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# THE EXACT PROBABILITIES OF BRANCHING PATTERNS UNDER TERMINAL AND SEGMENTAL GROWTH HYPOTHESES

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Information about the way of branching of dendritic arborizations may be obtained by comparing the frequency distributions of observed branching patterns with theoretical distributions based on well-defined growth models. Two models usually get much attention in geomorphological and (neuro)biological studies, viz. terminal growth and segmental growth. Formulae to construct the exact probability distributions for both growth models are presented. It is shown that ranking and lumping of the individual branching patterns enable the analysis of very large arborizations with relatively few data. The application of the Kolmogorov goodness-of-fit test for discrete distributions to the analysis is discussed.

*1. Introduction.* The dendritic processes of neuronal cells form arborizations whose structural parameters are dependent on the type of the cells and their age. These processes attain their final structures by successively forming bifurcations and changing their length and shape. If one is interested in these growth phenomena it often appears to be impossible to trace the individual structural development *in vivo*. The study of tree structures in fixed histological tissue (at a certain stage of development) then offers an alternative approach. An interesting question that can be raised with respect to growth phenomena concerns the existence of certain rules associated with the growth process. These rules may define the metrical parameters as well as the topological characteristics of the structure. However, here we shall elaborate growth models only as far as they concern the topological aspects.

The probability that a certain type of branching pattern occurs is dependent on the rules underlying the way it has been grown. Therefore, the frequency distribution of observed branching patterns can offer the possibility of distinguishing between different growth processes by comparing this observed distribution with theoretical ones. In previous neurobiological studies (e.g. Berry *et al.*, 1975; Berry and Bradley, 1976; Smit *et al.*, 1972) much attention has been paid to two growth models, viz. terminal growth and segmental growth. Terminal growth involves random bifurcation of terminal segments only, whereas segmental growth involves random branching from all segments. In these studies the growth probabilities have been obtained by simulating the growth process. As such, the accuracy of these values is determined by the total number of computer runs in the simulation procedure, the number of branching patterns that can be encountered and the probability values of each branching pattern. The second point may severely restrict the accuracy because the number of branching patterns is rapidly increasing with the degree of the structure (number of its terminal segments). Moreover, if each branching pattern corresponds to one class in the probability distribution, the number of classes would readily become unwieldy.

In this paper we present exact growth probabilities which prevent the inaccuracies inherent to simulated values. In addition, we propose a way of lumping the observed branching patterns to reduce the number of classes such that the frequency distributions of even 'large' structures can be managed. Special attention will be paid to a ranking scheme of these branching patterns by which they can be presented as a countable series where each pattern is identified by an integer number. This scheme (see also Harding, 1971) is based upon the topological properties of the structures. The identification of the 'real' growth process by comparing the observed and theoretical (as derived in this paper) probability distributions forms, in fact, a hypothesis-testing procedure. In a separate paper (Verwer and Van Pelt, submitted) this procedure will be illustrated in detail with examples based on data obtained from dendritic structures of neurons in the cerebral cortex of rats. The probabilities of rooted tree-shapes generated by random terminal bifurcation have already been deduced by Harding (1971) in a study on evolutionary trees. For the sake of completeness his results are also included.

*2. Characterization of Branching Patterns.* Much theoretical research in tree analysis has been performed in disciplines other than neuroscience (e.g. mathematics, geomorphology and phylogeny). As a consequence, the terminology has not been standardized but may depend on the field of research. For convenience, we shall summarize our terminology, not pretending that it is the most neutral one. Points and segments form basic elements of a branching pattern and are defined as follows (see also Figure 1).

*Segment*: part of the structure between two consecutive points. We can subdivide segments into (a) intermediate segments, i.e. between two consecutive bifurcation points, (b) terminal segments, i.e. between a bifurcation point and a terminal point, and (c) root segments or zeroth-order segments, i.e. between the origin and the first bifurcation point.

*Open bifurcation*: bifurcation into two intermediate segments.

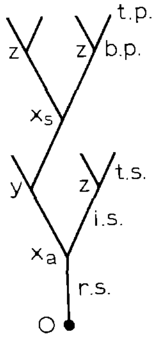


Figure 1. Nomenclature of the elements of a rooted tree. We distinguish the origin (0); bifurcation points, i.e. asymmetrical open bifurcation ($x_a$), symmetrical open bifurcation ($x_s$), half-open bifurcation ($y$) and closed bifurcation ($z$); terminal points (t.p.); and segments, i.e. root segment (r.s.), intermediate segment (i.s.) and terminal segment (t.s.).

*Half-open bifurcation*: bifurcation into an intermediate and a terminal segment.

*Closed bifurcation*: bifurcation into two terminal segments.

This distinction of bifurcation points corresponds to the one Berry and Pymm (1981) have introduced in their study on vertex analysis. They defined primary, secondary and tertiary vertices which are identical to the closed, half-open and open bifurcation points respectively.

*nth-order bifurcation point*: point where $n$th-order segments originate. Throughout this paper the order of segments must be interpreted within the context of a centrifugal ordering method. Thus, starting from the root segment (order zero), the order of each consecutive segment is incremented by one. For a discussion about the different ways of order assignment to segments we refer to Uylings *et al.* (1975).

*nth-order subtrees*: structures emanating from an $n$th-order bifurcation point.

*Degree of a tree*: number of its terminal segments.

