

BRANCH GEOMETRY IN *CORNUS KOUSA* (CORNACEAE): COMPUTER SIMULATIONS¹

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Computer simulations similar to actual trees were constructed using simple branching rules. Branch orientation with respect to the direction of gravity was a fundamental consideration. In *Cornus kousa* BUERG. ex HANCE, several types of branches develop from winter buds, varying from orthotropic shoots to plagiotropic ones. Based on actual observations and measurements of branching structures with a wide range of orientations, we made a flexible geometrical model consisting of five forking branches that varied in outgrowth depending on the direction of the shoot with respect to gravity. Repetition of the branching by computer generated a realistic tree pattern, which was close to the shape of a young *C. kousa* tree. Reproductive shoots seem to be under a branching rule that was a modification of vegetative branching, although the reproductive branch size was considerably smaller than the vegetative one, and reproductive branching was bifurcated instead of five-forked. We conclude that all branchings in orthotropic and plagiotropic shoots in the vegetative phase and shoots in the reproductive phase are formed under the same branching rule, but each has different parameter values.

Key words: branch geometry; branching; computer simulation; *Cornus*; Cornaceae; gravity; model; tree architecture; tree shape.

Numerous models of tree architecture have been performed (reviewed in Waller and Steingraeber, 1985; Fisher, 1992) and have variously emphasized branching patterns and three-dimensional geometry. One approach is based on the fact that a new branch growing from the mother shoot of a tree is geometrically determined by two parameters, branching angle and branch length. Repetition of the branching generates complex and distinctive tree forms. The overall complex shape of trees can be determined by surprisingly few parameters and thus relatively little genetic information, as was first demonstrated by computer-based simulations of tree architecture (Honda, 1971).

In addition to branching angle and branch length, tree branching geometry is influenced by environmental factors, especially gravity. The orientation of each shoot and the plane of branching are usually influenced by the direction of gravity. We have already generated three branching models of increasing geometrical complexity that account for the influence of gravity (Table 1). The H model (horizontal plane model) simulates trees of *Terminalia catappa* and *Cornus alternifolia* (Fisher and Honda, 1977, 1979a, b; Honda and Fisher, 1978a, b; Honda, Tomlinson, and Fisher, 1981). The P model (perpendicular plane model) is modified by gravitropism (the effect of gravity on growth) and simulates trees of *Cameraria latifolia* and *Tabernaemontana* sp. (Honda, Tomlin-

son, and Fisher, 1982). The most general geometrical model is the I model (inclined plane model) that simulates trees of *Tabebuia rosea* (Borchert and Honda, 1984), which needed an additional angle parameter for determination of branching plane in three-dimensional space.

We extend the study and simulation of tree architecture in the present paper by expanding upon the models cited above. While previously simulated species basically consist of bifurcating branching patterns, the Japanese strawberry tree, *Cornus kousa* BUERG. ex HANCE consists of five-forked branching (Figs. 1,2). Here, a more flexible model is needed and is derived from the I model with modifications based on detailed measurements of the branching angles and the branch length. The model simulates the geometry of all branching patterns of shoots in vegetative and reproductive phases.

MATERIALS AND METHODS

Plants and methods to measure branch angle and branch length—*Cornus kousa* was used for measurements of branching angle and branch length. The system of classifying the types of branching is illustrated in Fig. 3. Positions of vegetative branching events can be recognized by observation of two successive scars of foliage and scale leaves, even when lateral shoots are absent (Fig. 3, Types D and E). Positions of reproductive branching events can be recognized by observation of equal forking (pseudodichotomy), a scar of an inflorescence, or three successive foliage scars of normal leaves, outer scale and inner scale leaves (Fig. 3, Types F and G). Branching angles were measured by a circular protractor with a plumb for determining the vertical line. In vegetative shoots, branching angles and branch lengths of orthotropic branching (Fig. 4a) were measured in three individuals of 4–5 yr old trees cultivated in the open in a botanical garden in Tsukuba City. For plagiotropic branching (Fig. 4b), ten individuals of 15–20 yr old trees cultivated in the open in Tsukuba City were measured. Divergence angle ω was calculated from measurement of 2ω

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TABLE 1. Previous geometrical models for branching.^a

Model	Branching plane contains a mother shoot and —	Direction of the branching plane: the branching plane —	Effect of gravity	Example	Reference
H model	Two daughter shoots. The same as I model with $\omega = \pm 90^\circ$.	Is perpendicular to the vertical plane. ^b The mother shoot is in the direction of the steepest line in a slope of the branching plane.	Affected through the vertical plane.	<i>Terminalia catappa</i> , <i>Cornus alternifolia</i>	Honda, 1971; Fisher and Honda, 1977, 1979a, b; Honda and Fisher, 1978a, b; Honda, Tomlinson, and Fisher, 1981
P model	Two daughter shoots.	Is perpendicular to the previous branching plane.	Independent. Modifiable to receive the gravity effect.	<i>Cameraria latifolia</i> , <i>Tabebuia bernaemontana</i> sp.	Honda, Tomlinson, and Fisher, 1982
I model	One daughter shoot.	Makes angle ω with the vertical plane. ^b	Affected through the vertical plane.	<i>Tabebuia rosea</i> , <i>Cornus kousa</i>	Borchert and Honda, 1984

^a A daughter shoot in these models has a deflection angle θ from the direction of the mother shoot and relative branch length R in general.

^b A vertical plane is defined as a plane that contains the mother shoot and is vertical in gravity.



Figs. 1, 2. Photographs of five-forked branchings. Note shoot 0 actually raises up from the plane determined by shoots 1 and 2. Arrow head, branching. Numerals 0–4 indicate shoots 0–4. Photographs taken from side-view in the plane of shoots 1 and 2. 1. Branching type B. 2. Branching type C.

(Fig. 5b). Deflection angles θ_0 , θ_1 , θ_2 , and θ_4 (Fig. 5b,f) were calculated from measurements of the angle between the mother shoot and the respective shoots, $(180^\circ - \theta_i)$ where $i = 0, 1, 2$, and 4. Deflection angle θ_3 was calculated from the formula $\theta_3 = \theta_0 + \varphi_3$, where φ_3 is the measured angle between shoot 0 and shoot 3.

In reproductive shoots, branching angles and branch lengths were measured in nine branch complexes of trees growing naturally in the open in Hakone, Kanagawa Prefecture, which were presumably 50–70 yr old. Deflection angle θ was calculated from the angle 2θ that was actually measured. Branch length between two successive forkings was measured, and node number between them was counted. Then, branch growth per year was calculated by dividing branch length by the number of nodes since one internode is produced per year in the reproductive phase.

Branch geometry—A mother shoot (AB) makes a daughter shoot (BP) in three-dimensional space (Fig. 5a). To obtain the position of a daughter shoot, we used the I model, which was described in Borchert and Honda (1984). When shoots are represented as straight lines, each daughter shoot is determined by three parameters: deflection angle θ ; divergence angle ω ; and length ratio R of branch BP to the standard branch, the longest branch in a branching (shoot 0 or shoot 4). When notations are used as the terminal coordinates of a mother shoot and a daughter shoot, $A = (x_A, y_A, z_A)$, $B = (x_B, y_B, z_B)$, $P = (x_P, y_P, z_P)$, and $u = x_B - x_A$, $v = y_B - y_A$, $w = z_B - z_A$, $L = (u^2 + v^2 + w^2)^{1/2}$ and $M = (u^2 + v^2)^{1/2}$, the end point of a daughter shoot is represented as follows:

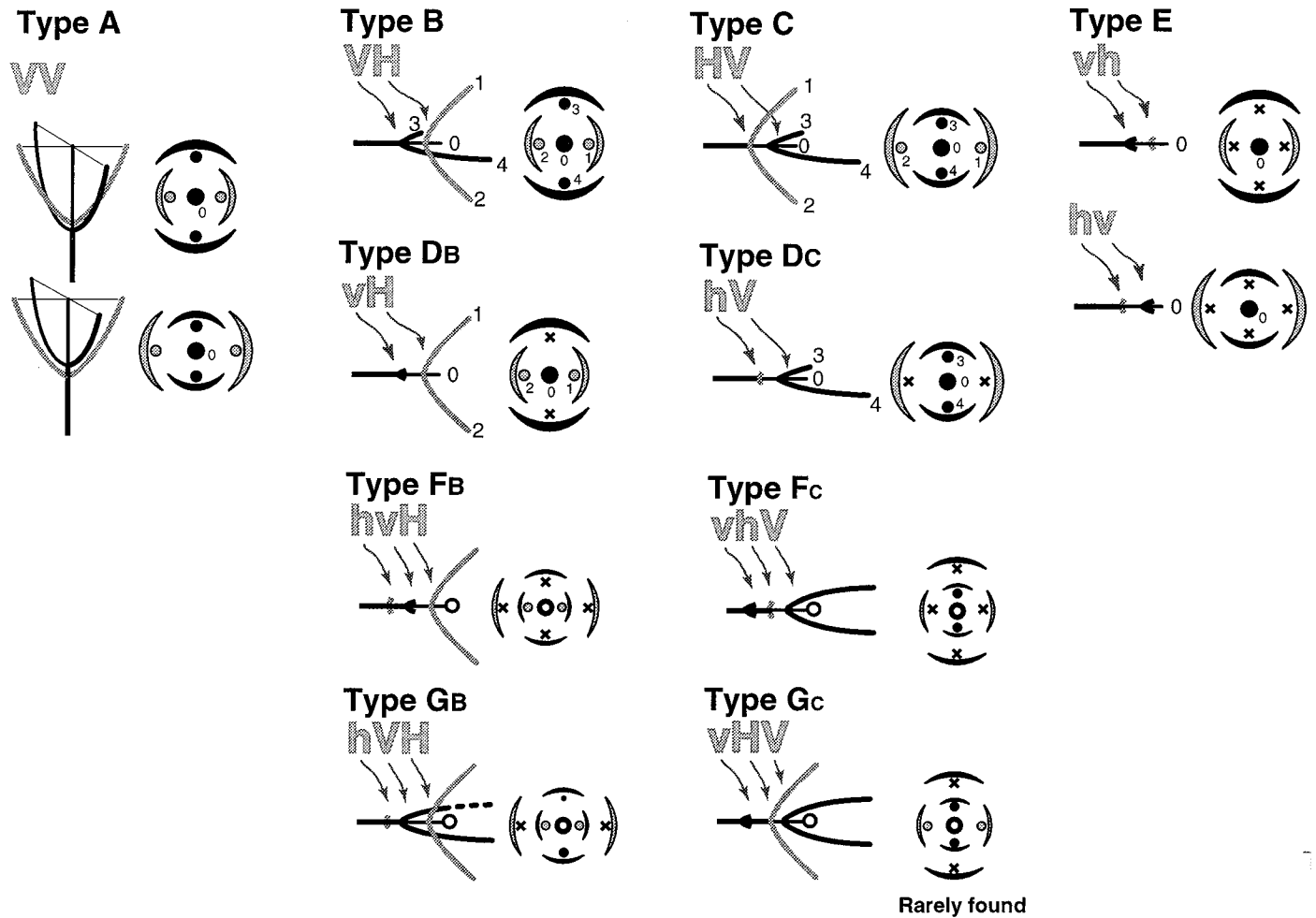


Fig. 3. Summary of branching types in *Cornus kousa*. Two nodes (foliage leaf and scale leaf) in a vegetative branch produce branching types A-D. Two nodes in a reproductive shoot produce branching type E. Three nodes (foliage leaf, outer scale leaf, and inner scale leaf) in a reproductive branch produce branching types F and G. V and H are vertical and horizontal nodes having lateral shoots, respectively. Small letters (v, h) indicate nodes that make no lateral shoot and have only buds. Crescents (from outer to inner) indicate positions of foliage and scale leaves. Solid circle indicates position of a shoot. Open circle indicates position of inflorescence. Cross indicates no shoot. Shoot 0, apical; shoot 1 and shoot 2, horizontal; shoot 3 (upper) and shoot 4 (lower) in a vertical plane. This scheme is a modification of that presented in Hatta (1980).

$$\left. \begin{aligned}
 x_p &= x_B + R[u \cos \theta - \{L(v/M)\sin \omega + w(u/M) \\
 &\quad \times \cos \omega\} \sin \theta] \\
 y_p &= y_B + R[v \cos \theta + \{L(u/M)\sin \omega - (v/M)w \\
 &\quad \times \cos \omega\} \sin \theta] \\
 z_p &= z_B + R[w \cos \theta + M \cos \omega \sin \theta].
 \end{aligned} \right\} (1)$$

We often discuss the direction of a mother shoot in relation to gravity using the angle of inclination of a mother shoot (ρ) as shown in Fig. 5a. The inclination angle is presented as $\cos \rho = w/L$. When the mother shoot is vertical ($x_B = x_A, y_B = y_A$), u, v , and M are all zero and Eqs. 1 are not used because 0/0 appears. The formulae may be used for vertical mother shoots, after the following replacements are made: $u/M = -1$ and $v/M = 0$.

Computer programs—The computer programs were written in FORTRAN and BASIC languages with modification of an earlier branching program (Honda, Tomlinson, and Fisher, 1981). Branch interaction, in which branches interfere with each other when they are close together, was similar to Honda, Tomlinson, and Fisher (1981). A sphere of in-

terference was used here instead of a cylinder. The interference radius was half of the terminal branch length. Calculations were performed by a personal computer (PC9801RX with a numerical data processor, NEC Co., Tokyo), and results were drawn by an XY-plotter (MP4300, Graphtech Co., Tokyo). For paired stereo views, the simulation was rotated 5° for the second image.

SUMMARY OF THE PREVIOUS INVESTIGATION

Phyllotaxis of *C. kousa* is decussate (Hatta, 1986). A pair of opposite leaves are produced at a terminal node, and a lateral shoot grows from the axil of each leaf. The orientation of the paired lateral shoots in a plagiotropic branch complex is either horizontal (H) or vertical (V).

At the end of a growing season a winter bud forms and consists of scale leaves. The scale leaves also produce shoots from their axils. Because a foliage leaf node is in close contact with the scale leaf node, a winter bud seems to produce a five-forked branching as shown in Fig. 4.

