

# Ratio of tree branch lengths: The equitable distribution of leaf clusters on branches

(*Terminalia*-branching/branch angle/effective leaf area/optimization/adaptive geometry)

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**ABSTRACT** The theoretical optimal ratios of branch lengths, which produce the most equitable distribution (minimum deviation) of leaf clusters in a computer-simulated branch system, are similar to the observed ratios in real trees of *Terminalia*. In another study, observed values for branch angles in this species were shown to be similar to theoretical optimal values that produce the maximum effective leaf area. The relationship between these two fundamental parameters of bifurcation and tree geometry and their effect on effective leaf area and distribution of leaves are discussed.

The overall shape of a tree is basically determined by two parameters, branch angle and ratio of branch lengths. This concept was realized in a theoretical treelike body that consisted of repeating bifurcations (1) and was later adapted with modifications to a real tree, *Terminalia catappa* L. (2). This species has certain architectural features that make it ideal for quantitative studies of tree geometry, and, in addition, its branching pattern is widespread among many tropical dicotyledonous trees (3). Recently, we have shown that the observed branch angles in *T. catappa* are very similar to optimal theoretical angles that produce the maximum effective leaf area (maxEA). This strongly suggests that branch angles are adapted for the maximum exposure of leaf surface to sunlight (4, 5). Does the other parameter, the ratio of branch lengths, have an adaptive significance? The theoretical ratios of branch lengths that produce maximal effective leaf area are far from the observed ones in *T. catappa*, and the theoretical branch pattern looks highly unstable with respect to mechanical design (5).

In the present report, we consider the equitability of distribution of leaf clusters on branches—that is, the uniformity of effective leaf area of individual leaf clusters in a branch complex. The observed ratios of branch lengths in *T. catappa* are shown to be very similar to theoretical ones that produce the most equitable distribution of leaf area within a branch complex. The biological meaning of the equitable distribution of leaf clusters will be considered, and the relationship between two important adaptive features of tree geometry, the maxEA and the most equitable distribution of leaf clusters, will be discussed.

## ASSUMPTIONS

**Computer Simulation of Branching.** The description of bifurcation used here is described (1); a branch unit (a mother unit,  $P_A P_B$ ) forks to produce two daughter branch units ( $P_B P_1$  and  $P_B P_2$ ). The branch angles are defined as  $\theta_1$  and  $\theta_2$ , the angles that  $P_B P_1$  and  $P_B P_2$  make with  $P_A P_B$ , respectively. The ratios of branch lengths are defined as  $R_i = P_B P_i / P_A P_B$  ( $i = 1$ , and 2). Repetition of bifurcation is governed by described

branching rules (2). A lateral branch complex or a branch tier consisting of the five lateral branch complexes is built up, simulating the branching pattern of *T. catappa*. A feature of this species is the dorsiventrality of lateral branch complexes that produce a pagoda-shaped crown, because the complexes arise as whorls from the main vertical leader axis. In the present report, except where otherwise indicated, we do not distinguish branch length ratios between the first order branching and the following ones as we did earlier (2)—i.e.,  $R_{01} = R_1$  and  $R_{02} = R_2$ .

The calculations are carried out by an electronic digital microcomputer with a disk memory (P652 and DAS 604, Olivetti). Simulations are drawn by an x-y plotter (WX535, Watanabe Sokuki, Tokyo).

## Hypothetical Variation of the Ratios of Branch Lengths.

We assume that there is a constant ratio of branch lengths that is based on the decrease of branch lengths in a geometrical ratio from the proximal to the distal branch units in a tree. This seemed reasonable according to the results of computer simulations of tree-like bodies (1) and was confirmed by actual observations of real trees [ref. 6; S. Oohata (personal communication)]. Now we will vary hypothetically the two ratios of branch lengths,  $R_1$  and  $R_2$ . They are not completely independent of each other; when  $R_1$  is large,  $R_2$  should be small because the amount of material from which two daughter branch units are made may be constant. Therefore, we assume  $R_1 + R_2$  is constant during hypothetical variation of the branch length ratio. When  $R_1$  is varied, we will use

$$p = \frac{R_1}{R_1 + R_2}$$

instead of  $R_1$ . Then  $R_2 / (R_1 + R_2)$  is expressed as  $1 - p$ .