A two-dimensional (2D) branching pattern is characterized by its 2D-topological type in the way its segments bifurcate (e.g. Shreve, 1966; Scheidegger, 1967; Smart, 1969). All 2D-topological types of the same degree (number of terminal segments) are grouped into a 2D-topological set. Therefore, $T^n = \{\tau_i^n | i = 1, \ldots, N_\tau^n\}$, if $n$ denotes the degree, $T^n$ the topological set, $\tau_i^n$ member $i$ of that set and $N_\tau^n$ the total number of topological types in $T^n$. Neuronal branching patterns, however, are three-dimensional and must be characterized by three-dimensional (3D)-topological types. This characterization must be invariant with respect to rotations of the structure and all subtrees in the 3D-space. The projection of a 3D-structure onto a 2D-plane can again be identified by a 2D-topological type. However, the same 3D-structure may give rise to several 2D-topological types dependent on the position of the 3D-structure with respect to the projecting plane. In fact, all 2D-topological types that may be transformed into each other by reflection of pairs of subtrees of a bifurcation represent the same 3D-structure. We shall denote all these 2D-topological types with the term *ambilateral type* [in analogy to the terminology of Smart (1969)]. A 3D-topological type can now be uniquely represented by its ambilateral type which is defined in the 2D-plane. On behalf of visualization we shall depict (Figure 2) an ambilateral type by that 2D-topological type in which all pairs of subtrees of a bifurcation are oriented such that the first subtree according to clockwise scanning has the lowest rank (Section 4).

We can now define the set $A^n$ of ambilateral types with $n$ terminal segments as $A^n = \{\alpha_i^n | i = 1, \ldots, N_\alpha^n\}$, where $\alpha_i^n$ is a particular ambilateral type and $N_\alpha^n$ is the total number of ambilateral types in set $A^n$. The set $A^n$ can be decomposed into subsets $A^{r,s}$ $(n = r + s)$ which contain all ambilateral types whose first-order subtrees each have $r$ and $s$ terminal segments (by definition, $r \leq s$).

3. *General Relations*. The number $N_\tau^n$ of 2D-topological types in set $T^n$ is completely defined by the degree $n$ via the relation given by Caley in

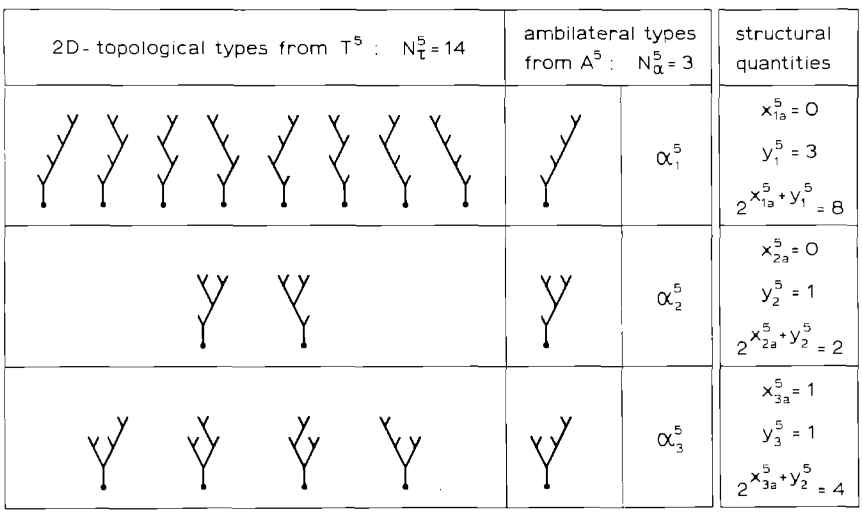


Figure 2. Illustration of the 2D-topological types of the set $T^5$, the corresponding ambilateral types of the set $A^5$ and some structural parameters. The number of 2D-topological types corresponding to one ambilateral type is given by the formula in column 3 [see also equation (9)].

1859 (cf. Shreve, 1966):

$$N_{\tau}^{n} = (2n-1)^{-1} \cdot \binom{2n-1}{n}. \tag{1}$$

The number $N_{\alpha}^{n}$ of ambilateral types in set $A^n$ is given by the recurrent relation (Harding, 1971)

$$N_{\alpha}^{n} = 1/2 \cdot \sum_{r=1}^{n-1} N_{\alpha}^{r} \cdot N_{\alpha}^{n-r} \text{ if } n \text{ is odd,}$$

$$\tag{2}$$

$$= 1/2 \cdot \sum_{r=1}^{n-1} N_{\alpha}^{r} \cdot N_{\alpha}^{n-r} + 1/2 \cdot N_{\alpha}^{n/2} \text{ if } n \text{ is even.}$$

Evidently, $N_{\alpha}^{1} = 1$.

The total number ($m$) of bifurcation points in $\alpha_i^n$ is given by

$$m = x_i^n + y_i^n + z_i^n. \tag{3}$$

Here, $x_i^n$ denotes the number of open bifurcations, $y_i^n$ the number of half-open bifurcations and $z_i^n$ the number of closed bifurcations. The numbers of open and closed bifurcation points are related via

$$z_i^n = x_i^n + 1. \tag{4}$$

Finally, a half-open bifurcation gives rise to one terminal segment and a closed bifurcation to two terminal segments thus:

$$n = y_i^n + 2 \cdot z_i^n. \tag{5}$$

From equations (3), (4) and (5) it is easy to see that $m = n - 1$.

*4. Ranking of Ambilateral Types.* A ranking scheme of ambilateral types such that each type can be identified by an integer number was first described by Harding (1971). The rules for ranking can be summarized as follows:

(i) The ambilateral types are ranked according to their degree.

(ii) The ranking of the types within a given set $A^n$ is based upon the subset-membership of these types such that members of the subset $A^{i,n-i}$ precede members of the subset $A^{j,n-j}$ if $i < j$.

(iii) All ambilateral types within the subset $A^{i,n-i}$ $(i \leqslant n-i)$ are arranged such that the ranking within $A^i$ is the coarse one and the ranking within $A^{n-i}$ is the fine one; this means that first a particular subtree from $A^i$ is combined with all subtrees from $A^{n-i}$ before combinations with the next subtree from $A^i$ are ranked.

In Table I all ambilateral types of the sets $A^1$ through $A^9$ are arranged. Note that the structure is represented by a code where each bifurcation is indicated by a pair of parentheses enclosing the degrees of both subtrees of that bifurcation. For the sets $A^4$ through $A^8$ the arrangement is illustrated in Figure 3. Ranking rules (i) and (ii) define a natural ordering of the ambilateral types. Rule (iii) is the result of an arbitrary choice which is reflected in the general number sequence 46, 47, 48 and 89–94.

