

## TOPOLOGICAL PROPERTIES OF BINARY TREES GROWN WITH ORDER-DEPENDENT BRANCHING PROBABILITIES

■ J. VAN PELT and R. W. H. VERWER  
Netherlands Institute for Brain Research,  
Meibergdreef 33,  
1105 AZ Amsterdam, The Netherlands.

This paper describes a growth model for binary topological trees. The model defines the branching probability of all segments in the tree. The branching probability of a segment is formulated as a function of two variables, one indicating its type (intermediate or terminal), the other representing its order, i.e. the topological distance to the root segment. The function is determined by two parameters, namely the ratio of branching probabilities of intermediate and terminal segments and the strength of the order dependency, implemented in an exponential form. Expressions are derived for the calculation of probabilities of partitions as well as ambilateral tree types. Special attention is paid to symmetry properties of the partitions and it is indicated which part of the parameter domain results in predominantly symmetrical trees.

*1. Introduction.* Naturally grown branching patterns (e.g. neuronal dendrites, axonal terminal fields and rivers) often show great variability in their shapes. It is still often possible to distinguish characteristic features in their shapes on a first visual examination. For instance, pyramidal neurons are easily distinguishable from non-pyramidal ones. As such, one is usually able to classify branching patterns on these aspects. An intuitive classification on basis of the topology of the branching patterns, however, is not easy to make. This is caused by the fact that in most cases no topology (i.e. arrangement of segments in the formation of the tree) is in principle excluded from occurring. Only a statistical analysis of the topological patterns is able to show that their frequencies of occurrence may differ significantly between trees or sets of trees. The considerable interest in the topological properties of branching patterns, as shown in recent literature, is based on the idea that these frequencies of occurrence can be linked with developmental aspects, i.e. the way a 'growing' tree attains its final structure (Hollingworth and Berry, 1975; Dacey and Krumbein, 1976; Harding, 1971; Van Pelt and Verwer, 1983, 1985). By constructing growth models for branching patterns one is able to correlate formal growth rules with the topological variability in a set of branching patterns. Recently, the usefulness of this approach has been explicitly argued for by MacDonald (1984). Although one has to be aware that these formal growth rules may differ

substantially from the detailed dynamics of the real growth process, the study of the resulting variability can very well reveal global statistical properties of the dynamics on a larger time scale. Moreover, it may explain the difference between groups of branching patterns in terms of the global (formal) rules under which each pattern has developed. Generally, these formal rules will be based on a notion of the real growth process and as such may be different for each field of research. In neurobiology, for instance, much attention is paid to the branching patterns of neuronal cells. The formal growth rules which have been formulated to model the development of their topological patterns (Berry *et al.* 1975; Van Pelt and Verwer, 1983) can be summarized as:

- (1) a branching pattern consists of segments and we distinguish intermediate and terminal segments;
- (2) a branching event is defined as the division of a segment into two segments by a branching point from which a third new segment protrudes;
- (3) growth is considered as a series of branching events, one at a time;
- (4) each branching event in a tree is a realization of a stochastic process, defined on all segments in that tree, in which each segment has a certain probability to branch.

The growth process is now defined by specifying the branching probabilities of all segments. In a recent study (Van Pelt and Verwer, 1985) the following rule has been applied:

- (5) each intermediate segment of a branching pattern has a branching probability  $p_i$  and each terminal segment has a branching probability  $p_t$ .

In the following we shall mainly use the ratio  $R = p_i/p_t$  or the ratio  $Q = R/(R + 1) = p_i/(p_i + p_t)$  and we shall refer to this model as the one-parameter model. Van Pelt and Verwer (1985) have calculated the probability distributions of partitions (i.e. degrees of subtree pairs) and ambilateral tree types (i.e. 3-D topological tree types) on basis of these formal rules and they showed that the distributions were highly dependent of the ratio  $R$ . For two specific values of  $R$ , i.e.  $R = 0$  (terminal growth) and  $R = 1$  (segmental growth) this dependency was already shown in previous studies, qualitatively by Berry *et al.* (1975) and quantitatively by Van Pelt and Verwer (1983). A subtree is defined as the part of a tree that proceeds from one of its segments (acting as a root segment of that subtree) up to the tips of the tree. The pair of subtrees emerging from a bifurcation point is called a subtree pair. Although the incorporation of the parameter  $R$  has offered the possibility of adapting the model to frequency distributions of experimentally obtained branching patterns by varying  $R$  (Verwer *et al.*, submitted), it appeared that the model was limited in predicting very symmetrical trees