**Calculation of the Effective Leaf Area.** The cluster of 7–10 approximately horizontal leaves at the end of each branch unit can be approximated by a horizontal circular disk of a constant radius at that point. We will define the radius of a circular disk in relative terms by using  $r$ , the ratio of the radius to the length of the longest distal unit of the simulated branch complex when  $R_1 = 0.94$  and  $R_2 = 0.87$ , which are the observed values in real trees. Taking the shape and length of the leaves into account, we find that  $r = 0.8$  gives a reasonable approximation (4, 5). The radius of disks is determined as noted above and kept constant during the varying of  $R_1$  and  $R_2$  in computer simulations. The total leaf area of the lateral branch complex (or the branch tier) consists of many overlapping circular disks. The effective leaf area (EA), the area exposed to direct vertical illumination, is based on a projection of the branch complex (or tier) onto the horizontal plane. This projection is divided into Dirichlet domains (7, 8), the boundaries of which are intersecting lines be-

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Abbreviations: EA, effective leaf area; maxEA, maximum EA;  $p$ , ratio of branch length ratios;  $r$ , radius of leaf cluster;  $s$ , deviation;  $\min s$ , minimum  $s$ .

tween neighboring pairs of circles. The area of each domain ( $a_j$ ) is calculated, and EA is defined as  $EA = \sum_j a_j$ .

**Variation in Distribution of Leaf Clusters on Branches.** For the purpose of examining the variation in the distribution of leaf clusters on branches, we define

$$s = \sqrt{\frac{\sum_j (a_j - \bar{a})^2}{C}}$$

where  $C$  is the number of end points of the branch unit (the number of leaf clusters or the number of domains) in a lateral branch complex or branch tier and  $\bar{a}$  is the average area over all domains ( $\bar{a} = EA/C$ ). The scale is adjusted so that  $\bar{a}$  is unity. We will call  $s$  the deviation hereafter, bearing in mind that it indicates the degree of *lack* of equitable distribution of leaf clusters on branches. A small value of  $s$  means that the areas of Dirichlet domains are quite uniform; in other words, the end points of branch units are uniformly distributed. On the other hand, a large value of  $s$  means that the areas of Dirichlet domains are uneven, and the end points of branch units are crowded in some regions and sparse in the other regions. The biological meaning of  $s$  will be considered later.