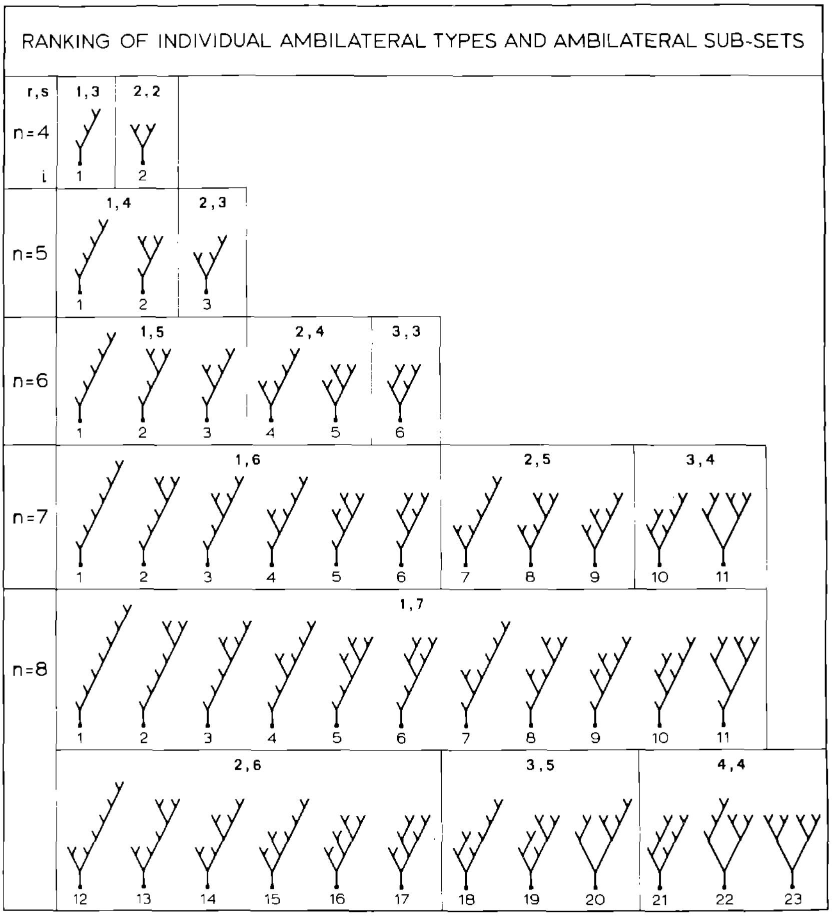


Figure 3. Illustration of the ambilateral types of the sets $A^n$ ($n = 4$–$8$). The relative number of the type within the set is denoted by $i$ whereas $(r, s)$ indicates the subset.

TABLE I

Probabilities of Ambilateral Types $\alpha_i^n$ for Terminal Growth $P_t(\alpha_i^n)$ and for Segmental Growth $P_s(\alpha_i^n)$

| General number | Relative number $i$ within $A^n$ | Degrees of tree and first-order subtrees $n(r, s)$ | Branching code | Terminal growth probability $P_t(\alpha_i^n)$ | Segmental growth probability $P_s(\alpha_i^n)$ |
|---|---|---|---|---|---|
| 1 | 1 | 1 | 1 | 1.00000 | 1.00000 |
| 2 | 1 | 2(1, 1) | 2 | 1.00000 | 1.00000 |
| 3 | 1 | 3(1, 2) | 3 | 1.00000 | 1.00000 |
| 4 | 1 | 4(1, 3) | 4(1 3) | 0.66667 | 0.80000 |
| 5 | 2 | 4(2, 2) | 4(2 2) | 0.33333 | 0.20000 |
| 6 | 1 | 5(1, 4) | 5(1 4(1 3)) | 0.33333 | 0.57143 |
| 7 | 2 | 5(1, 4) | 5(1 4(2 2)) | 0.16667 | 0.14286 |
| 8 | 3 | 5(2, 3) | 5(2 3) | 0.50000 | 0.28571 |
| 9 | 1 | 6(1, 5) | 6(1 5(1 4(1 3))) | 0.13333 | 0.38095 |
| 10 | 2 | 6(1, 5) | 6(1 5(1 4(2 2))) | 0.06667 | 0.09524 |
| 11 | 3 | 6(1, 5) | 6(1 5(2 3)) | 0.20000 | 0.19048 |
| 12 | 4 | 6(2, 4) | 6(2 4(1 3)) | 0.26667 | 0.19048 |
| 13 | 5 | 6(2, 4) | 6(2 4(2 2)) | 0.13333 | 0.04762 |
| 14 | 6 | 6(3, 3) | 6(3 3) | 0.20000 | 0.09524 |
| 15 | 1 | 7(1, 6) | 7(1 6(1 5(1 4(1 3)))) | 0.04444 | 0.24242 |
| 16 | 2 | 7(1, 6) | 7(1 6(1 5(1 4(2 2)))) | 0.02222 | 0.06061 |
| 17 | 3 | 7(1, 6) | 7(1 6(1 5(2 3))) | 0.06667 | 0.12121 |
| 18 | 4 | 7(1, 6) | 7(1 6(2 4(1 3))) | 0.08889 | 0.12121 |
| 19 | 5 | 7(1, 6) | 7(1 6(2 4(2 2))) | 0.04444 | 0.03030 |
| 20 | 6 | 7(1, 6) | 7(1 6(3 3)) | 0.06667 | 0.06061 |
| 21 | 7 | 7(2, 5) | 7(2 5(1 4(1 3))) | 0.11111 | 0.12121 |
| 22 | 8 | 7(2, 5) | 7(2 5(1 4(2 2))) | 0.05556 | 0.03030 |
| 23 | 9 | 7(2, 5) | 7(2 5(2 3)) | 0.16667 | 0.06061 |
| 24 | 10 | 7(3, 4) | 7(3 4(1 3)) | 0.22222 | 0.12121 |
| 25 | 11 | 7(3, 4) | 7(3 4(2 2)) | 0.11111 | 0.03030 |