with high probability. As has been discussed by Van Pelt and Verwer (1985), symmetrical trees have increasing probability for smaller values of the ratio  $R$ , but their probability is far from being one at  $R = 0$ . Very often during fitting of the model parameter to dendritic data (unpublished observations) the sample likelihood  $L$  was increasing monotonically for decreasing values of the parameter  $R$ . Thus, the best fit was found at  $R = 0$  but the lack of a peak for  $R > 0$  and the fact that  $dL/dR < 0$  for  $R = 0$  indicated that the frequency of symmetrical trees in the observed sample was higher than terminal growth ( $R = 0$ ) predicts. Goodness-of-fit tests performed with data of basal dendrites of pyramidal cells resulted in a rejection of the segmental growth model (Verwer and Van Pelt, 1983). Although the terminal growth model could not be rejected, it appeared that the observed sample contained consistently more symmetrical branching patterns than was predicted by the latter model. The aim of the present work was to extend the growth model such that it is able to describe probability distributions in which more symmetrical trees have a high probability to occur. For this purpose we have added an extra formal growth rule to the ones already formulated.

- (6) An order can be assigned to each segment in a tree which is equal to the number of segments on the path from the root segment up to this segment. The root segment has order zero. The branching probability of a segment depends on its order.

This rule is based upon the notion that in the outgrowth of dendritic trees mechanisms may play a role which result in order-dependent branching. For instance, high-order segments (most distal from the root) may profit from their property to 'feel' more free space to grow into, such that there is an overall centrifugal effect on the branching probability. On the other hand, synthesis of new material takes place in the cell body, and transport phenomena may result in a predominance of low-order segments to branch which results in an overall centripetal effect on the branching probability. In the present study, the detailed form of the order dependency of the branching probability is built in the model in a formal way, i.e. not argued from any possible dynamical mechanism, and such that both centrifugal and centripetal effects can be described. Moreover, if the order dependency is set to zero the model reduces to the one-parameter model (Van Pelt and Verwer, 1985).

*2. The Model.* The order dependency of the branching probability of a segment will be introduced by the factor  $2^{-S\gamma}$ , in which  $\gamma$  denotes the order and the parameter  $S$  modulates the strength of the order dependency such that for  $S = 0$  it disappears and for  $S > 0$  and  $S < 0$  the branching probability decreases (respectively increases) with increasing order  $\gamma$ . The branching

probability of a terminal segment  $p_t$  and an intermediate segment  $p_i$  is equal to

$$p_t = \frac{1}{C} \cdot 2^{-S\gamma} \quad \text{and} \quad p_i = \frac{1}{C} \cdot R \cdot 2^{-S\gamma}, \quad \text{respectively.} \quad (1)$$

The ratio  $R$  of the branching probabilities for intermediate and terminal segments is maintained as in previous studies but now only concerns segments of equal order. The constant  $C$  allows for normalization such that the total branching probability of the tree is 1 and it depends not only on the parameters  $R$  and  $S$  but also on the particular arrangement of the segments in the tree. As a consequence of the order dependency of the branching probabilities we now have to know how the segments are distributed over the orders.

Let us take a set of trees of degree  $n$ , grown according to the above mentioned rules and let us define on that set the functions  $T(\gamma|n)$  and  $I(\gamma|n)$ . The function  $T(\gamma|n)$  describes the probability that in a randomly chosen tree from a set of  $n$ th-degree trees a randomly chosen terminal segment is of the order  $\gamma$ . The function  $I(\gamma|n)$  describes the probability that in a randomly chosen tree from a set of  $n$ th-degree trees a randomly chosen intermediate segment is of the order  $\gamma$ . The maximum order of a segment in a  $n$ th-degree tree can be  $n - 1$  since the root segment is of order zero, thus

$$\sum_{\gamma=0}^{n-1} I(\gamma|n) = 1 \quad \text{and} \quad \sum_{\gamma=0}^{n-1} T(\gamma|n) = 1, \quad (2)$$

while  $I(n - 1|n) = 0$  because a segment of highest order is always a terminal one and  $T(0|n) = 0$  for  $n > 1$  as the root always bifurcates for  $n > 1$ . A tree of degree  $n$  has  $n$  terminal segments (by definition) and  $n - 1$  intermediate segments. The mean number of terminal and intermediate segments of order  $\gamma$  per tree is thus equal to

$$E[N_t^n(\gamma)] = n \cdot T(\gamma|n) \quad \text{and} \quad E[N_i^n(\gamma)] = (n - 1) \cdot I(\gamma|n), \quad (3)$$

respectively. The growth rules, applied to a virtual tree, composed of these mean number of segments, require also a normalization such that

$$\frac{1}{C(n)} \cdot \sum_{\gamma=0}^{n-1} \{E[N_t^n(\gamma)] + R \cdot E[N_i^n(\gamma)]\} \cdot 2^{-S\gamma} = 1. \quad (4)$$