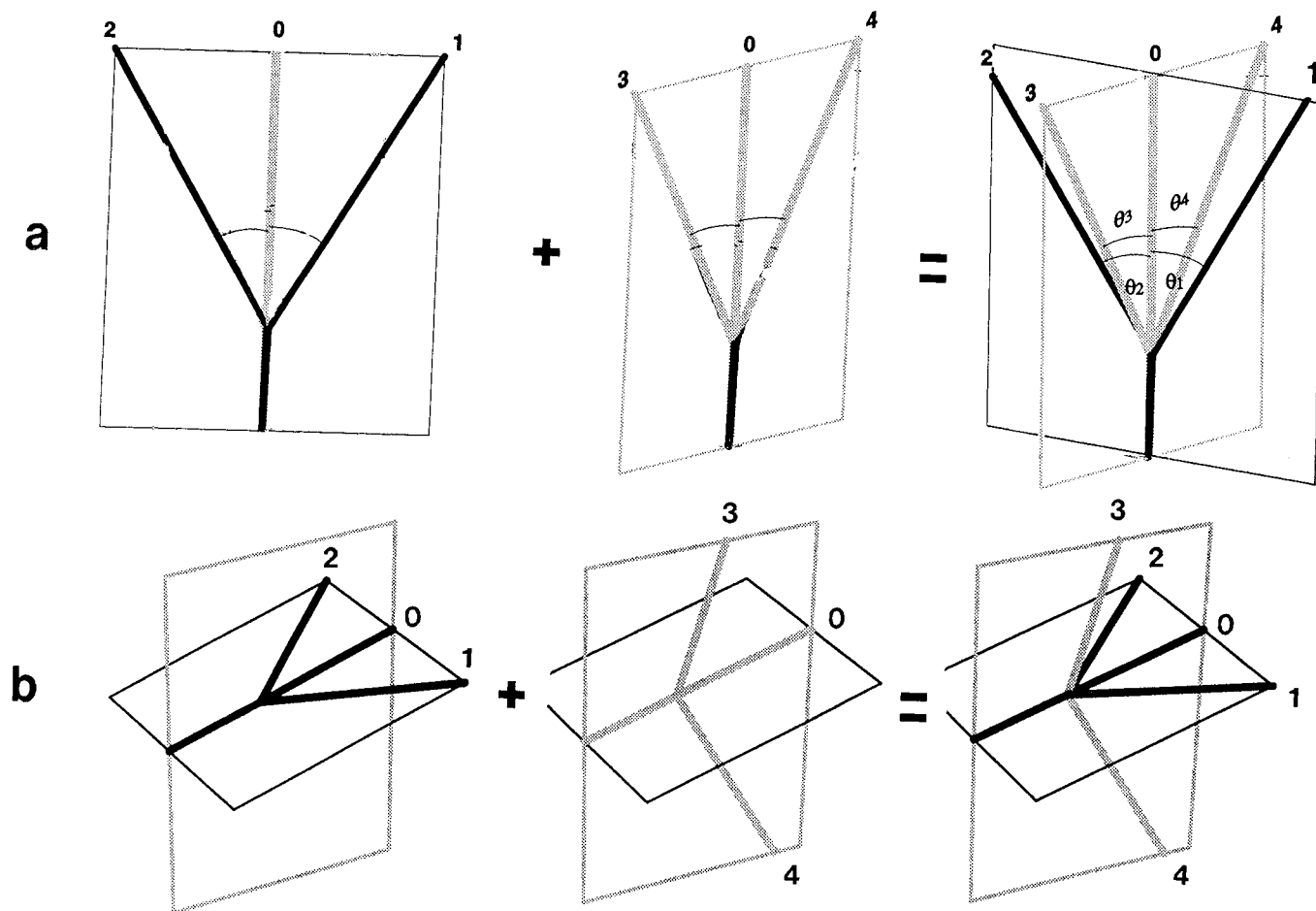


Fig. 4. A branching that forms five daughter shoots in the vegetative phase consists of successive two three-forked branchings from axils of foliage leaves and of scale leaves, respectively. (a) orthotropic branching. (b) plagiotropic branching.

Branching types—The five-forked branchings were described by Hatta (1980) as eight branching types: A, B, C, D₁, D₂, E, F₁, and F₂. However, further observation refined this classification so that the original notations of D₁, D₂, F₁, and F₂ were changed to D_B, D_C, F (F_B or F_C) and G (actually G_B as described later), respectively (H. Hatta, H. Honda, and J. B. Fisher, unpublished data). We will describe vegetative branching first. An erect stem has branching type A as shown in Fig. 3 and Fig. 4a. A plagiotropic shoot has two possible branching types, VH and HV, which correspond to the branching types B and C, respectively (Figs. 3, 4b). VH or HV is a notation where the first and second letters show orientation of the proximal foliage and distal scale node, respectively. A foliage leaf sometimes produces no shoot (we use a small letter v or h in this case to show the orientation). vH and hV correspond to branching types D_B and D_C, respectively. Branching type E occurs when a winter bud produces no lateral shoot (vh and hv in Fig. 3).

In a branch complex with reproductive branchings, the winter bud has two nodes from which a pair of outer scale leaves and a pair of inner scale leaves grow. The apex of a main shoot stops growing and becomes a terminal inflorescence. Because a foliage node is followed directly by a winter bud, three successive nodes are in

direct contact: foliage leaves, outer scale leaves, and inner scale leaves. We can describe branching orientation in the reproductive shoot by three letters, hvH (type F_B) and vhV (type F_C). Foliage leaf nodes lack shoots. Most outer scale leaf nodes lack shoots. Some of the outer scale nodes sometimes produce shoots as hvH (type G_B), whereas they rarely produce vhV (type G_C).

Transition of the branching types—The sequence of transition is generally A → B, C → D_B, D_C → E, F (F_B or F_C), G (actually G_B). We measured quantitatively the actual frequency of transformations of branching types (H. Hatta, H. Honda, and J. B. Fisher, unpublished data). On the basis of the data, we made the plausible transition rule as shown in Fig. 6 and Table 2. For example, when a mother shoot of type A makes daughter shoots, daughter shoot 0 is type A and daughter shoots 1–4 are all type B/C₁. Here, we distinguish type B/C₁ from type B/C as shown in Fig. 6. Shoots of type B/C₁ grow vigorously and establish the main axes in lateral branches.

Because we are mainly interested in the canopy shape, it is enough to consider branching types A, B, C, D_C, and F (F_B or F_C), because other types do not influence the canopy shape. Type D_B does not make an extensive branch complex, because shoot 4 of type D_B is dormant

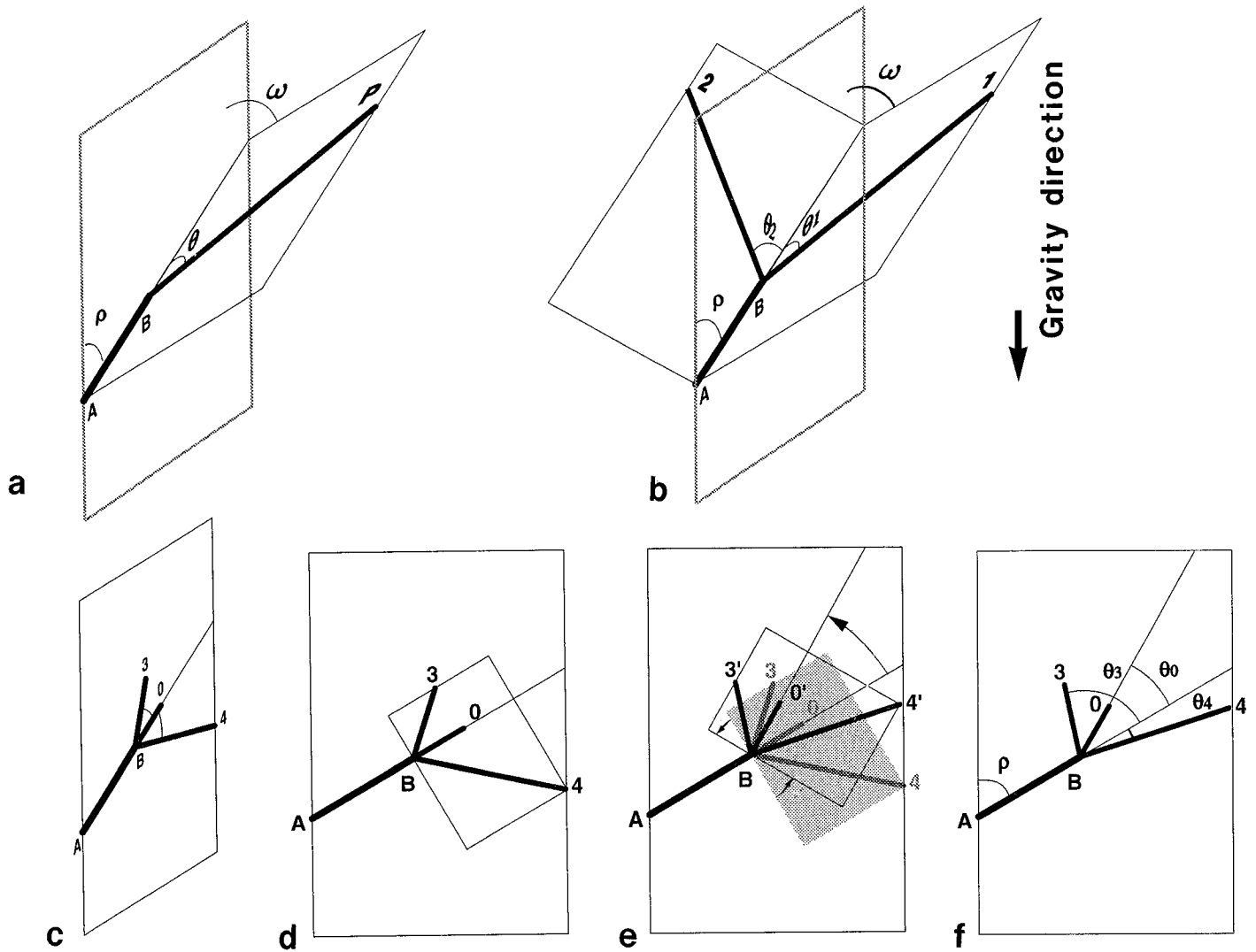


Fig. 5. Diagrams of branching. (a) I model, inclined plane model. The direction of the terminal point of P of a daughter shoot is determined by deflection angle θ and divergence angle ω . The angle of inclination of branch AB from the vertical line is ρ . (b) The I model makes, in vegetative shoots, a horizontal branching plane including shoots 1 and 2, which is folded by $90^\circ - \omega$ in gravity. (c and d) In a vertical branching plane, the model includes shoots 0, 3, 4 in its most simple form. (e and f) Typically shoot 0 raises up by θ_0 , and shoots 3 and 4 similarly raise up, thus keeping the angles with shoot 0 constant.