TABLE I. (cont.)

| General number | Relative number | $n(r, s)$ | Branching code | Terminal growth probability | Segmental growth probability |
|---|---|---|---|---|---|
| 26 | 1 | 8(1, 7) | 8(1 7(1 6(1 5(1 4(1 3))))) | 0.01270 | 0.14918 |
| 27 | 2 | 8(1, 7) | 8(1 7(1 6(1 5(1 4(1 2))))) | 0.00635 | 0.03730 |
| 28 | 3 | 8(1, 7) | 8(1 7(1 6(1 5(2 3)))) | 0.01905 | 0.07459 |
| 29 | 4 | 8(1, 7) | 8(1 7(1 6(2 4(1 3)))) | 0.02540 | 0.07459 |
| 30 | 5 | 8(1, 7) | 8(1 7(1 6(2 4(2 2)))) | 0.01270 | 0.01865 |
| 31 | 6 | 8(1, 7) | 8(1 7(1 6(3 3))) | 0.01905 | 0.03730 |
| 32 | 7 | 8(1, 7) | 8(1 7(2 5(1 4(1 3)))) | 0.03175 | 0.07459 |
| 33 | 8 | 8(1, 7) | 8(1 7(2 5(1 4(2 2)))) | 0.01587 | 0.01865 |
| 34 | 9 | 8(1, 7) | 8(1 7(2 5(2 3))) | 0.04762 | 0.03730 |
| 35 | 10 | 8(1, 7) | 8(1 7(3 4(1 3))) | 0.06349 | 0.07459 |
| 36 | 11 | 8(1, 7) | 8(1 7(3 4(2 2))) | 0.03175 | 0.01865 |
| 37 | 12 | 8(2, 6) | 8(2 6(1 5(1 4(1 3)))) | 0.03810 | 0.07459 |
| 38 | 13 | 8(2, 6) | 8(2 6(1 5(1 4(2 2)))) | 0.01905 | 0.01865 |
| 39 | 14 | 8(2, 6) | 8(2 6(1 5(2 3))) | 0.05714 | 0.03730 |
| 40 | 15 | 8(2, 6) | 8(2 6(2 4(1 3))) | 0.07619 | 0.03730 |
| 41 | 16 | 8(2, 6) | 8(2 6(2 4(2 2))) | 0.03810 | 0.00932 |
| 42 | 17 | 8(2, 6) | 8(2 6(3 3)) | 0.05714 | 0.01865 |
| 43 | 18 | 8(3, 5) | 8(3 5(1 4(1 3))) | 0.09524 | 0.07459 |
| 44 | 19 | 8(3, 5) | 8(3 5(1 4(2 2))) | 0.04762 | 0.01865 |
| 45 | 20 | 8(3, 5) | 8(3 5(2 3)) | 0.14286 | 0.03730 |
| 46 | 21 | 8(4, 4) | 8(4(1 3)4(1 3)) | 0.06349 | 0.03730 |
| 47 | 22 | 8(4, 4) | 8(4(1 3)4(2 2)) | 0.06349 | 0.01865 |
| 48 | 23 | 8(4, 4) | 8(4(2 2)4(2 2)) | 0.01587 | 0.00233 |
| 49 | 1 | 9(1, 8) | 9(1 8(1 7(1 6(1 5(1 4(1 3)))))) | 0.00317 | 0.08951 |
| 50 | 2 | 9(1, 8) | 9(1 8(1 7(1 6(1 5(1 4(2 2)))))) | 0.00159 | 0.02238 |
| 51 | 3 | 9(1, 8) | 9(1 8(1 7(1 6(1 5(2 3))))) | 0.00476 | 0.04476 |
| 52 | 4 | 9(1, 8) | 9(1 8(1 7(1 6(2 4(1 3))))) | 0.00635 | 0.04476 |
| 53 | 5 | 9(1, 8) | 9(1 8(1 7(1 6(2 4(2 2))))) | 0.00317 | 0.01119 |
| 54 | 6 | 9(1, 8) | 9(1 8(1 7(1 6(3 3)))) | 0.00476 | 0.02238 |
| 55 | 7 | 9(1, 8) | 9(1 8(1 7(2 5(1 4(1 3))))) | 0.00794 | 0.04476 |
| 56 | 8 | 9(1, 8) | 9(1 8(1 7(2 5(1 4(2 2))))) | 0.00397 | 0.01119 |
| 57 | 9 | 9(1, 8) | 9(1 8(1 7(2 5(2 3)))) | 0.01190 | 0.02238 |
| 58 | 10 | 9(1, 8) | 9(1 8(1 7(3 4(1 3)))) | 0.01587 | 0.04476 |