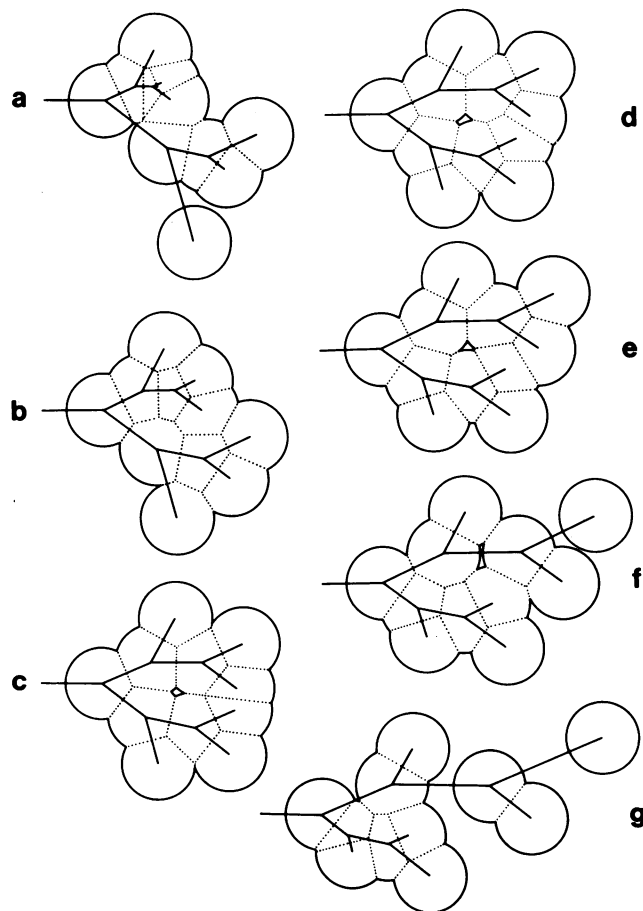


FIG. 1. Variations of the pattern of a lateral branch complex ( $N = 3$ ) viewed from above. The natural observed values in *T. catappa* were given to all parameters except for  $p$ ;  $R_1 + R_2 = 1.81$ ,  $r = 0.8$ ,  $\theta_1 = 24.4^\circ$ , and  $\theta_2 = -36.9^\circ$ .  $p = 0.30$  (a), 0.40 (b), 0.50 (c), 0.52 (d), 0.555 (e), 0.615 (f), and 0.70 (g). The pattern of d, e, and f is, respectively, that similar to nature, that for minimum  $s$  (min  $s$ ), and that for maxEA. Boundaries (.....) divide the total leaf area into Dirichlet domains.

## RESULTS

One branch complex of branch order  $N = 3$  of *T. catappa* was simulated as shown in Fig. 1d using observed natural values for the parameters in which  $R_1 = 0.94$  and  $R_2 = 0.87$ .  $R_1$  was varied under the condition of  $R_1 + R_2 = 1.81$  because the amount of material for the two daughter branches should be kept constant during all comparisons as described in *Assumptions*. Several patterns are shown in Fig. 1. EA of the respective patterns was calculated and plotted in Fig. 2 (broken line). The maxEA was obtained at  $p$  (which is proportional to  $R_1$  here) = 0.615 and its pattern is shown in Fig. 1f. The value of  $p$  for maxEA is far from the natural observed value ( $p = 0.519$ ), and the pattern seems unstable with respect to mechanical design. Next, the  $s$  of the respective patterns was calculated and plotted in Fig. 2c. The minimum  $s$  (min  $s$ ) occurs at  $p = 0.555$  and its pattern is shown in Fig. 1e. The value of  $p$  for min  $s$  is closer to the natural observed value and the pattern is similar to Fig. 1d.

$R_1 + R_2 = 1.81$  in the case of *T. catappa* and we obtained  $p = 0.555$  for min  $s$ . Then to what degree is the value of  $p$  for min  $s$  dependent on  $R_1 + R_2$ ? When  $R_1 + R_2$  was varied slightly ( $R_1 + R_2 = 1.61, 1.71, 1.91, \text{ and } 2.01$ ), the values of  $p$  for min  $s$  were obtained. The results are shown in Figs. 2 and 3a. It should be noticed that  $p$  for min  $s$  is minimal around  $R_1 + R_2 = 1.81$ —i.e.,  $p$  for min  $s$  is not affected severely even if the value of  $R_1 + R_2$  fluctuates around 1.81.

The leaf cluster at the end of each branch is approximated by a circular disk of a constant radius. For the determination of the radius, we use  $r = 0.8$ , which gives a reasonable approximation as mentioned in *Assumptions*. How much does the value of  $r$  affect  $p$  for min  $s$ ? The values of  $p$  for min  $s$  were calculated in the cases of  $r = 0.6, 0.7, 0.9, \text{ and } 1.0$  and shown in Fig. 3b. The  $p$  value for min  $s$  is minimal around  $r = 0.8$ . However, this value of  $p$  is only slightly affected as  $r$  fluctuates around 0.8.

The results mentioned above are in the case of the branch order  $N = 3$ . In the other cases ( $N = 1, 2, \text{ and } 4$ ), the values of  $p$  for min  $s$  are obtained and shown also in Fig. 3c. We can have two slightly different simulations when  $N = 4$ , as described in rule 6 of Fisher and Honda (2).

