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Trees and Streams: The Efficiency of Branching Patterns

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Extending the analysis of branching patterns of the drainage net of rivers, originated by Horton, the relation of average numbers and lengths of tree branches to size of branch was investigated. Size of branch was defined by branch order, or its position in the hierarchy of tributaries. It was found that, as in river drainage nets, there is a definite logarithmic relation between branch order and lengths and numbers.

This definite relation is quantitatively comparable, within limits, among river networks, tree branching systems, and several random-walk models in both two and three dimensions. Such a relation appears to be the most probable under the applicable constraints. Moreover the most probable arrangement appears to minimize the total length of all stems in the branching system within other constraints and so, to that extent, achieves a certain efficiency.

1. Introduction

The stem system of a plant forms a structural support serving to expose photosynthetic organs to sunlight and at the same time to provide the routes for removing photosynthetic products from them. While the structural support requires stems of increasing size toward the central trunk of a plant, that requirement alone seems insufficient to account for the regularity and similarity of the main branching network typical of a variety of plants. Rather, there appears to be an inherent economy in the structure of the branch network. The principle of economy or least-work under particular constraints inherent in the whole system is postulated as a controlling element in the organization of the branching pattern of plants.

The branching form is analogous to the drainage system of a river in that the network of streams and tributary rills serves various parts of the drainage area as routes for carrying surface runoff from the basin eventually to the ocean. The network of stream channels is also comprised of trunk streams and tributary branches. Because there is a modest fund of knowledge about the branching of stream channels available, it is of interest to inquire about the similarities and differences among various kinds of branching networks, particularly the comparison of networks of three dimensions and of two.

Service to a large number of individual leaves, or in the case of a river drainage basin, a large number of unit areas, could be accomplished by a variety of stem patterns. There could be, for example, an individual branch going to each unit but all branches converging to a single central locus. Such a pattern would eliminate stems of intermediate size. Another possibility would be to have a large number of petioles emanating from each branch of moderate size thus eliminating the need for stems of small size. Or these combinations might occur haphazardly even on a single plant inasmuch as there is usually a plethora of latent or deciduous buds, most of which never develop.

2. River Drainage Networks and Network Nomenclature

A great impetus in the study of river channel morphology was provided by the findings of R. E. Horton (1945) who recognized the geometric relations between the number and lengths of stream channels of various sizes. The term "branch order" (or stream order in the case of rivers) is a measure of the position of a branch in the hierarchy of tributaries. It is best described by a sketch as in Fig. 1(a) The first-order branches are those which have no tributaries. The second-order branches are those which have as tributaries only first-order stems. However, each second-order branch is considered to extend headward to the tip of the longest tributary that it drains. Which tributary to call the headward extension of a given second-order branch, where differences in length are insignificant, is a matter of choice.

The third-order branch receives as tributaries only first and second-order channels, and it also is considered to extend headward to the end of the longest tributary. It can be seen, then, that in practice, after the second-order branches are labeled and third-order branches identified, one of the previously marked second-order branches is renumbered to make it the headward extension of the third-order branch.

When the number of streams of a given order and their average lengths are plotted against order on semi-logarithmic paper, straight-line relationships are obtained of which the graphs in Fig. 1(b) are typical. The slopes of these lines have particular significance. In the plot of number of branches against order [Fig. 1(b)] the slope of the line signifies the ratio of the number of first-order branches to each second-order one. This is the bifurcation ratio, or branching ratio. In river-channel systems it varies within narrow limits, averaging around 3·5 for basins in a wide variety of physiographic and climatic settings. The meaning of this ratio can best be visualized by saying

