v \cos \theta_j + \left(\frac{L\, u \cos \delta - v\, w \sin \delta}{M} \right) \sin \theta_j \right]$$

$$z_j = z_B + R_k(w \cos \theta_j + M \sin \delta \sin \theta_j),$$

where $j = 2i + 1$, $k = 2$; u, v, w, L, M as above. θ_j and δ must have the same sign. Coordinates for branch point P_{2i} are calculated as in the *H*-model.

LITERATURE CITED

BORCHERT, R. 1976. The concept of juvenility in woody plants. Acta Hort. **56:**21–36.

———. 1978. Feedback control and age-related changes of shoot growth in seasonal and nonseasonal climates. Pages 497–515 *in* P. B. TOMLINSON and M. H. ZIMMERMANN, eds. Tropical trees as living systems. Cambridge University Press, Cambridge.

BORCHERT, R., and N. A. SLADE. 1981. Bifurcation ratios and the adaptive geometry of trees. BOT. GAZ. **142:**394–401.

BORCHERT, R., and P. B. TOMLINSON. 1984. Architecture and crown geometry in *Tabebuia rosea* (Bignoniaceae). Amer. J. Bot. (in press).

EWERS, F. W., and M. H. ZIMMERMANN. 1984. The hydraulic architecture of balsam fir (*Tsuga canadensis*). Can. J. Bot. (in press).

FISHER, J. B., and H. HONDA. 1977. Computer simulation of branching pattern and geometry in *Terminalia* (Combretaceae), a tropical tree. BOT. GAZ. **138:**377–384.

FRIJTERS, D., 1978. Principles of simulation of inflorescence development. Mechanisms of developmental integration of *Aster novae angliae* L. and *Hieracium murorum* L. Ann. Bot. **42:**549–560.

GREEN, P. B., and R. S. POETHIG. 1982. Biophysics of the extension and initiation of plant organs. Pages 485–509 *in* S. SUBTELNY and P. B. GREEN, eds. Developmental order: its origin and regulation. 40th Symposium of the Society for Developmental Biology. Liss, New York.

HALLÉ, F., R. A. A. OLDEMAN, and P. B. TOMLINSON. 1978. Tropical trees and forests: an architectural analysis. Springer, Berlin.

HONDA, H. 1971. Description of the form of trees by the parameters of the tree-like body: effects of the branching angle and the branch length on the shape of the tree-like body. J. Theoret. Biol. **31:**331–338.

HONDA, H., and J. B. FISHER. 1978. Tree branch angle: maximizing effective leaf area. Science **199:**888–890.

HONDA, H., P. B. TOMLINSON, and J. B. FISHER. 1981. Computer simulation of branch interaction and regulation by unequal flow rates in botanical trees. Amer. J. Bot. **68:**569–585.

———. 1982. Two geometrical models of branching of botanical trees. Ann. Bot. **49:**1–11.

LEGAY, J. M. 1980. Mise en place de l'architecture du Gui (étude longitudinale). Bull. Soc. Bot. France, Actual Bot. **127**(2):33–40.

LINDENMAYER, A. 1982. Developmental algorithms: lineage versus interactive control mechanisms. Pages 219–245 *in* S. SUBTELNY and P. B. GREEN, eds. Developmental order: its origin and regulation. 40th Symposium of the Society for Developmental Biology. Liss, New York.

LÜCK, J., and H. B. LÜCK. 1982. Modellbildungen zur pflanzlichen Verzweigung (eine Übersicht). Ber. Deut. Bot. Ges. **95:**75–97.

MCMAHON, T. A. 1975*a*. The mechanical design of trees. Sci. Amer. **223**(7):97–102.

———. 1975*b*. Using body size to understand the structural design of animals: quadrupedal locomotion. J. Appl. Physiol. **39:**619–627.

MEINHARDT, H. 1976. Morphogenesis of lines and nets. Differentiation **6:**117–123.

TOMLINSON, P. B. 1983. Tree architecture. Amer. Sci. **71:**141–149.

WHITE, J. 1979. The plant as a metapopulation. Annu. Rev. Ecol. Syst. **10:**109–145.

———. 1981. The allometric interpretation of the self-thinning rule. J. Theoret. Biol. **89:**475–500.

WILSON, B. F., and R. R. ARCHER. 1979. Tree design: some biological solutions to mechanical problems. BioScience **29:**293–298.

ZIMMERMANN, M. H. 1978. Hydraulic architecture of some diffuse-porous trees. Can. J. Bot. **56:**2286–2295.

ZIMMERMANN, M. H., and C. L. BROWN. 1971. Trees: structure and function. Springer, Berlin.