When we calculated the theoretical branch angles that produce the maxEA, an isolated branch complex did not give reasonable values of the branch angles (Fig. 5, ref. 5). Therefore,

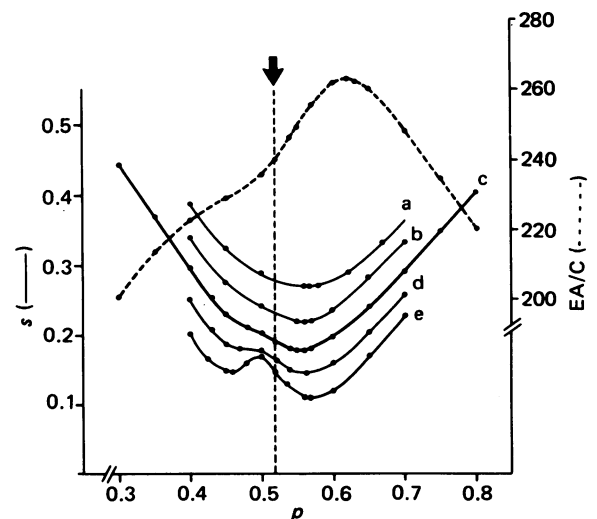


FIG. 2. EA in relative units and  $s$  versus  $p$ . ---, EA when  $R_1 + R_2 = 1.81$ . —,  $s$  when  $R_1 + R_2 = 1.6$  (a), 1.71 (b), 1.81 (c), 1.91 (d), and 2.01 (e). Arrow indicates the observed  $p$  value (0.519). Other parameter values are the same as Fig. 1.

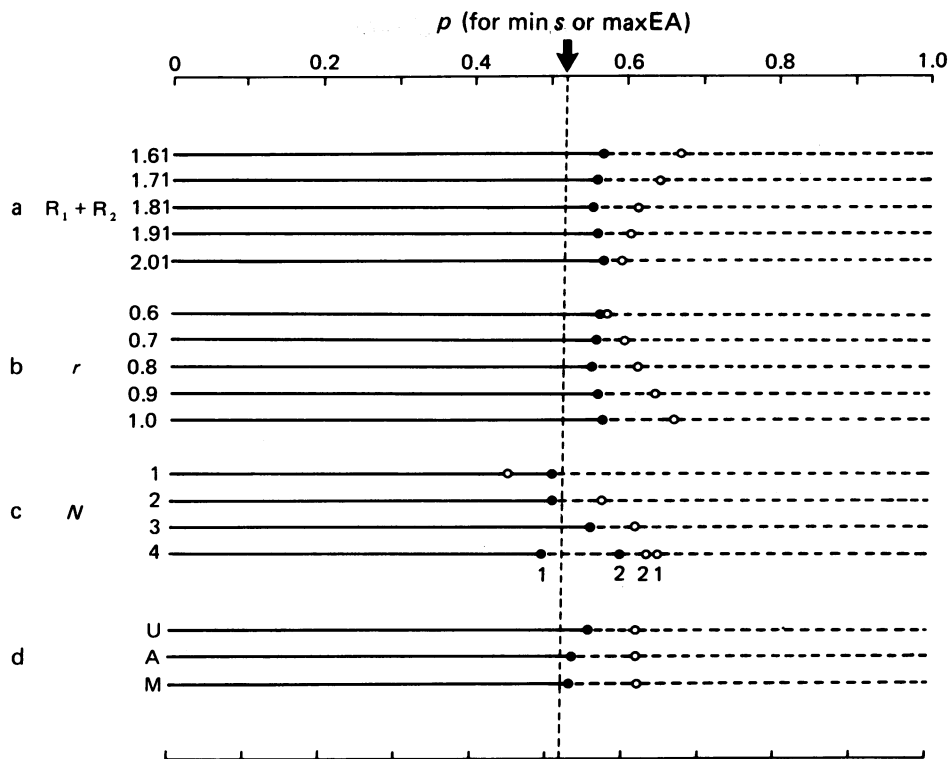


FIG. 3. Values of  $p$  for min  $s$  (●) and for maxEA (○), depending on  $R_1 + R_2$  (a),  $r$  (b), and  $N$  (c) of one lateral branch complex.  $d$  is the case of a branch tier consisting of the five branch complexes, uniform (U), alternate (A), and mixed (M) symmetries as defined by Fisher and Honda (5). The parameter values, except where otherwise indicated, are the same as in Fig. 1. Arrow indicates the observed  $p$  value (0.519).