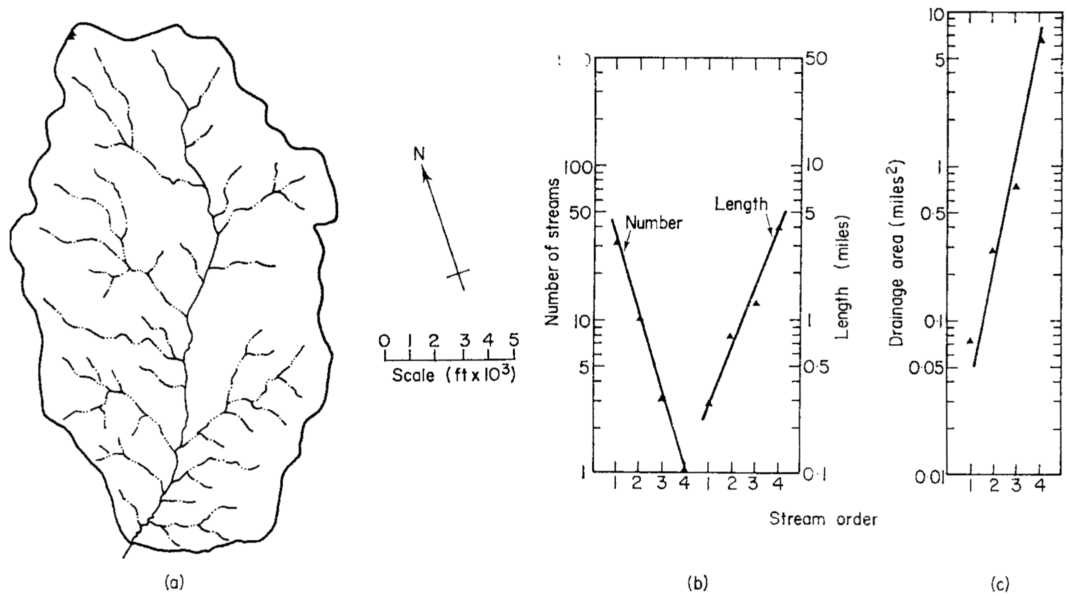

FIG. 1. Drainage network and branching characteristics of a drainage basin having an area of 6·6 miles², Watts Branch above Glen Hills, near Rockville, Maryland. (a) drainage network map; (b) number and lengths of streams of various orders; (c) average drainage area of streams of each order. ———·———, First order; ———··———, second order; ———···———, third order; ————————, fourth order.

that any stream of a given order has either three or four branches of the next lower order.

The slope of the line in the plot of average stream length against order signifies the ratio of the length of a second-order channel to the average length of its first-order tributaries. It is called the "length ratio", and for rivers has a value which generally averages about 2·3. That is, any branch tends to be 2·3 times as long as the average of its tributaries of the next lower order.

In river systems there is also a regularity in the relation of drainage basin size and stream order as indicated in Fig. 1(c).

3. Analysis of Tree Branching Patterns

The same definitions and plotting procedure can be applied to analyze the branch patterns of a plant. For the usual tree, which is too large to allow handling of every individual branch and twig, I started at the tip of the lowest large branch which could be conveniently reached from the ground or a stepladder and measured the length of each branch or twig progressively toward the main trunk, keeping track of the order of each sub-branch and twig as it occurred along the main branch. Having completed the measurement of those main branches which could be reached, the relative sizes of all main stems were estimated by eye and assigned an estimated order number by comparison with those for which detailed measurements were available.

A typical set of data after the average lengths had been computed is given in Table 1. This sample is for a conifer but for deciduous trees similar data were recorded for average numbers of petioles on branches of various orders.

The measured data on order, number, and average lengths are plotted in Fig. 2 for two conifers one of which was discussed in Table 1. On the fir tree, one fourth-order branch was measured completely and it was only part of the tree. By visual comparison the number of fourth-order branches could be counted and the order of the main trunk estimated. Data plotted in Fig. 2 are for twigs and branches only, and the measurements of needles are not plotted. The present paper does not deal with either leaves or root hairs; probably quite different parameters are operating. The method of estimating total number from a sample may, however, have some validity.