and does not make a sympodial axis as other types B, C, and D_C (Fig. 3). Furthermore, the frequency of type D_B in branching complexes is quite low. Type E is small and does not fork. Types G_B and G_C are only found infrequently. In addition, types B and C are not distinguishable geometrically because they are essentially forked at one point. Therefore, we sought to make a geometrical branch model that can represent types A, B/C, D_C , and F (F_B or F_C).

RESULTS

Measurements for the model parameters—Orthotropic branching in the vegetative phase—When a stem is vertical, the shoot forks in two vertical branching planes that are perpendicular to each other (Fig. 4a). Deflection angles and length ratios of daughter shoots were measured and results are shown in Table 3. Absolute mother

branch length in average was 60.3 ± 19.2 cm (mean and standard deviation, $N=18$).

Plagiotropic branching in the vegetative phase—Generally speaking, shoots generated from a plagiotropic shoot show a small degree of negative gravitropism, that is, the new shoots have a tendency to become more vertical. Plagiotropic branching consists basically of two branching planes, horizontal and vertical, where shoots 1 and 2 belong to a horizontal plane and shoots 3 and 4 to a vertical one (Figs. 4b,5). Because shoots 1 and 2 in the horizontal plane are affected by negative gravitropism, the horizontal plane is folded slightly along the direction of the mother shoot (Fig. 5b). The average divergence angle ω (79.1°) was less than the 90° of a perfect horizontal plane by 10.9° (Table 3). Deflection angles (42.8° , 41.6°) of plagiotropic shoots were close to those of or-

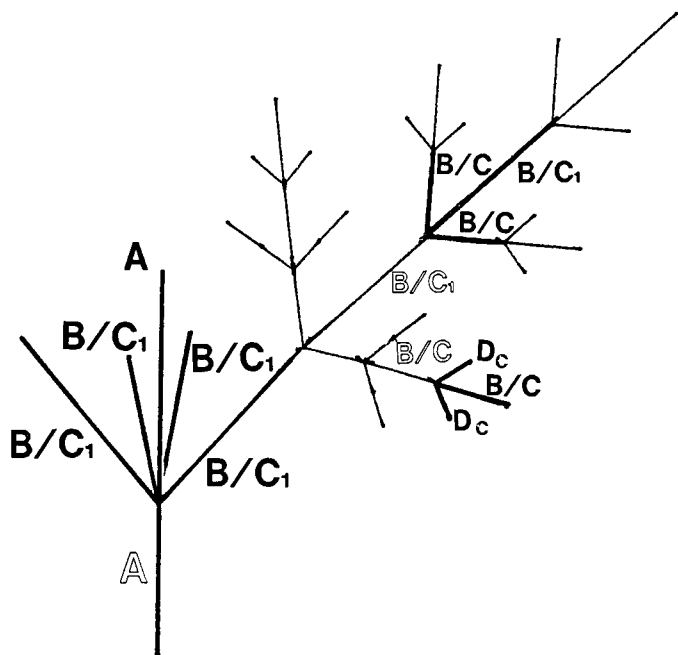


Fig. 6. Assignment of vegetative branching types according to the transition rules of Table 2. Branching types are illustrated in Fig. 3. The reproductive branch complex is not shown.

thotropic shoots (42.8°). Length ratios of shoots 1 and 2 to shoot 4 are given in Table 3.

The central daughter shoot (shoot 0) in the vertical branching plane (Fig. 5e) grows more vertically than the mother shoot (AB). Deflection angles from the direction of the mother shoot (θ_0 in Fig. 5f) were measured (Fig. 7a). This angle (θ_0) correlated with the angle of inclination of a mother shoot (ρ). The exact regression line is determined by the method of least squares using $\theta_0 = a\rho + b$ and is indicated by the broken line in Fig. 7 (broken line). Since we hypothesize that shoot 0 in plagiotropic branching is inclined by a constant angle from the continuation of the mother shoot from vertical, we calculated a generalized regression line for which $\theta_0 = \rho - b$. For this hypothetical generalized model, the regression line is $\theta_0 = \rho - b$, because the inclination angle of shoot 0 (b) is $\rho - \theta_0$. Note that the slope is 1.0 in the model. The generalized regression line determined by the method of least squares was $\theta_0 = \rho - 20.7^\circ$ as shown in Fig. 7a (solid line) and Table 3. The generalized and exact regression lines were close to each other as shown in Fig. 7a. For our simulations, we approximate the inclination of shoot 0 by the generalized regression, i.e., 20.7° from the vertical line. The same procedure of regression lines was applied to deflection angles θ_3 and θ_4 , then we get the generalized regression lines (Fig. 7b, c and Table 3). For simulations, the angles between shoots 3 and 0, and shoots 4 and 0 were calculated by using the generalized regression lines. Calculations resulted in 43.0° ($\theta_3 - \theta_0$) and 43.6° ($\theta_4 + \theta_0$), respectively (see Fig. 5f). These angles were close to those of the orthotropic branchings (42.8°). Therefore, shoots 0, 3, and 4 in plagiotropic branching became more vertical, respectively, without changing their mutual geometrical relationship (Fig. 5d, e). That is, shoots 0, 3 and 4 rotated around the point B,

TABLE 2. Matrix of branching types in new daughter shoots.^a

New daughter shoot	Mother branching type			
	A	B/C ₁	B/C	D _c
Shoot 0	A	Repr	Repr	Repr
Shoot 1	B/C ₁	B/C	D _c	—
Shoot 2	B/C ₁	B/C	D _c	—
Shoot 3	B/C ₁	Repr	—	—
Shoot 4	B/C ₁	B/C ₁	B/C	D _c

^a Each type is illustrated in Fig. 3 and their relationships are shown in Fig. 6. B/C, branching type B or C. B/C₁, a branching type growing vigorously in type B/C. Repr, reproductive branching type (type E, F_B, F_C or G_B). —, no daughter shoots grow.

but the angle between shoots 3 and 0 and the angle between shoots 4 and 0 did not change.

The lengths of shoot 0, shoot 3, and shoot 4 (L_0 , L_3 , and L_4) were measured (Fig. 8). Shoot 4 became progressively dominant over (longer than) shoot 0 as the mother shoot departed from the vertical line. The length ratios of shoot 0 and shoot 3 (L_0 and L_3) to shoot 4 (L_4) were constant when $\rho > 50^\circ$. Shoot 4 did not vary much in length as the mother shoot departed from vertical (data are not shown). Shoot 0 greatly decreased in length until around $\rho = 50^\circ$ (Fig. 8a). Shoot 3 had a similar tendency as shoot 0 (Fig. 8b).

Reproductive shoots—The branching angle between two daughter shoots of a fork was $2\theta = 48.2^\circ \pm 8.33^\circ$

TABLE 3. Measurements of vegetative shoots used for computer simulations.