| | | | | | |
|---|---|---|---|---|---|
| 59 | 11 | 9(1, 8) | 9(1 8(1 7(3 4(2 2)))) | 0.00794 | 0.01119 |
| 60 | 12 | 9(1, 8) | 9(1 8(2 6(1 5(1 4(1 3))))) | 0.00952 | 0.04476 |
| 61 | 13 | 9(1, 8) | 9(1 8(2 6(1 5(1 4(2 2))))) | 0.00476 | 0.01119 |
| 62 | 14 | 9(1, 8) | 9(1 8(2 6(1 5(2 3)))) | 0.01429 | 0.02238 |
| 63 | 15 | 9(1, 8) | 9(1 8(2 6(2 4(1 3)))) | 0.01905 | 0.02238 |
| 64 | 16 | 9(1, 8) | 9(1 8(2 6(2 4(2 2)))) | 0.00952 | 0.00559 |
| 65 | 17 | 9(1, 8) | 9(1 8(2 6(3 3))) | 0.01429 | 0.01119 |
| 66 | 18 | 9(1, 8) | 9(1 8(3 5(1 4(1 3)))) | 0.02381 | 0.04476 |
| 67 | 19 | 9(1, 8) | 9(1 8(3 5(1 4(2 2)))) | 0.01190 | 0.01119 |
| 68 | 20 | 9(1, 8) | 9(1 8(3 5(2 3))) | 0.03571 | 0.02238 |
| 69 | 21 | 9(1, 8) | 9(1 8(4(1 3)4(1 3))) | 0.01587 | 0.02238 |
| 70 | 22 | 9(1, 8) | 9(1 8(4(1 3)4(2 2))) | 0.01587 | 0.01119 |
| 71 | 23 | 9(1, 8) | 9(1 8(4(2 2)4(2 2))) | 0.00397 | 0.00140 |
| 72 | 24 | 9(2, 7) | 9(2 7(1 6(1 5(1 4(1 3))))) | 0.01111 | 0.04476 |
| 73 | 25 | 9(2, 7) | 9(2 7(1 6(1 5(1 4(2 2))))) | 0.00556 | 0.01119 |
| 74 | 26 | 9(2, 7) | 9(2 7(1 6(1 5(2 3)))) | 0.01667 | 0.02238 |
| 75 | 27 | 9(2, 7) | 9(2 7(1 6(2 4(1 3)))) | 0.02222 | 0.02238 |
| 76 | 28 | 9(2, 7) | 9(2 7(1 6(2 4(2 2)))) | 0.01111 | 0.00559 |
| 77 | 29 | 9(2, 7) | 9(2 7(1 6(3 3))) | 0.01667 | 0.01119 |
| 78 | 30 | 9(2, 7) | 9(2 7(2 5(1 4(1 3)))) | 0.02778 | 0.02238 |
| 79 | 31 | 9(2, 7) | 9(2 7(2 5(1 4(2 2)))) | 0.01389 | 0.00559 |
| 80 | 32 | 9(2, 7) | 9(2 7(2 5(2 3))) | 0.04167 | 0.01119 |
| 81 | 33 | 9(2, 7) | 9(2 7(3 4(1 3))) | 0.05556 | 0.02238 |
| 82 | 34 | 9(2, 7) | 9(2 7(3 4(2 2))) | 0.02778 | 0.00559 |
| 83 | 35 | 9(3, 6) | 9(3 6(1 5(1 4(1 3)))) | 0.03333 | 0.04476 |
| 84 | 36 | 9(3, 6) | 9(3 6(1 5(1 4(2 2)))) | 0.01667 | 0.01119 |
| 85 | 37 | 9(3, 6) | 9(3 6(1 5(2 3))) | 0.05000 | 0.02238 |
| 86 | 38 | 9(3, 6) | 9(3 6(2 4(1 3))) | 0.06667 | 0.02238 |
| 87 | 39 | 9(3, 6) | 9(3 6(2 4(2 2))) | 0.03333 | 0.00559 |
| 88 | 40 | 9(3, 6) | 9(3 6(3 3)) | 0.05000 | 0.01119 |
| 89 | 41 | 9(4, 5) | 9(4(1 3)5(1 4(1 3))) | 0.05556 | 0.04476 |
| 90 | 42 | 9(4, 5) | 9(4(1 3)5(1 4(2 2))) | 0.02778 | 0.01119 |
| 91 | 43 | 9(4, 5) | 9(4(1 3)5(2 3)) | 0.08333 | 0.02238 |
| 92 | 44 | 9(4, 5) | 9(4(2 2)5(1 4(1 3))) | 0.02778 | 0.01119 |
| 93 | 45 | 9(4, 5) | 9(4(2 2)5(1 4(2 2))) | 0.01389 | 0.00280 |
| 94 | 46 | 9(4, 5) | 9(4(2 2)5(2 3)) | 0.04167 | 0.00559 |

Each ambilateral type $\alpha^n_i$ is identified by its general number, its number $i$ within the set $A^n$, its degree $n$ and the degrees of its first-order subtrees $(r, s)$ and its branching code. All ambilateral types from the sets $A^1$–$A^9$ are given.

*5. Exact Probability Distributions for Two Growth Models.* During its growth a tree structure of degree $n$ has been successively a member of the ambilateral sets $A^1, \ldots, A^n$. The rules governing the growth process determine completely the probability of occurrences of all types within an ambilateral set.

*5.1. Probabilities of occurrence of ambilateral types.*

*5.1.1. Terminal growth model.* The terminal growth probability $P_t(\alpha_i^n)$ (probability of the occurrence of an ambilateral type $\alpha_i^n$ provided that the structure has been formed by means of terminal growth) can be expressed by means of the recurrent relation of Harding (1971):

$$P_t(\alpha_i^n) = 2^{1-\delta_{rs}\cdot\delta_{jk}} \cdot (n-1)^{-1} \cdot P_t(\alpha_j^r) \cdot P_t(\alpha_k^s)$$

$$\text{if } (n > 1), \quad P_t(\alpha_1^1) = 1 \text{ and } \delta_{uv} = \begin{vmatrix} 0 \text{ if } u \neq v \\ 1 \text{ if } u = v \end{vmatrix}. \tag{6}$$

Here, $\alpha_j^r$ and $\alpha_k^s$ are the first-order subtypes of $\alpha_i^n$. The term $2^{1-\delta_{rs}\cdot\delta_{jk}}$ has been used to formulate the special case that both subtrees are identical. Attempts to reformulate these probabilities in a non-recurrent expression have not been successful so far. Values of $P_t(\alpha_i^n)$ for ambilateral types of the sets $A^1$ through $A^9$ are given in Table 1, column 5.