Experience has shown that the bifurcation ratio, or slope of the line in Fig. 2, is the same for the whole tree as for a representative sample. It was estimated that for the fir tree there is one stem (main trunk) of fifth-order. A check on the validity of this estimate is provided by extending (solid line) the plot representing the relation of order to average stem length (right-hand diagram Fig. 2) to the place it intersects an abscissa value of order 5. There

TABLE 1

Number and average lengths of branches of various orders and other data for Fig. 2

Species:	Fir (Abies concolor)
Location:	10350 W. 13th Pl., Denver, Colorado, August 1964
Size and age:	Diameter breast high, 0·2 ft; 12 yrs (est.); height 10 ft (est.)
Needles or leaves:	Average 0·08 to 0·17 ft in length; needles solitary

Order of branch	Number of branches	Average length (ft)
1	88	0·27
2	21	·77
3	4	1·8
4	1	4·9

Main trunk estimated as fifth order.

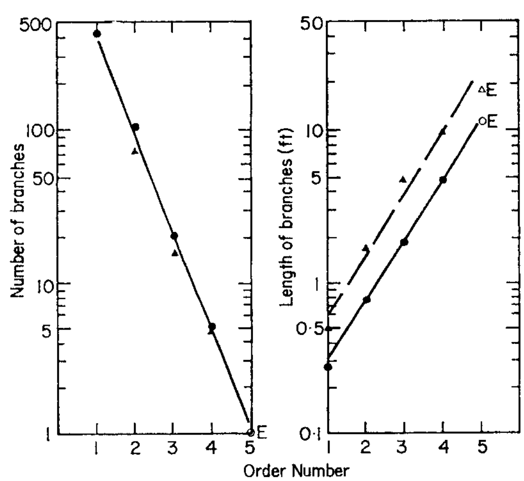

FIG. 2. Numbers and average lengths of branches of various orders. ●, On a 10-ft high fir tree (*Abies concolor*); ▲, a pine 19-ft high (*P. taeda*). In the left-hand plot, the branching ratio = 4·8; in the right-hand plot, the length ratio = 2·5 for the pine (— — —) and 2·7 for the fir (———). Open symbols marked E indicate estimated values.

the length of the fifth-order stem is read from the graph to be 11·5 feet, which is in reasonable agreement with the field estimate of the height of the whole tree, 10 feet.

For the whole fir tree, then, one can estimate that there are 430 twigs of first order, 100 of second order, 20 of third order and about 5 of fourth order. With data on the number of petioles or needles per unit length of various branches and knowing the average length of branches of different size, it would be possible to estimate quickly the total number on the whole tree. A similar method was used to estimate the total number of miles of river and stream channel in the whole United States (Leopold, Wolman & Miller, 1964, p. 142).

For the particular fir tree used in Fig. 2 the bifurcation ratio is 4·8 and the length ratio 2·7.

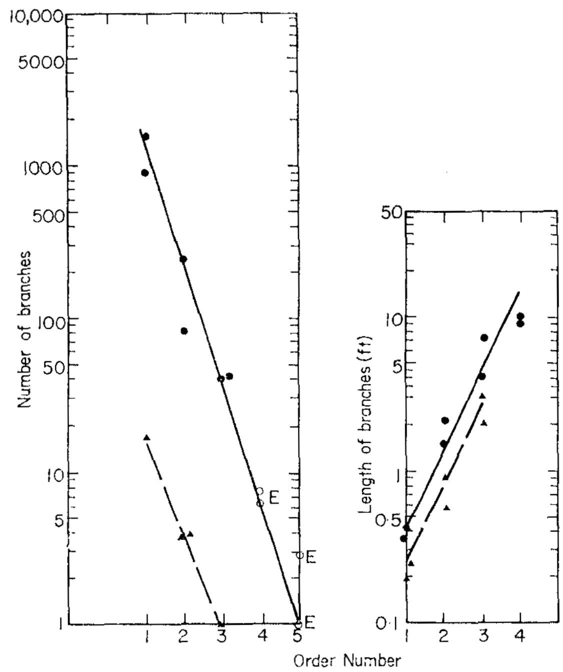

FIG. 3. Branching characteristics of two species of deciduous trees. ●, Two ash (*Fraxinus* sp.) of moderate size (diameter at breast height = 0·34 ft); ▲, a small tulip (*Liriodendron tulipifera*), height 3·3 ft. In the left-hand plot, the branching ratio = 6·5 for the ash (———) and 4·7 for the tulip (— — —). In the right-hand plot, the length ratio = 3·4 for the ash (———) and 3·6 for the tulip (— — —). Open symbols marked E indicate estimated values.