Parameters	Mean + SD or regression line	Range of ρ	N	Figures
In orthotropic branching				
$\theta_1, \theta_2, \theta_3, \theta_4$	$42.8^\circ \pm 6.8^\circ$	$\sim 0^\circ$	64	
$L_1/L_0, L_2/L_0, L_3/L_0, L_4/L_0$	0.608 ± 0.301	$\sim 0^\circ$	72	
In horizontal plane of plagiotropic branching ^a				
ω	$79.1^\circ \pm 10.47^\circ$	$18^\circ\text{--}80^\circ$	49	
θ_1	$42.8^\circ \pm 9.05^\circ$	$18^\circ\text{--}80^\circ$	51	
θ_2	$41.6^\circ \pm 7.70^\circ$	$18^\circ\text{--}80^\circ$	51	
L_1/L_4	0.481 ± 0.192	$18^\circ\text{--}80^\circ$	51	
L_2/L_4	0.493 ± 0.180	$18^\circ\text{--}80^\circ$	51	
In vertical plane of plagiotropic branching ^b				
θ_0	$\rho - 20.7^\circ$	$18^\circ\text{--}80^\circ$	52	Fig. 7a
θ_3	$\rho + 22.3^\circ$	$18^\circ\text{--}80^\circ$	49	Fig. 7b
θ_4	$-\rho + 64.3^\circ$	$18^\circ\text{--}80^\circ$	51	Fig. 7c
L_0/L_4	$-0.0230\rho + 1.187$ ($r = -0.690$)	$18^\circ\text{--}50^\circ$	28	Fig. 8a
	0.112 ± 0.0612	$50^\circ\text{--}80^\circ$	26	
L_3/L_4	$-0.000713\rho + 0.491$ ($r = -0.455$)	$18^\circ\text{--}50^\circ$	28	Fig. 8b
	0.153 ± 0.0689	$50^\circ\text{--}80^\circ$	23	

^a Exact regression lines: $\omega = -0.106\rho + 84.15^\circ$ ($r = -0.143$, $N = 49$); $\theta_1 = 0.329\rho + 36.37^\circ$ ($r = 0.216$, $N = 51$); $\theta_2 = 0.0352\rho + 39.89^\circ$ ($r = 0.0673$, $N = 51$); $L_1/L_4 = -0.000827\rho + 0.5211$ ($r = -0.0634$, $N = 51$); $L_2/L_4 = 0.00154\rho + 0.4189$ ($r = 0.1242$, $N = 51$).

^b Generalized regression line for deflection angles. See text. Exact regression lines: $\theta_0 = 0.863\rho - 14.0^\circ$ ($r = 0.857$, $N = 52$); $\theta_3 = 0.807\rho + 31.5^\circ$ ($r = 0.770$, $N = 49$); $\theta_4 = -0.453\rho + 37.8^\circ$ ($r = -0.627$, $N = 51$).

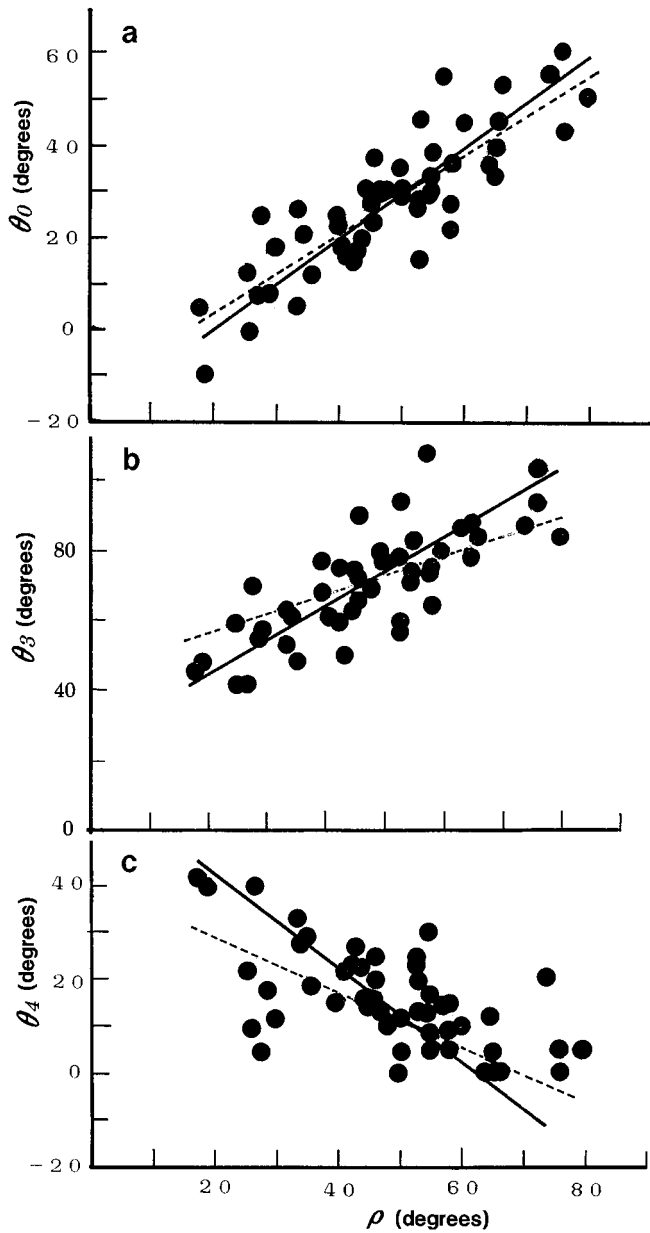


Fig. 7. Deflection angle θ_0 , θ_3 , and θ_4 (in a, b, and c, respectively) in vegetative shoots vs. inclination angle of mother shoot (ρ) (See Fig. 5f). Solid lines in figures are generalized regression lines. Broken line is the exact regression line by the method of least squares. See Table 3.

($N = 141$); for simulations we used $\theta = 24.1^\circ$. Branch length ratio of a daughter shoot to a mother one was 1.04 ± 0.305 ($N = 160$ from seven branch complexes). The averaged time interval between successive forkings was 2.08 ± 0.83 yr ($N = 349$). The branch length of one year's growth was 0.923 ± 0.326 cm ($N = 349$).

Computer simulations of *Cornus kousa*—*Simulation of a branching in the vegetative phase*—Computer simulations were performed using real measurements for the parameter values in Eqs. 1. We calculated all branching angles ($\theta_0, \dots, \theta_4$) and all branch length ratios (L_0, \dots, L_4) from the angle of inclination of a mother shoot (ρ). Then,

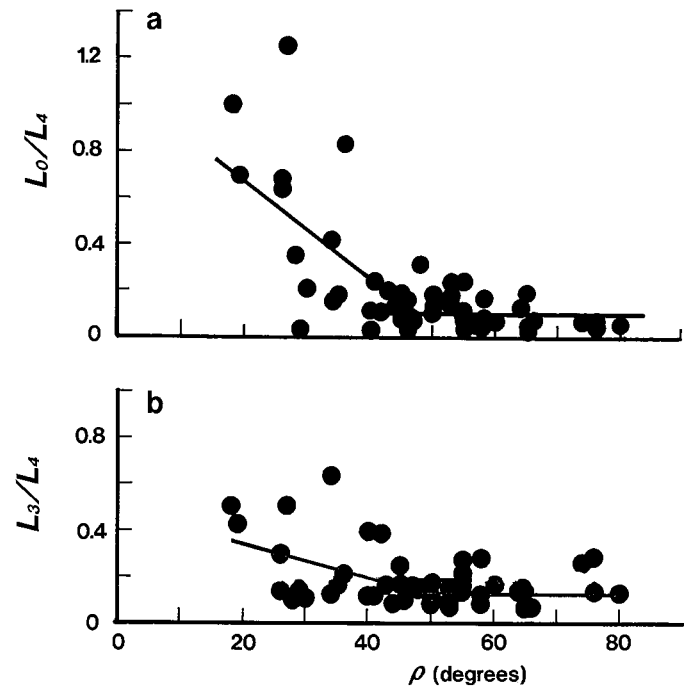


Fig. 8. Vegetative branch length ratios of shoots 0 and 3 (in a, b) with respect to shoot 4 in vertical plane (See Fig. 5f) vs. inclination angle of mother shoot (ρ). Solid lines are regressions and averages. (See Table 3.)

the coordinates of the five end points of daughter shoots in three-dimensional space were calculated by Eqs. 1. The results are shown in Fig. 9. Our geometrical model generated branching types A and B/C (Fig. 3) by variation of parameter value ρ . Branching type D_C (Fig. 3) was obtained by giving zero value to parameters L_1 and L_2 .