we used a branch tier consisting of the five lateral branch complexes (4), which is more like the real tree. Here, even a branch complex gives reasonable values of  $p$  for min  $s$ . In a branch tier, there are many kinds of arrangements of branch complexes, because there can be mirror image symmetry among branch complexes in a tier. The three types were defined as uniform, alternate, and mixed symmetries as described (5). Calculations of the values of  $p$  for min  $s$  in the three symmetries were also performed (Fig. 3d). They are as close or closer to the observed  $p$  value as those of a single branch complex (Fig. 3a-c). Branch patterns for min  $s$  and maxEA of a tier of alternate symmetry,  $N = 3$ , are shown in Fig. 4.

All the  $p$  values for maxEA, in addition to the  $p$  values for min  $s$ , were also calculated and are shown in Fig. 3. For all cases presented here, the  $p$  values for min  $s$  are closer to the observed value of  $p$  in *T. catappa* than those for maxEA. The condition of min  $s$  appears to determine the  $p$  value, at least to a greater degree than that of maxEA.

Although we see how the feature of min  $s$  affects  $p$ , we should remember that branch angles were reasonably predicted by the condition of maxEA (4, 5). Will the adaptive feature of min  $s$  give a reasonable prediction of the branch angles? The branch angles  $\theta_1$  and  $\theta_2$  for min  $s$  were calculated in the several cases and are represented in Fig. 5 in comparison with those for maxEA. In the case of one branch complex, the theoretical values of  $\theta_1$  and  $\theta_2$  for maxEA and min  $s$  are both far from those in nature. We must consider the more natural case of a branch tier. As shown in Fig. 5, the theoretical values of  $\theta_1$  and  $\theta_2$  for maxEA are generally closer to the observed values than those for min  $s$ , thus indicating that the adaptive feature of maxEA determines  $\theta_1$  and  $\theta_2$  to a greater degree than min  $s$ .

We have the two parameters of tree geometry, branch angles ( $\theta_1$  and  $\theta_2$ ) and  $p$  in relation to the two adaptive features, maxEA and minimum variation in the distribution of leaf clusters (min  $s$ ). We might vary both parameters simultaneously

to search for the optimal state if possible. However, this would require an enormous amount of calculation. As an alternative, we vary the branch angles and the  $p$  value alternately. First, the branch angles are fixed at the observed values and the  $p$  value for min  $s$  is calculated. Next, the calculated  $p$  value is fixed and the  $\theta_1$  and  $\theta_2$  for maxEA are calculated. And next, the calculated  $\theta_1$  and  $\theta_2$  are fixed and the  $p$  value for min  $s$  is calculated, and so forth. These steps are repeated and the results are shown in Fig. 6 (dotted circles). A similar procedure was followed except that the feature of min  $s$  is used for both determinations of the branch angles and  $p$  value; this procedure gives the results shown in Fig. 6 (open circles). These results can be contrasted to those derived by the same procedure, but in which the feature of maxEA is used throughout as shown in Fig. 6 (solid circles). The calculated  $\theta_1$  and  $\theta_2$  in the case of alternate calculation of  $p$  for min  $s$  and of  $\theta_1$  and  $\theta_2$  for maxEA are closer to the observed values than those derived by the other methods of calculation, although the calculated  $p$  value is not so close to the observed value.