The 19-foot pine tree shown on Fig. 2 was also estimated to be of fifth order. Data on number of branches agree closely with those for the 10-foot fir but branch length for any given order are greater for the pine than for the fir.

Some additional examples are given in Fig. 3, presenting two species of deciduous trees. Estimated points on the graphs are marked "E".

It can be seen that all the graphs for trees are generally similar to the graph for the river in Fig. 1, and that differences among conifers and among deciduous trees seem to be no less than between conifers and deciduous. However, the present paper is intended merely to call attention to certain general similarities and many more samples than I now have available would be necessary for an analysis of variance.

4. Opposing Tendencies and the State of Mutual Accommodation

In river channel morphology a wide spectrum of alternative hydraulic adjustments are possible to accommodate the increasing flow or discharge as the river grows downstream by the joining of tributaries. The river as a whole can be visualized as an open system in steady state. The quasi-equilibrium or steady state condition has been found susceptible of analysis by considering its energy distribution analogous to thermodynamic entropy (Leopold & Langbein, 1962; Leopold *et al.*, 1964, pp. 266–275). The steady state in the river system represents a balance between the opposing tendencies for minimum power expenditure in the whole system and equality of the distribution of power throughout the system.

By analogy it seems possible that the branching patterns of trees and of other biologic forms are governed by opposing tendencies which are analogous to minimum energy expenditure and uniform energy utilization. In the case of trees it might be supposed that the former involves minimizing the total length of all branches and stems. The uniformity of energy utilization might concern providing a photosynthetic surface which tends, under certain constraints, to obtain the most efficient use of sunlight. Such efficiency might be visualized as combining (a) maximum number of area-hours of exposure to direct sunlight, and (b) the most uniform number of area-hours during progress of the sun's passage during the day.

5. Total Stem Length in Some Different Branching Patterns

Various branching arrangements can be visualized which would serve a given number of unit areas. Each of these arrangements has a different value of total length of all stems. Serving a given number of unit areas would mean, in the tree, carrying nutrients to and supporting the leaves. In the river drainage basin it would mean draining each part of the total area.

Consider first the problem posed in Fig. 4, in which three points, A, B and C, are to be joined in such a way that points A and B are to be fed by, supported by, or otherwise served by single point C. The three diagrams

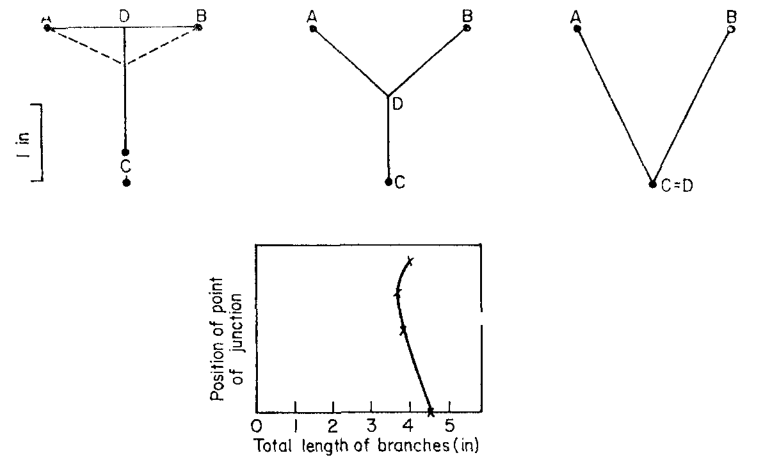

FIG. 4. Effect of position of junction point of a Y on the total stem length. Three possible arrangements are shown at the top; below is a graph of position of the junction point in relation to total stem length. The ordinate scale for the graph is identical with the graphical length of ordinate in the diagrams above.

represent merely some of the alternative lengths and angles at which branches could be constructed depending on the choice of the junction point D. The graph shows the relation of position of junction and the total length of branches. A minimum point exists, not very sensitive, but nevertheless real, in which point D is about a third of the maximum distance down the length of branch D–C.