Simulation of a whole tree in the vegetative phase—To perform computer simulations of development of a whole tree, we used the sequence of transitions of branching types which develop from one another. The timing of actual transition from one type to another was not deterministic but stochastic in the real tree. As an approximation, we used a plausible, deterministic transition rule based on branch position, as already mentioned (Fig. 6 and Table 2). Based on this transition rule, we performed computer simulations of branch complexes. Figs. 10 and 11 show simulated developmental stages of a whole tree and a lateral branch, where each dominant shoot in the respective branchings was assumed to have the same length as that of its mother shoot.

Simulation of reproductive shoots—Most reproductive branchings belong to type F, which is a pseudodichotomy. The apical bud produces a terminal inflorescence (Fig. 3). Planes of successive forkings are vertical ($\omega = 0^\circ, 180^\circ$) or perpendicular ($\omega = \pm 90^\circ$) to the previous vertical plane (Fig. 12). In reproductive branching, the horizontal plane is not folded as in vegetative branching (Fig. 5b). Values 90° (and -90°) and 0° (and 180°) are used for divergence angle ω alternately in successive branchings (Fig. 12). For simulation we used deflection

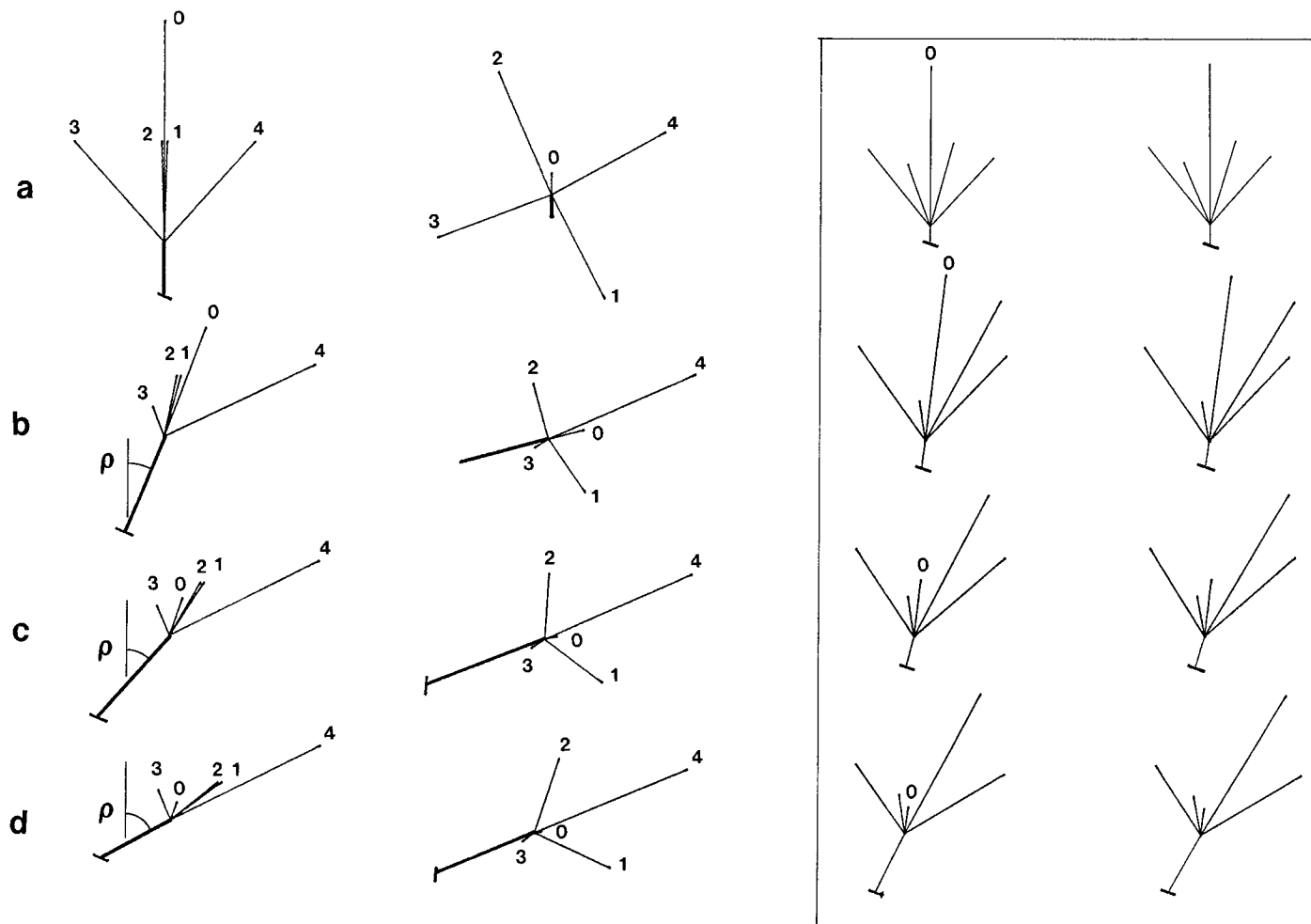


Fig. 9. Computer simulations of branching of vegetative shoots with the inclined angle of the mother shoot (ρ) set at 0° (a), 22° (b), 42° (c), and 62° (d). Side, top, and stereo views are displayed from left to right. The direction of gravity is to the bottom of the page (side and stereo views) and approximately perpendicular to the page (top view). Numerals 0–4 indicate shoot 0 – shoot 4.

angle $\theta = 24.1^\circ$, and the branch length ratio of a daughter shoot to a mother one was 1.0.

Simulated developmental stages of reproductive branching are shown in Fig. 13. Gravity influenced the growth direction of shoots 3 and 4 in vertical plane. The model in which shoots 3 and 4 raise up vertically against gravity had been used in the vegetative shoots as already mentioned. The same model was used here in reproductive shoots where the angle 2θ between two daughter shoots remains constant. We made a simulation to show the effect of gravity on a branching complex (Fig. 13a–g). Fig. 13h is the case without raising-up of shoots against gravity and should be compared with Fig. 13f.

To show the transition from a vegetative to a reproductive phase, a reproductive branch complex was simulated upon a vegetative branch (Fig. 14). The size of reproductive shoot is considerably smaller because the reproductive branch length is ~ 2 cm, whereas the length of shoot 4 in a vegetative branch complex is ~ 30 cm.

DISCUSSION

Variation of branching in an individual tree—Based on detailed observations and quantitative measurements

of actual shoots of various orientations, we made the basic model of branching that was affected by gravity.

The intrinsic branching pattern of vegetative shoots of *C. kousa* was five-forked branching in orthotropic shoots (Fig. 4a). When the mother shoot departed from the vertical, the orthotropic shoots transformed to plagiotropic ones (Fig. 4b) that produced a branching consisting of vertical and horizontal branching planes (Fig. 5b, f). The geometrical consequence of the transformation was clearly demonstrated by computer simulations of the basic model (Fig. 9).

Gravity affected the direction of branching differently in vertical and horizontal branching planes. In the vertical plane, shoot 0 raised up vertically against gravity (until the inclination angle = 20.7° , Fig. 7a). Shoots 3 and 4 also raised up along with shoot 0. Shoots 0, 3, and 4 behaved just like a three-forked solid body (Fig. 5e). The relative geometrical relationship among them did not change during changes in orientation. On the other hand, the horizontal plane was folded (angle ω , from 90° to 79.1°) as its mother shoot inclined away from the vertical, while the deflection angles θ_1 and θ_2 were constant (Fig. 5b). Shoot 0 in the vertical plane became more vertical