### DISCUSSION

The theoretical  $p$  values which are calculated in a branch complex and a branch tier to produce min  $s$  are closer to the observed value than are the  $p$  values that produce maxEA. The theoretical branch angles producing min  $s$  and those producing maxEA are both far from the observed values in the case of one isolated branch complex. In the case of a branch tier, the branch angles that produce maxEA are closer to the observed values than are those that produce min  $s$ . These results are summarized in Table 1.

For determining the most natural  $\theta_1$  and  $\theta_2$ , we must consider a branch tier instead of one branch complex. This could be expected because  $\theta_1$  and  $\theta_2$  have a greater influence on interactions among neighboring lateral branch complexes in a tier than does  $p$ .

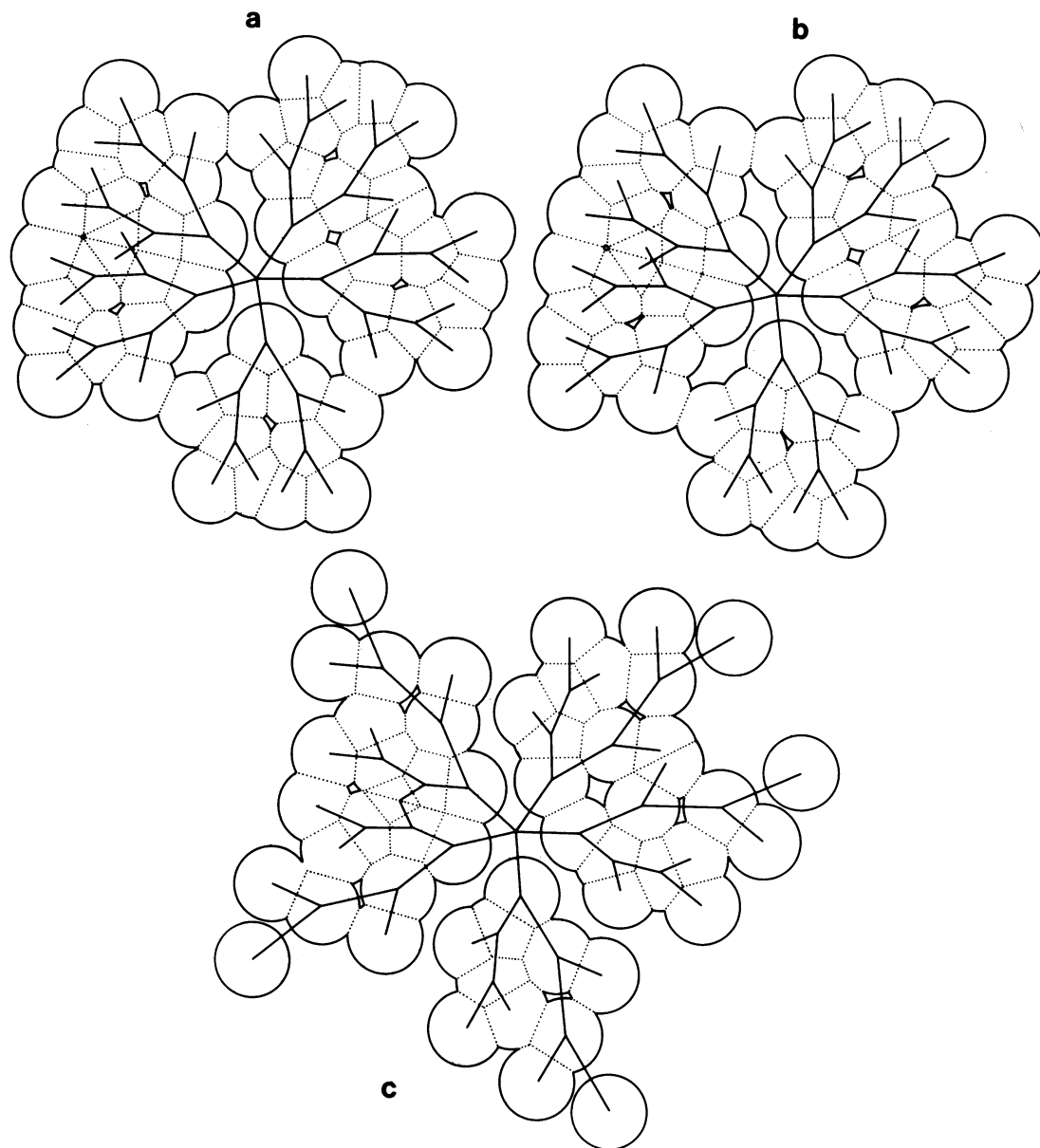


FIG. 4. Patterns of branch tier of alternate symmetry with  $N = 3$ . (a) Pattern similar to nature,  $p = 0.52$ ; (b) pattern for  $\min s$ ,  $p = 0.533$ ; (c) pattern for  $\max EA$ ,  $p = 0.617$ . Other parameter values are similar to those in Fig. 1.

We will now consider the biological meaning of the deviation,  $s$ . The value of  $s$  indicates the degree of inhomogeneity of the areas of Dirichlet domains in a branch complex (or tier). Therefore, it also indicates the unevenness of distribution of end points of the branch units to which each leaf cluster is attached. In the case of a large  $s$ , the end points of branch units are crowded in some regions and sparse in the other regions. Ecologically, this means that some leaf clusters are greatly shaded by adjacent ones whereas other clusters are fully exposed to sunlight, resulting in uneven illumination and heat load. On other hand, in the case of a small  $s$  we expect that costs of intercluster competition for sunlight are more equitably distributed, on branches at least, than in the case of a large  $s$ .