Thus to minimize total branch lengths, the branches in the example would not meet in a T as in the left diagram, nor in a V as in the right, but in a Y in which the stem of Y is about two-thirds of its total height.

Consider now the simple case of a square, eight units on each side, consisting of 64 unit areas, and one wishes to serve each unit area from a point centered in the square. One possible pattern would be to have a separate branch proceed from the central point to each of the 64 units, as suggested in Fig. 5(a). Another would be to have four principal branches connected to the center and from the ends of each branch there would radiate 16 shorter stems, as in Fig. 5(b). A still further subdivision involving sub-branches is pictured in Fig. 5(c). The total lengths of stems in the three patterns are respectively approximately 200, 124 and 88 length units. The order number of the largest branches in the three patterns are respectively first, second and third order.

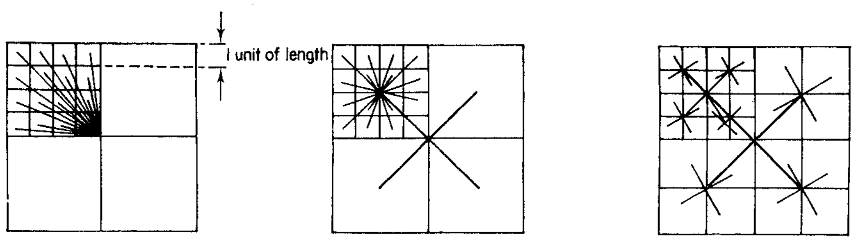

FIG. 5. Possible branching patterns to serve 64 unit areas from a central point. (a) Separate individual stems from the center to each unit; total length of stems $\doteq$ 200 units. (b) Four principal branches, from each of these radiale 16 stems; total length of stems $\doteq$ 124 units. (c) Four principal and 16 sub-branches and radiating stems; total length of stems = 88 units.

Clearly, an increase in the maximum order of the branching pattern serves the same number of unit areas with a progressively smaller total length of stem. Branching, therefore, represents an increase in efficiency in considering total stem length. It is understood that constraints are exerted limiting the bifurcation.

The same number of unit areas may be served if the unit areas are distributed around certain three-dimensional forms rather than merely over a plane. For example, consider a cylinder having an area, exclusive of the circular ends, equal to 64 units of area. Let a central stem be in the position of the axis of the cylinder and from this axis there radiate orthogonally stems to each of the 64 units of the surface. This would be a branch network of second order. It would require approximately the following total stem lengths depending on the ratio of cylinder height to radius.

Height/radius	Total stem length
1·1	303
2·5	205
10	74

Thus leaves of unit area making up the outer surface of a tall thin cylinder could be served by a branching system of second order slightly more efficiently than by a second order branching system with leaves arranged in a square on a plane surface. But if the cylinder were fat and not tall it would be less efficient than a plane surface. Further, the cylinder would be less efficient for exposing the leaves to the passing sun because part of the cylinder would always be on the shady side.

No doubt one of the constraints imposed on the branching is the requirement that the subaerial stem system of a plant must give structural support to the various parts. Another might be effect of length on flow characteristics of liquid. Other types of constraints also suggest themselves.

6. Branching Systems and Random Walks

In the natural world there are usually a large number of interacting processes at work, including a host of variables. Feedback mechanisms tend to constrain any individual process which may cause a local perturbation in a system. There are also a large number of examples; that is, there are many hills, many streams, many trees. So large is the number of factors and so many are the examples that, though the average or modal condition of any system may be described, the description must be in statistical terms. An understanding of the phenomena must stem from a stochastic rather than deterministic approach. All the detailed local causes and effects operating on a given example cannot be known. In such circumstances random occurrences may play a large role and thus random models involving specific probability statements can often produce the same general characteristics which occur in the mean or modal condition of the field prototype.