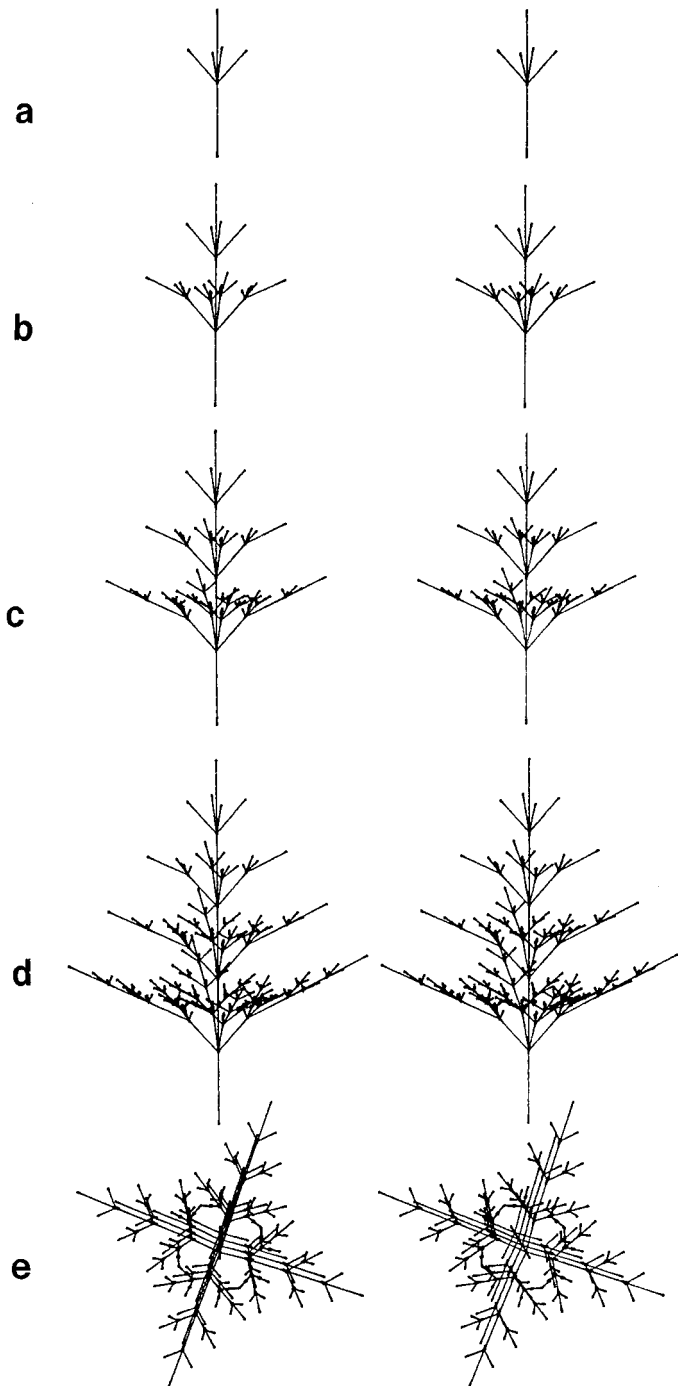


Fig. 10. Computer simulations of the whole shape of vegetative shoots. Stereo side views of the first (a), the second (b), the third (c), and the fourth generations (d) of simultaneous branching. Top view of the fourth branching generation (e) is also shown. The direction of gravity is to the bottom of the page (a-d) and almost perpendicular to the page (e).

by the inclination angle = 20.7° (Fig. 7), and all plagiotropic shoots occurred when their inclination angle from vertical was $>20^\circ$ (Fig. 8). These two angles were similar to each other. The shoot seems to have a critical inclination angle that detects the vertical. When the inclination angle is less than $\sim 20^\circ$, the shoot apparently does

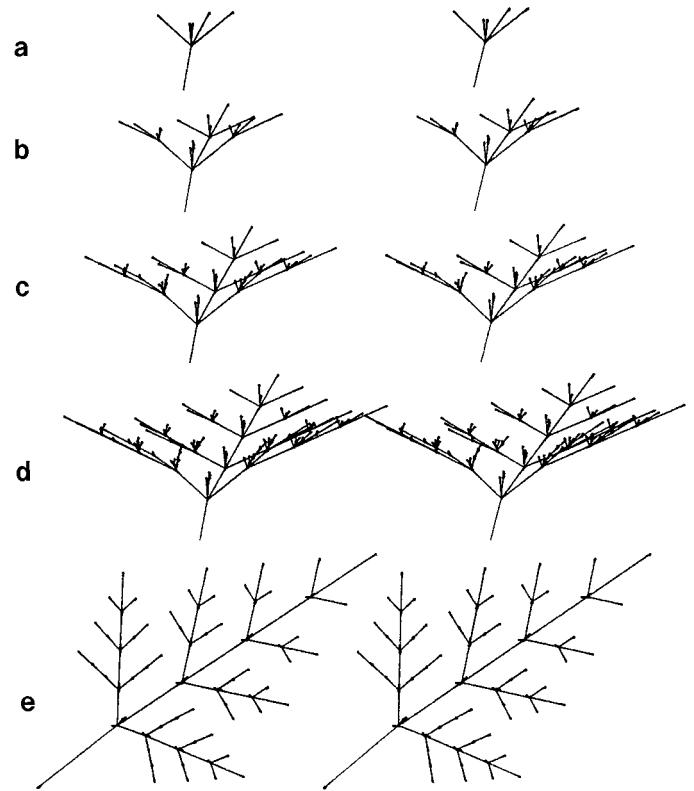


Fig. 11. Computer simulations of the vegetative stages of a lateral branching complex. Stereo side views of the first (a), the second (b), the third (c), and the fourth branching generations (d) are shown. Top view of the fourth branching generation (e) is also shown. The direction of gravity is to the bottom of the page (a-d) and almost perpendicular to the page (e).

not distinguish the direction of inclination from the vertical.

Reproductive shoots differed in geometry from vegetative shoots because their size was smaller than the vegetative one, and reproductive branching was bifurcated instead of five-forked. Reproductive shoots were also under the branching rule with different parameter values (ω

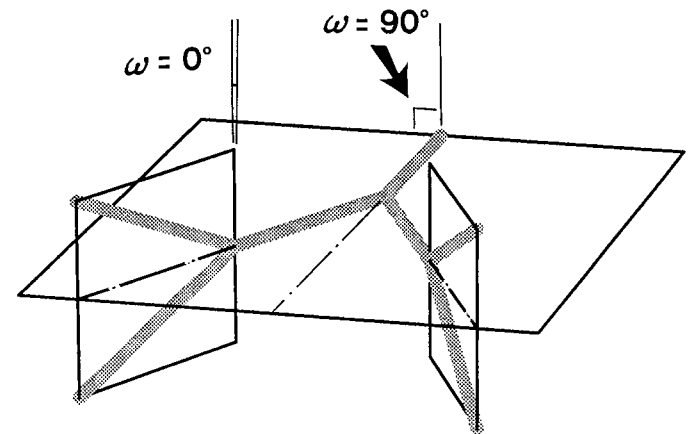


Fig. 12. Reproductive shoots with successive planes of forking along a shoot. Divergence angle $\omega = \pm 90^\circ$ for horizontal forking and $\omega = 0^\circ, 180^\circ$ for vertical forking in this figure.

= 0° , 180° and $\pm 90^\circ$). Reproductive shoots also raised up vertically opposite the direction of gravity, but we did not measure this quantitatively because reproductive shoots were too small to be measured accurately. The results of generalized regression line of vegetative branchings were used here for the simulation of reproductive branchings.

Comparison of computer simulations with actual trees—Realistic simulations produced by a model demonstrate that its parameters and rules for branching are applicable and appropriate. Such a test is particularly important in geometrical models that undergo many iterations where seemingly slight variations in branching angles or ratios can result in very different architectures (Honda, 1971; see also other approaches in Room, Maillette, and Hanan, 1994 and Prusinkiewicz and Lindenmeyer, 1990).

Computer simulation of whole tree shape in the vegetative phase of *Cornus* (Fig. 10) seems to be realistic for a young tree. A simulated lateral branch complex (Fig. 11) displays the same pattern of extensive sympodial growth as an actual lateral branch complex, although objective or quantitative evaluations of the similarity are difficult. If we look at the single branching in detail (Figs. 1,2), we find that, as the mother shoot departs from the vertical line, the plane including shoots 1 and 2 changed independently of the erection of shoot 0. Shoot 0 is not included in the plane of shoots 1 and 2, but shoot 0 raises up vertically from the plane as seen in actual trees from side view of branchings of type B and type C (Figs. 1,2). This behavior is successfully simulated by our model as shown in side view of Fig. 9c, d.