One of the roles of branches in a tree is the transport of materials between the trunk and leaves. The transport of materials and products of photosynthesis from leaf clusters may be very poorly balanced among branches of the same order when the  $s$  value is larger. For example, compare the two branches of the first bifurcation in lateral branch complexes of Fig. 1 *a* and *g*. One of the branches has a large total EA belonging to all its

descendent branch units, whereas the other branch has a small EA.

In addition to the above-mentioned aspects of ecology and physiology, we can relate  $s$  to the mechanical stability of the branch system. Branches in a tree have the important, if not primary, role of mechanically supporting the leaves and twigs in addition to transporting materials and establishing the geometry of the EA. The weight of every leaf cluster should be similar to one another, irrespective of large or small EA, rather

Table 1. Summary of the computer simulations of optimal branching parameters in *Terminalia catappa*

Branching system	$p$ for		$\theta_0, \theta_2$ for	
	$\min s$	$\max EA$	$\min s$	$\max EA$
One branch complex	0	X	X	X
Tier of five complexes	0	X	X	0

0, Theoretical value(s) that is closer to the observed value(s); X, theoretical value(s) that is far from or not closer to the observed value(s).

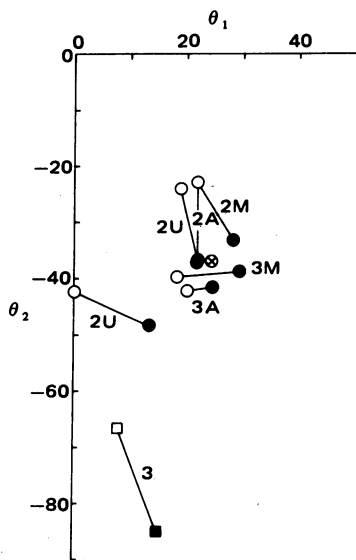


FIG. 5. Branch angles  $\theta_1$  and  $\theta_2$  (in degrees) that produce the maxEA (●, ■) or the min  $s$  (○, □) in comparison with the observed ones (⊙). The natural observed values in *T. catappa* are given to all parameters except for  $\theta_1$  and  $\theta_2$ ;  $R_1 = 0.94$ ,  $R_2 = 0.87$ ,  $R_{01} = 0.86$ ,  $R_{02} = 0.85$ ,  $r = 0.8$ , and  $\alpha = 138.5$  (2). ■ and □, One branch complex of  $N = 3$ ; ● and ○, a branch tier of five complexes. U, A, and M, symmetries as mentioned in the legend to Fig. 3; 2 and 3,  $N = 2$  and  $N = 3$ , respectively.