Drainage networks of stream channels have been generated by random-walk models and these have characteristics quantitatively similar to field examples (Leopold & Langbein, 1962, pp. A14-19). Specifically, relations between numbers and average lengths of branches and the orders similar to the graphs of Fig. 1 are produced. The idea suggests itself, then, that random models in three dimensions might be devised which would have some of the same characteristics as the branching network of trees. The value of such models might be in the inferences they suggest concerning any differences in patterns resulting from opposite versus alternate buds, and from the percentage of buds that develop.

Three-dimensional models were too complicated to visualize in detail in diagrams drawn on paper so actual models were built, using a child's Tinker-Toy. This toy consists basically of wooden wheels drilled with holes located around the circumference and in the plane of the wheel. Wooden sticks of various lengths can be fitted into these holes so that they project off the wheel in radial directions. There are eight radial holes in each wheel and one in the axial direction.

Many rules for the construction of branching structure might be devised, but the following were typical of the ones chosen for the models here described. The face cards were removed from a deck, leaving all aces to tens inclusive. After each draw the card was replaced and the deck shuffled.

Question	*Drawn*	*Rule*
Whether to add or not to add a stem	red	Pass to next wheel
	black	Put two branching stems into the wheel
Length of stem to be added	odd	Add long stem
	even	Add short stem
Angle orientation of wheel	A–2	0° to given plane
	3– 4	22°
	5– 6	45°
	7– 8	67°
	9–10	90°

The game begins with a single vertical stalk set on a base for convenience. A wheel is placed on its upper end so that the stalk sticks into one of the radial holes. A card is drawn. If it is black two sticks are placed in the wheel radiating out of it at 45 and 135° from the horizontal. The black draw in other words, gives two stems or a bifurcation. The length of the added stems are determined by the odd–even rule, and the orientation of the whole wheel relative to a predetermined direction is governed by the value of the card. The rule just described involves equal chance for adding two 45° sprouts or no sprouts at all.

The end of each sprout was taken consecutively over the whole tree, a card being drawn for each sprout existing. Then the process was repeated and in each repetition there would be a larger number of sprouts. The model was considered ended when the total number of available wheels or sticks was used, usually 40 of each. The analysis of numbers and average lengths of each order was carried out as in the drainage basin analysis described in connection with Fig. 1. Data for this particular set of rules are plotted in the lower diagram of Fig. 6.

Other rules were made up, primarily by changing the number of added stems on the draw of a black card. Equal probabilities were tested for 0 or 2 sprouts, 0 or 3 sprouts, 0 or 1 or 2 or 3 sprouts, 0 or a long sprout consisting of two alternate and 1 terminal short sprout. The numbers and average lengths as function of order are shown graphically in Figs 6 and 7.

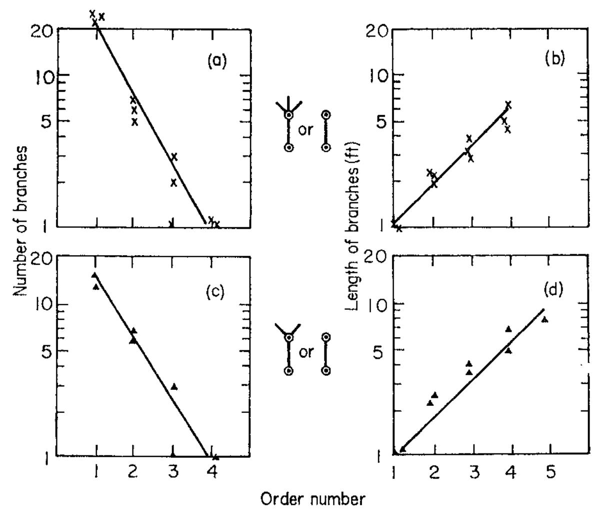

FIG. 6. Tinker-toy trees by random walks. (a) and (b) show data pertaining to a model in which the choice was to add three stems or no stems. (c) and (d) the choice was to add two stems or no stems. For (a) the branching ratio = 2·8; for (b) the length ratio = 1·8; for (c) the branching ratio = 2·5; for (d) the length ratio = 1·8.