The computer simulation of a reproductive branch complex (Fig. 13f, g) shows a compact spherical branch complex, raising up in gravity as did actual reproductive branch complexes. We can recognize the effect of gravity in the branching model when Fig. 13f is compared to Fig. 13h, in which the effect of gravity was not introduced in the simulation.

Here, we present a model that simulates actual trees of *Cornus*. This model could be useful in examining the theoretical effects of changes in parameters related to geometry with respect to gravity or mechanical stability as reviewed in Fisher (1992) or using more recent approaches for determining optimization of branching patterns (Farnsworth and Niklas, 1995). Such studies of gravitropism and biomechanics can be carried out in the future but will have to be related to experimental studies on actual trees.

Relationship among the geometrical models of branching—In general, any direction of a new shoot can be defined by two angles in three-dimensional space. The I model (Borchert and Honda, 1984) is a case in which the direction of a daughter shoot is defined by angles ω and θ based on the direction of a mother shoot in gravity. Therefore, the I model is the most generalized branching model. The H model (Honda, 1971; Fisher and Honda, 1977) is a case of the I model with $\omega = \pm 90^\circ$. The P model (Honda, Tomlinson, and Fisher, 1982) is similar to a model of the successive alternation of two I models with $\omega = 0^\circ$, 180° and $\omega = \pm 90^\circ$ (Fig. 12), but differs

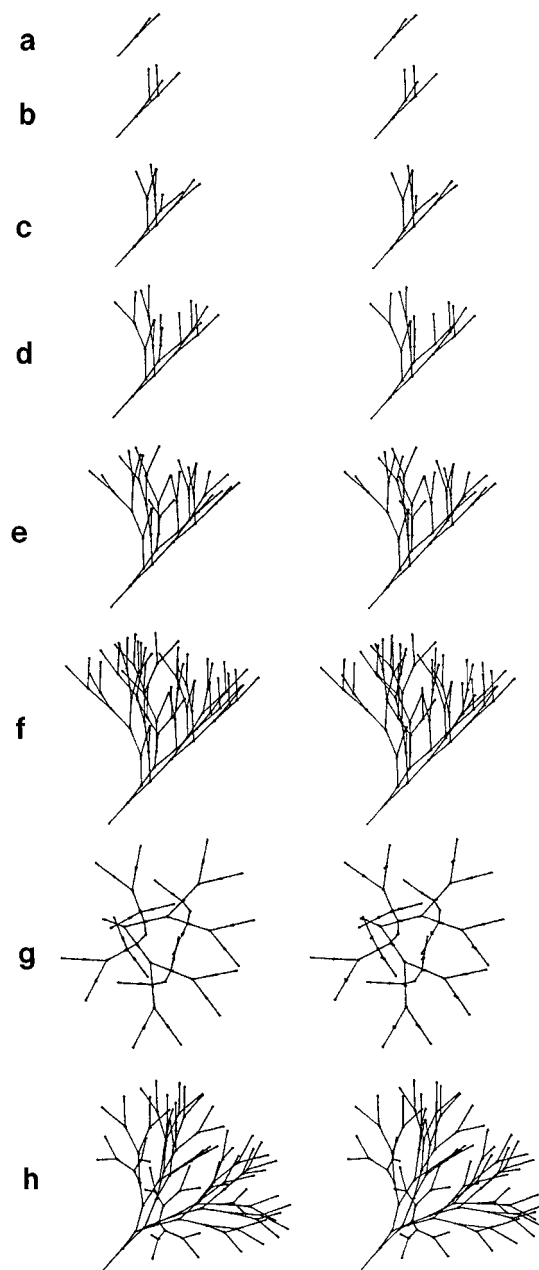


Fig. 13. Computer simulations of the growth of reproductive shoots. Stereo side view of the first to the sixth branching generations (a-f) are shown. Top view of the sixth branching generation is also shown (g). Simulations a-g use the model in which a shoot in the vertical plane raises up vertically until its inclination angle = 20.7° in the computer simulation. Computer simulation without the raising-up model (h) is shown for comparison with f. The direction of gravity is to the bottom of the page (a-f and h) and almost perpendicular to the page (g).

as will be mentioned later. These models can be described by the relation of two planes (the branching and the vertical planes in Table 1): the branching plane includes a mother shoot and one or two daughter shoots, and the vertical plane includes a mother shoot. In the H model, the branching plane is perpendicular to the vertical plane, and the mother shoot is in the direction of the steepest line on a slope of the branching plane. In the P model, the branching plane is perpendicular to the *previous*

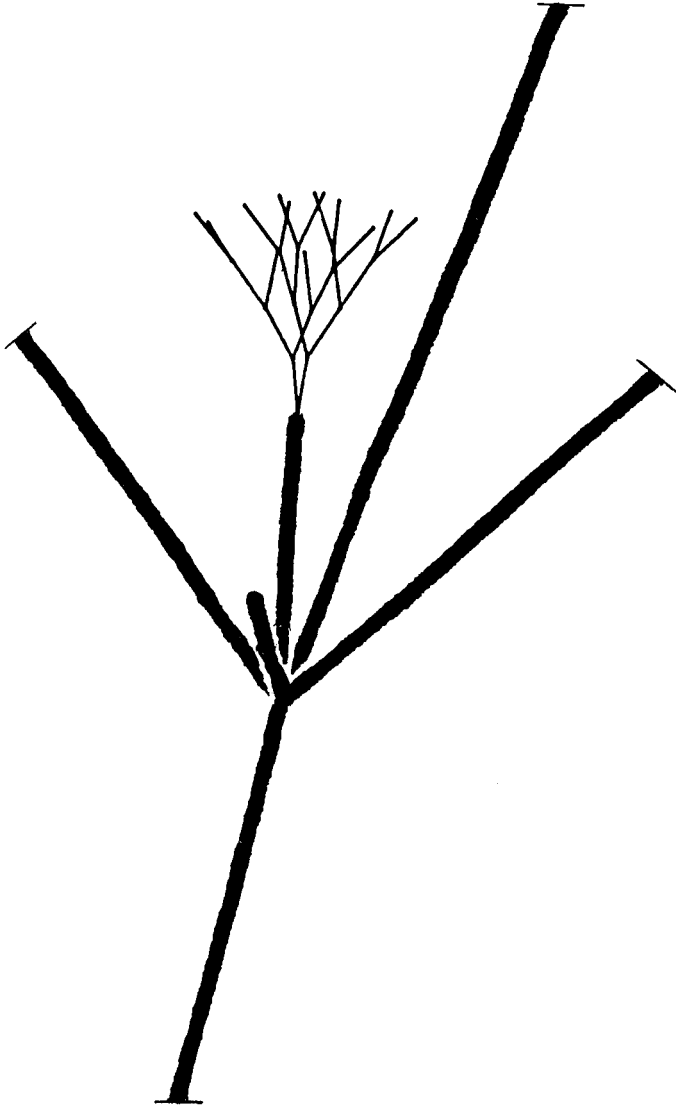


Fig. 14. A simulated developmental stage of reproductive branching that begins at the end of a vegetative branch.

branching plane (including the mother shoot, the shoot of the mother's sister, and the shoot of grandmother). The original P model bears no relation to the vertical plane and thus is independent of gravity direction. The P model could be modified to include the gravity effect (Honda, Tomlinson, and Fisher, 1982). In the I model, a branching plane (including a mother and a daughter shoot) makes angle ω with the vertical plane as shown in Fig. 5a.

Although the branching model for *Cornus* is more complex in geometry and branching types than our previous models (Table 1), it supports our view that relatively little information is needed to establish the distinctive branching pattern and shape of a tree. Tree form is

determined by bud outgrowth and fate (branching types), orientation angles of a shoot, and relative shoot length. These geometrical features are determined by pre-existing shoots (mother shoots) as seen in Tables 2 and 3. Complexity of form arises after numerous interactions or orders of branching occur. Consequently, we suggest that distinctive canopy shape can be genetically determined by relatively localized control of bud growth and orientation and by the extent of growth (the number of branching events), or what Room, Maillette, and Hanan (1994) refer to as internal factors. Canopy shape is also affected by environment or external factors (Fisher, 1992; Room, Maillette, and Hanan, 1994), which were not dealt with in our study.

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