than proportional to EA; a small EA of a cluster is due to its large overlapping area. When the  $s$  value is large (e.g., Fig. 1 *a* and *g*), the form of a branch complex looks unstable in mechanical design because of the uneven distribution of the moments of mass that are defined as a leaf cluster's weight multiplied by the length of its branch unit. Long branch units would be more easily broken by strong mechanical perturbation (i.e., wind) than short ones because mechanical stability depends not only on the distribution of the load, but also on the geometry of the beam (branch) carrying the load. On the other hand, the geometry or quality of the wood in the branch could compensate for the uneven distribution of moments, such that the branch unit would be stable from a mechanical point of view.

We are interested in whether or not the adaptive features of min  $s$  and maxEA are consistent with each other in a branching pattern. We should mention that the EAs of Figs. 1 *e* and 4 *b*, which are the patterns at min  $s$ , are reduced by 4.5% and 9.5% of their respective maxEAs (Figs. 1 *f* and 4 *c*). At present we cannot determine whether or not these reduced rates are significant. Nevertheless, we know that *T. catappa* gets an equitable distribution of leaf clusters via optimizing branch length ratios at little cost to EA. Similarly, it gets a maxEA via optimizing the branch angles at little cost to the equitable distribution of leaf clusters.

We conclude that in *T. catappa* two important parameters of branch geometry (presumably under genetic control) have

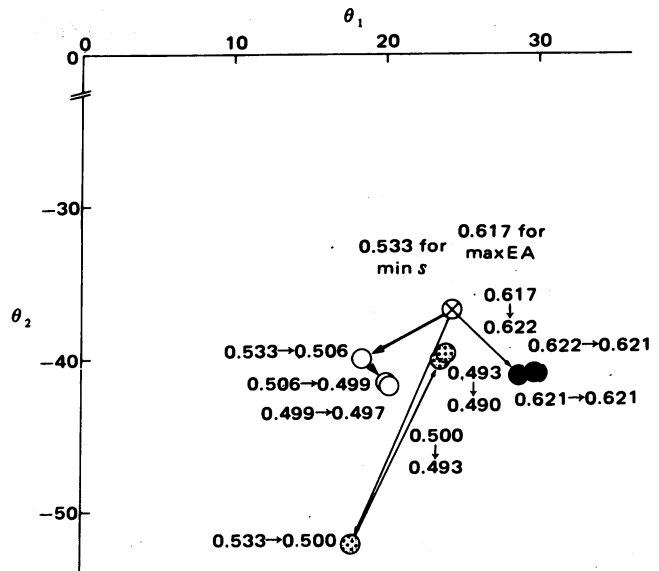


FIG. 6. Alternate calculations of the branch angles (in degrees) and  $p$ . Numerals are the  $p$  values. Large arrows indicate changes under the principle of min  $s$ . Small arrows indicate changes under the principle of maxEA. ⊙, The case of determinations of  $\theta_1$ ,  $\theta_2$  for maxEA and  $p$  for min  $s$ . First,  $\theta_1$  and  $\theta_2$  are fixed at the observed values and  $p$  for min  $s$  is calculated. Next, the calculated  $p$  is fixed and  $\theta_1$  and  $\theta_2$  are calculated for maxEA . . . etc. ○, The case of determinations of  $\theta_1$ ,  $\theta_2$ , and  $p$  by using the condition of min  $s$  throughout; ●, the case of determinations of  $\theta_1$ ,  $\theta_2$ , and  $p$  by using the condition of maxEA throughout; ⊙, the observed values of  $\theta_1$  and  $\theta_2$ .

been evolutionarily selected for the most efficient presentation of leaf surface within the constraints of the pattern of branching. This has resulted in a maxEA with the most uniform distribution of leaf clusters, thus distributing biophysical costs, such as shading, transport of materials, heat load from insolation, and moments of mass, throughout the system.

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