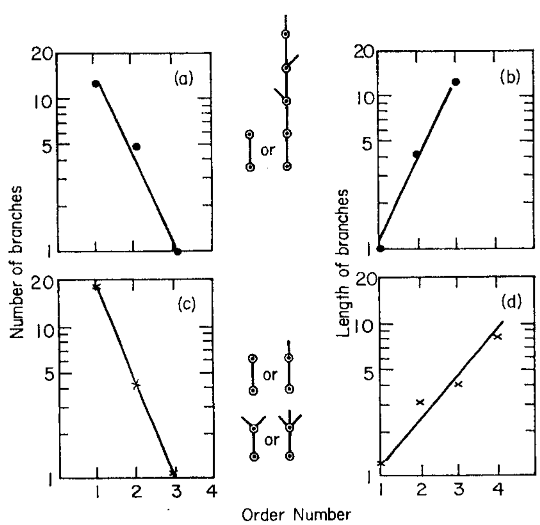

FIG. 7. Tinker-toy trees by random walks. (a) and (b) show data from a model in which the choice was to add an alternate branching stem or no stem; In (c) and (d) the choice was among adding none, one, two, or three stems. For (a) the branching ratio = 3·6; for (b) the length ratio = 3·6; for (c) the branching ratio = 4·4; for (d) the length ratio = 2·0.

The data plotted include one or several trials of each rule. It was found that successive trials under the same rules give very comparable results, for the data converge rapidly with replication.

Table 2 presents the average values of the bifurcation and length ratios for a variety of field examples and random models. The values of each ratio are quite comparable among the various types of examples. Bifurcation ratio averages about 3·8 which is only slightly larger than the value 3·5 for river networks for which a large number of data are available compared with a small number of examples of all other categories. The length ratio averages 2·6.

TABLE 2

Average values of branching characteristics of several field examples and random models

	Bifurcation ratio† Average values	Length ratio‡ Average values
Two-dimensional		
River networks	3·5	2·3
Random models of river networks	4·1	2·5
Theory§		2 to 4
Three-dimensional		
Trees	5·1	3·4
Roots	3·2	2·4
Tinker-toy random models	3·3	2·3

† Bifurcation ratio defined as the average number of branches of a given order per branch of next higher order.

‡ Length ratio defined as ratio of average length of branches of a given order to average length of next higher order.

§ Leopold & Langbein, 1962, p. A15.

7. Area-hours Exposed to Direct Sunlight by a Simple Plant

In the preceding pages I have been concerned with the tendency for efficiency by the minimization of the total length of all the branches of a plant. Presumably there are opposing tendencies which constrain the branching pattern. In a plant one tendency probably concerns both uniformity and maximization of the sunlight hours on each unit of leaf area. As a first rudimentary approach to this, a question was posed as follows.

For a given plant does totality of sunlight expressed as area-hours equal or exceed that which would occur if an equal leaf-area were arranged in some other geometric form? For example, why do many plants stagger their leaves en echelon rather than arrange them in the form of a uniform umbrella?

The single test described here hardly scratches the surface of a large problem, but because it apparently has not received much attention previously, my few observations may merit mention here.

A sunflower plant 2·6 feet high, growing in full sunlight, was selected. Each of the 21 leaves was painted with a large number for identification. Attaching a camera to the end of a long pole to keep distances equal, a series of seven photographs was taken in the plane of the sun's passage over this plant in midsummer at angles from the horizontal of 33°, 66°, 77°, 90°, etc. A stadia rod was included in the photo for scale. The area of each leaf seen by the camera from each position was planimetered on the photograph. Use of these areas as a measure of direct radiation neglects the reflected light which reaches photosynthetic surfaces and, more importantly, the variation of the energy received when the sun is at different angles from its zenith.