*5.1.2 Segmental growth model.* Dacey and Krumbein (1976) have proven that as a result of segmental growth all 2D-topological types in set $T^n$ have an equal probability of occurrence. This means that the segmental growth probability for 2D-topological types $P_s(\tau_i^n)$ (probability of the occurrence of a topological type $\tau_i^n$ provided that the structure has been formed by means of segmental growth) equals [by means of equation (1)]:

$$P_s(\tau_i^n) = \frac{1}{N_\tau^n} = \frac{2n-1}{\binom{2n-1}{n}}. \tag{7}$$

The probability of the occurrence of ambilateral type $\alpha_i^n$ is now completely determined by the number $N_{eq}(\alpha_i^n)$ of topological types in set $T^n$ that belong to the same ambilateral type $\alpha_i^n$, giving the formula

$$P_s(\alpha_i^n) = \frac{N_{eq}(\alpha_i^n)}{N_\tau^n}. \tag{8}$$

The number of equivalent structures $N_{eq}(\alpha_i^n)$ can be expressed in terms of the common structural parameters $x_{ia}^n$ and $y_i^n$ by

$$N_{eq}(\alpha_i^n) = 2^{x_{ia}^n} \cdot 2^{y_i^n}. \tag{9}$$

Here, $x_{ia}^n$ denotes the number of open bifurcations into two different ambilateral subtrees (asymmetrical bifurcation) and $y_i^n$ the number of half-open bifurcations. To prove equation (9) we observe that in the 2D-plane there are $2^{x_{ia}^n}$ ways to define the members of $x_{ia}^n$ pairs of 2D-subtrees as left or right ones and $2^{y_i^n}$ ways to define $y_i^n$ terminal segments as left or right branches of the bifurcation. Evidently, all these $2^{x_{ia}^n+y_i^n}$ choices give rise to the same ambilateral type, whereas every choice corresponds to one particular 2D-topological type (cf. Figure 2). Combining equations (1), (8) and (9) we now get

$$P_s(\alpha_i^n) = 2^{x_{ia}^n+y_i^n} \cdot \frac{2n-1}{\binom{2n-1}{n}}. \tag{10}$$

According to equations (4) and (5) and the relation $x_i^n = x_{is}^n + x_{ia}^n$, where $x_{is}^n$ denotes the number of open bifurcations into two identical ambilateral subtrees (symmetrical bifurcation), equation (10) can also be written in terms of $x_i^n$ and $x_{is}^n$ as

$$P_s(\alpha_i^n) = 2^{-(x_i^n+x_{is}^n)} \cdot \frac{2n-1}{\binom{2n-1}{n}} \cdot 2^{n-2}. \tag{11}$$

Values of $P_s(\alpha_i^n)$ for ambilateral types of the sets $A^1$ through $A^9$ are given in Table I, column 6.

*5.2. Probability distributions of ambilateral subsets.* We can express the probability of the occurrence of a structure in terms of probabilities of its first-order subtrees by separating the probabilities of the independent events of ambilateral subset membership $P(\alpha_i^n \in A^{r,s})$ and the joint occurrence of the two particular subtrees within the ambilateral subset $P(\alpha_j^r, \alpha_{-k}^s)$:

$$P(\alpha_i^n) = P(\alpha_i^n \in A^{r,s}) \cdot P(\alpha_j^r, \alpha_k^s). \tag{12}$$

*5.2.1. Terminal growth model.* The derivation of both probabilities of equation (12) for terminal growth results in

$$P_t(\alpha_i^n \in A^{r,s}) = \frac{2^{1-\delta_{rs}}}{n-1} \tag{13}$$

and

$$P_t(\alpha_j^r, \alpha_k^s) = 2^{\delta_{rs}(1-\delta_{jk})} \cdot P_t(\alpha_j^r) \cdot P_t(\alpha_k^s). \tag{14}$$

Equation (13) can be proven by summing the probabilities of all types within a subset $A^{r,s}$ using equation (6).

$$P_t(\alpha_i^n \in A^{r,s}) = \sum_{h|\alpha_h^n \in A^{r,s}} P_t(\alpha_h^n) = \text{[using equation (6)]}$$

$$(\text{if } r \neq s) = \frac{2}{n-1} \sum_{j,k} P_t(\alpha_j^r) \cdot P_t(\alpha_k^s) = \frac{2}{n-1},$$

$$(\text{if } r = s) = \frac{1}{n-1} \sum_{j \leq k} 2^{1-\delta_{jk}} \cdot P_t(\alpha_j^r) \cdot P_t(\alpha_k^s) = \frac{1}{n-1}$$

$$\left(\text{note that } \sum_{j \leq k} 2^{1-\delta_{jk}} \cdot X = \sum_{j<k} 2 \cdot X + \sum_{j=k} X = \sum_{\substack{j<k \\ j>k}} X + \sum_{j=k} X = \sum_{j,k} X\right).$$

Equation (14) follows directly from equations (6), (12) and (13).

*5.2.2. Segmental growth model.* For segmental growth the function $P_s(\alpha_i^n \in A^{r,s})$ can be derived in the following way. The set of 2D-topological types $T^n$ can be divided into subsets which are defined by the set-membership of the first-order subtrees of the members of $T^n$. If $T^{r,s}$ denotes the subset of topological types whose first-order subtrees belong to $T^r$ and $T^s$ resp. we get:

$$T^n = T^{1,n-1} \cup T^{2,n-2} \cup \ldots \cup T^{n-1,1}. \tag{15}$$

The number of types in the subset $T^{r,n-r}$ is defined by all combinations of types belonging to $T^r$ and $T^{n-r}$ and equals $N_\tau^r \cdot N_\tau^{n-r}$. Of course, the number $N_\tau^n$ of types in $T^n$ is equal to the sum of types in all subsets.

$$N_\tau^n = N_\tau^1 \cdot N_\tau^{n-1} + N_\tau^2 \cdot N_\tau^{n-2} + \cdots + N_\tau^{n-1} \cdot N_\tau^1. \tag{16}$$