Using the maximum area displayed by each leaf to the camera as a measure of its actual area, the total leaf surface of the plant was 3·86 ft^2. In the seven positions photographed the total possible area exposed to sunlight would be $7 \times 3{\cdot}86 = 27{\cdot}0$ ft^2 time units. The total planimetered leaf area from the seven camera positions was 13·7 ft^2. Thus 51% of the leaf area is exposed to direct sunlight on the average over the period of the whole day.

A hemisphere having the same surface area, 3·86 ft^2, would have a diameter of 1·57 feet. The comparable area exposed to direct sunlight by such a hemisphere would be the sum of its projected areas with sun angles in the same seven positions. The comparable value for the hemisphere of equal surface area would be 12·4 ft^2 or the equivalent hemisphere would expose on the average 46% of its area to direct sunlight over the period of the day. In this respect the plant is somewhat more efficient than would be the hemisphere.

The data allowed comparison of the plant and equivalent hemisphere for the seven sun angles separately. As would be expected, the percentage of leaf area receiving direct sunlight is somewhat irregular but exceeds that of the theoretic hemisphere in five of the seven sun angles.

The total length of petiole and stem (second order branching pattern) necessary to support 21 units of surface area on a hemisphere would be 16·4 feet. In the actual sunflower plant the 21 leaves were supported by 11·3 feet of petiole and stem. Thus the sunflower obtained more area-hours of direct sunlight than the hemisphere while at the same time it had a smaller total stem length than a comparable second order branching system in the hemisphere.

8. Interpretive Comment

Systems in which paths connect points distributed in space with some particular point or locus of points may take many forms. It is postulated here that the form which is most probable also tends to minimize the total length of all paths within the applicable constraints. The most probable pattern will consist of a progressively branching system in which there is at all potential points of branching some specific probability that branches will develop.

This postulate, inferred from the data presented, is not proven here theoretically, but it is in keeping with accepted theory that if entropy is considered to be proportional to the logarithm of a probability, the entropy of a system is maximum when the probabilities of alternative states are equal. Further, a system which satisfies the condition of least work is (depending on the constraints) one of a larger class of systems that are characterized by maximum probability (Leopold & Langbein, 1962, p. A7).

Earlier, in the case of river drainage networks and here, in some simple three-dimensional networks, it has been demonstrated that random models develop branching systems in which the branch lengths and the number of branches increase logarithmically with order number. This logarithmic relationship is one of optimum probability.

Geometric relationships of at least some branching forms show that minimum total length of all branches is associated with high values of bifurcation ratio and low values of length ratio. But the few models tested suggest that when the former exceeds 3·8 and the latter falls below 2·6, further change has but little effect on total branch length. It is inferred, then, that values taken from nature for these two ratios, being in close agreement respectively with the numbers just cited, are the result of the fact that these values typify the most probable branching configuration.

The patterns exhibited by alternate vs. opposite buds and coniferous needle arrangement as compared with leaves held on petioles, both have logarithmic relations between numbers and lengths of stem and branch order. Bifurcation and length ratios are respectively comparable for the examples studied.Thus the coniferous versus the deciduous arrangements do not seem to impose different magnitudes of constraint on the principal branching characteristics.

Whereas leaf systems would logically tend to present the largest surface area for the greatest portion of the day, root systems might be expected to tend toward filling a given volume with least total root length. Actually many root systems are so asymmetric that this imputed tendency may well be overshadowed by geotropism or other constraints.

One will immediately call to mind many specialized plants such as those of the desert in which the photosynthetic surfaces are deployed quite differently.

The constraints exerted by the environment appear in those cases to be dominant.

There are many other characteristics of branching patterns that suggest themselves as needing to be studied, particularly to relate them to the demonstrated logarithmic relation of numbers and lengths to order. For example, Murray (1927) observed that the weight of all of a plant above any particular stem cross-section is proportional to the cube of the circumference at that cross-section. Because circumference is correlated with order, it follows that the weight of all of a plant above a given point on a stem is a function of the order number of that stem. One may inquire, then, whether a particularly wide growth ring, a function of incremental circumference, is associated with greater than average number of buds developing, or with greater than usual lengths on each new stem. The former is related to bifurcation and the latter to length ratio.

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