Since with segmental growth all topological types within $T^n$ are equally probable (Dacey and Krumbein, 1976), the probability that a topological type belongs to the subset $T^{r,n-r}$ (or to the subset $T^{n-r,r}$) becomes

$$P_s(\tau_i^n \in T^{r,n-r}) = \frac{N_\tau^r \cdot N_\tau^{n-r}}{N_\tau^n}. \tag{17}$$

All the members of the subsets $T^{r,n-r}$ and $T^{n-r,r}$ are members of the ambilateral subset $A^{r,n-r}$. Thus the probability that an ambilateral type belongs to the subset $A^{r,n-r}$ is equal to

$$P_s(\alpha_i^n \in A^{r,n-r}) = 2^{1-\delta_{r,n-r}} \cdot \frac{N_\tau^r \cdot N_\tau^{n-r}}{N_\tau^n}. \tag{18}$$

The function $P_s(\alpha_j^r, \alpha_k^s)$ can be defined by writing equation (12) as

$$P_s(\alpha_j^r, \alpha_k^s) = \frac{P_s(\alpha_i^n)}{P_s(\alpha_i^n \in A^{r,s})}. \tag{12}$$

Substitution of equations (8), (9) and (18) herein gives

$$P_s(\alpha_j^r, \alpha_k^s) = 2^{x_{ia}^n + y_i^n} \cdot \frac{1}{N_\tau^r \cdot N_\tau^s} \cdot \frac{1}{2^{1-\delta_{rs}}}. \tag{19}$$

Substitution of $N_\tau^r$ and $N_\tau^s$ using equations (8) and (9) gives

$$P_s(\alpha_j^r, \alpha_k^s) = \frac{2^{x_{ia}^n + y_i^n}}{2^{x_{ja}^r + y_j^r} \cdot 2^{x_{ka}^s + y_k^s}} \cdot \frac{1}{2^{1-\delta_{rs}}} \cdot P_s(\alpha_j^r) \cdot P_s(\alpha_k^s). \tag{20}$$

Combining two subtrees $\alpha_j^r (r > 1)$ and $\alpha_k^s (s > 1)$ into $\alpha_i^n$ does not introduce new half-open bifurcation points; thus we can write

$$y_i^n = y_j^r + y_k^s. \tag{21}$$

However, the number of asymmetrical open bifurcation points $x_{ia}^n$ equals the sum of $x_{ja}^r$ and $x_{ka}^s$ only if both subtrees are of the same ambilateral type. Otherwise, a new asymmetrical open bifurcation has been formed.

$$x_{ia}^n = x_{ja}^r + x_{ka}^s + (1 - \delta_{rs} \cdot \delta_{jk}). \tag{22}$$

Substitution of (21) and (22) into (20) results in

$$P_s(\alpha_j^r, \alpha_k^s) = 2^{\delta_{rs} \cdot (1-\delta_{jk})} \cdot P_s(\alpha_j^r) \cdot P_s(\alpha_k^s). \tag{23}$$

Equation (23) holds also if $r = 1$ and/or $s = 1$. Now, the probability $P_s(\alpha_i^n)$ can also be expressed in the form of a recurrent relation

$$P_s(\alpha_i^n) = 2^{1-\delta_{rs} \cdot \delta_{jk}} \cdot \frac{N_T^r \cdot N_T^s}{N_T^n} \cdot P_s(\alpha_j^r) \cdot P_s(\alpha_k^s). \tag{24}$$

It appears that the difference between segmental and terminal growth [cf. equations (24) and (6)] is only reflected in the expressions for $P(\alpha_i^n \in A^{r,s})$, viz. equations (13) and (18). Values of these probabilities are presented in Table II.

TABLE II
Probabilities of Trees of Degree $n$ having First-order Subtrees of Degrees $r$ and $s$ $(n = r + s)$ for Terminal Growth $P_t(n = r + s)$ and for Segmental Growth $P_s(n = r + s)$, and Cumulative Probabilities

| | | Terminal growth | | Segmental growth | |
|---|---|---|---|---|---|
| $n$ | $r, s$ | $P_t(n = r + s)$ | Cumulative | $P_s(n = r + s)$ | Cumulative |
| 4 | 1, 3 | 0.6667 | 0.6667 | 0.8000 | 0.8000 |
| | 2, 2 | 0.3333 | 1.0000 | 0.2000 | 1.0000 |
| 5 | 1, 4 | 0.5000 | 0.5000 | 0.7143 | 0.7143 |
| | 2, 3 | 0.5000 | 1.0000 | 0.2857 | 1.0000 |
| 6 | 1, 5 | 0.4000 | 0.4000 | 0.6667 | 0.6667 |
| | 2, 4 | 0.4000 | 0.8000 | 0.2381 | 0.9048 |
| | 3, 3 | 0.2000 | 1.0000 | 0.0952 | 1.0000 |
| 7 | 1, 6 | 0.3333 | 0.3333 | 0.6364 | 0.6364 |
| | 2, 5 | 0.3333 | 0.6667 | 0.2121 | 0.8485 |
| | 3, 4 | 0.3333 | 1.0000 | 0.1515 | 1.0000 |
| 8 | 1, 7 | 0.2857 | 0.2857 | 0.6154 | 0.6154 |
| | 2, 6 | 0.2857 | 0.5714 | 0.1958 | 0.8112 |
| | 3, 5 | 0.2857 | 0.8571 | 0.1305 | 0.9417 |
| | 4, 4 | 0.1429 | 1.0000 | 0.0583 | 1.0000 |
| 9 | 1, 8 | 0.2500 | 0.2500 | 0.6000 | 0.6000 |
| | 2, 7 | 0.2500 | 0.5000 | 0.1846 | 0.7846 |
| | 3, 6 | 0.2500 | 0.7500 | 0.1175 | 0.9021 |
| | 4, 5 | 0.2500 | 1.0000 | 0.0979 | 1.0000 |
| 10 | 1, 9 | 0.2222 | 0.2222 | 0.5882 | 0.5882 |
| | 2, 8 | 0.2222 | 0.4444 | 0.1765 | 0.7647 |
| | 3, 7 | 0.2222 | 0.6667 | 0.1086 | 0.8733 |
| | 4, 6 | 0.2222 | 0.8889 | 0.0864 | 0.9597 |
| | 5, 5 | 0.1111 | 1.0000 | 0.0403 | 1.0000 |
| 11 | 1, 10 | 0.2000 | 0.2000 | 0.5789 | 0.5789 |
| | 2, 9 | 0.2000 | 0.4000 | 0.1703 | 0.7492 |
| | 3, 8 | 0.2000 | 0.6000 | 0.1022 | 0.8514 |
| | 4, 7 | 0.2000 | 0.8000 | 0.0786 | 0.9300 |
| | 5, 6 | 0.2000 | 1.0000 | 0.0700 | 1.0000 |

6. *Discussion.* In this paper expressions are presented for the exact probabilities of occurrence of particular ambilateral types [equations (6) and (11)] and of first-order bifurcation types [equations (13) and (18)] under the hypothesis of terminal and segmental growth respectively. Since these probabilities do not suffer from the inaccuracies inherent in simulated values they offer the best basis for statistical analysis. The ranking of ambilateral types considerably facilitates the identification of individual ambilateral types and subsets of them. This ranking scheme also implies an ordering of ambilateral subsets as defined in Section 4. An example of the probability distributions for both terminal and segmental growth is given in Figure 4. The preference for asymmetrical structures (with respect to the degrees of the subtrees of a bifurcation) as caused by segmental growth is striking, whereas terminal growth hardly gives rise to any preference at all.

Several goodness-of-fit tests are available to test discrete data (e.g. frequencies of observed ambilateral types) against hypothesized probabilities (Horn, 1977). Horn advised that the Kolmogorov test for discontinuous distributions (Conover, 1972) should preferably be used over the $\chi^2$ test, particularly when the number of data per class and the total number of observations is small. This preference is based on the property of the Kolmogorov test as explicitly utilizing the ordering of the classes whereas the $\chi^2$ test ignores this. As a consequence the Kolmogorov test can only be applied to data that can be classified according to a natural order. In our opinion one can speak of a natural order if an uncertainty in assignment of an observation to a class is physically correlated with the uncertainties in assignments to the immediate neighbouring classes. The

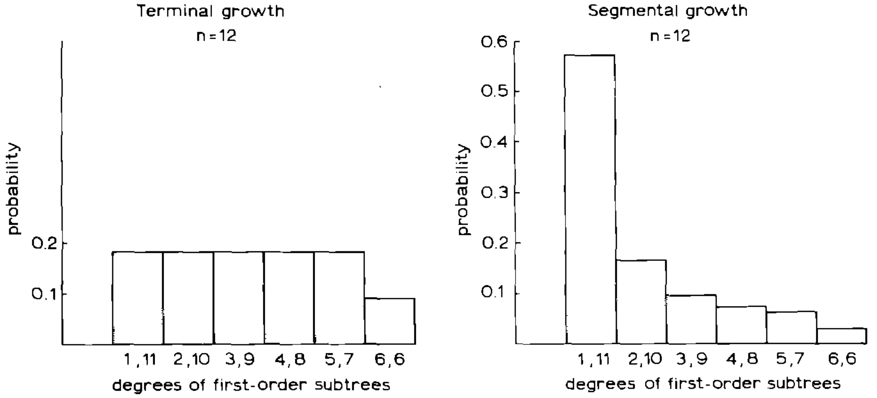


Figure 4. Probabilities of trees of degree 12 plotted against the degrees of the first-order subtrees for both terminal and segmental growth.

ordering of ambilateral types does fulfil this criterion as long as rule (iii) has not been used in the ranking scheme, i.e. up to and including ambilateral types with 8 terminal segments. Also, the ordering of the ambilateral subsets, defined by the first-order subtrees, does fulfil this criterion; however, in this case there are no limitations as concerned to the size of the trees. These properties enable the use of a Kolmogorov procedure as a hypothesis test. That means that growth tests on small structures (up to 9th degree) may be performed either on the observed frequencies of individual ambilateral types or on the frequencies of ambilateral subset memberships. For greater structures (with 9 or more terminal segments) only the last-mentioned procedure should be applied. Anyhow, for these larger structures the rapidly increasing number of possible ambilateral types forms a serious obstacle to the statistical analysis. The classification into ambilateral subsets implies an enormous data reduction; for example, the set $A^9$ has 46 ambilateral types whereas it contains only 4 subsets, viz. $A^{1,8}$, $A^{2,7}$, $A^{3,6}$ and $A^{4,5}$. The expected probabilities according to terminal and segmental growth hypotheses are given by equations (13) and (18) respectively and are explicitly shown in Table II for $n = 4$–11. It may be argued that classification according to

TABLE III
Number of Classes if Structures are Classified according to (a) their Ambilateral Type, (b) the Degrees of the First-order Subtrees and (c) the Degrees of all Pairs of Subtrees

| Degree $n$ | Number of classes (a) | (b) | (c) |
|---|---|---|---|
| 4 | 2 | 2 | 2 |
| 5 | 3 | 2 | 4 |
| 6 | 6 | 3 | 7 |
| 7 | 11 | 3 | 10 |
| 8 | 23 | 4 | 14 |
| 9 | 46 | 4 | 18 |
| 10 | 98 | 5 | 23 |
| 11 | 207 | 5 | 28 |
| 12 | 451 | 6 | 34 |
| 13 | 983 | 6 | 40 |

ambilateral subsets involves an undesired loss of information. However, application of the same classification procedure to the subtree pairs from higher-order bifurcation points removes much of this objection. For example, the observation of the ambilateral type 9(4(1 3)5(1 4(2 2))) means an event in subsets $A^{4,5}$, $A^{1,3}$, $A^{1,4}$ and $A^{2,2}$. Table III shows that such a classification also implies a considerable data reduction for trees of degrees higher than 8 whereas all information concerning the degrees of pairs of subtrees is preserved.

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