Each term in the sum describes the probability that one of the terminal or intermediate segments of order  $\gamma$  branches. The function  $C(n)$  defined as

$$C(n) = \sum_{\gamma=0}^{n-1} \{E[N_t^n(\gamma)] + R \cdot E[N_i^n(\gamma)]\} \cdot 2^{-S\gamma} \quad (5)$$

can be considered as the mean, unnormalized probability of branching of the whole tree of degree  $n$ . The advantage of defining the order dependency in an exponential form [equation (1)] is that the ratio between branching probabilities of consecutive segments (or segments in a subtree) is independent of the position of these segments (or subtree) in the tree. For instance, in a subtree with root segment of order  $\gamma_0$ , the branching probability of a segment depends on the order by the factor  $2^{-S(\gamma_0+\gamma')}$  if  $\gamma'$  indicates the relative order in the subtree. This means that the order dependency in the subtree is given by the factor  $2^{-S\gamma'}$ , while the constant  $2^{-S\gamma_0}$  acts as a scaling factor for the whole subtree. The subtree will develop on subsequent branching events as if it was a complete tree. The consequence of this property is that the functions  $T(\gamma | n)$  and  $I(\gamma | n)$  will not apply to the  $n$ th-degree trees only but also to  $n$ th-degree subtrees in higher-degree trees. Also the partition probabilities will be independent of the order in the tree since both subtrees of a pair are scaled in their total branching probability by the same factor  $2^{-S\gamma_0}$ . This recursive property implies that any subtree of order  $\gamma$  and degree  $m$  forms new segments at its root or in its subsequent subtrees of degrees  $r$  and  $m - r$  with probabilities proportional to  $R \cdot 2^{-S\gamma}$ ,  $2^{-S(\gamma+1)} \cdot C(r)$  and  $2^{-S(\gamma+1)} \cdot C(m - r)$ , respectively. Thus, branching of a (sub)tree of degree  $n$  at its root segment or in both subsequent subtrees occurs with probabilities

$$\frac{R \cdot 2^S}{R \cdot 2^S + C(r) + C(n - r)}, \frac{C(r)}{R \cdot 2^S + C(r) + C(n - r)} \text{ and } \frac{C(n - r)}{R \cdot 2^S + C(r) + C(n - r)}, \tag{6}$$

respectively. A recurrent relation for  $C(n)$  can be formulated immediately because the unnormalized branching probability  $C(n)$  of a tree can be expressed in the unnormalized branching probabilities of its root and both subsequent subtrees. A tree of degree  $n$  has a probability  $p(r, n - r)$  of having first-order subtrees of degree  $r$  and  $(n - r)$  and thus we have

$$C(n) = R + 2^{-S} \cdot \sum_{r=1}^{[n/2]} p(r, n - r) \cdot [C(r) + C(n - r)]. \tag{7}$$

The notation  $[x]$  denotes the integer part of  $x$ . The partition probabilities of degree  $n$  can be expressed in those of degree  $n - 1$  via

$$\begin{aligned} p(r, n - r) &= p(r - 1, n - r) \cdot \frac{C(r - 1)}{R \cdot 2^S + C(r - 1) + C(n - r)} \\ &+ (1 - \delta(r, n - r) + \delta(r, n - r - 1)) \cdot p(r, n - r - 1) \\ &\times \frac{C(n - r - 1)}{R \cdot 2^S + C(n - r - 1) + C(r)}, \end{aligned} \tag{8}$$

if  $1 < r \leq n - r$ .

The Kronecker delta  $\delta(x, y)$  equals 1 if  $x = y$  and 0 if  $x \neq y$ . The first term describes the probability of partition  $(r - 1, n - r)$  times the probability that the branching event occurs within the  $(r - 1)$ th-degree subtree. The second term describes the probability of partition  $(r, n - r - 1)$  times the probability that the branching event occurs within the  $(n - r - 1)$ th-degree subtree. The factor  $1 - \delta(r, n - r) + \delta(r, n - r - 1)$  equals 2 if both subtrees are of equal degree ( $r = n - r - 1$ ) which doubles the probability and equals 0 to cancel the second term if  $r = n - r$ . A  $(1, n - 1)$  partition may result from a branching event in the  $(n - 2)$ th-degree subtree of a  $(1, n - 2)$  partition or from branching of the root segment in a  $(n - 1)$ th-degree tree, thus

$$\begin{aligned}
 p(1, n - 1) &= 2^{\delta(1, n-2)} \cdot p(1, n - 2) \cdot \frac{C(n - 2)}{R \cdot 2^S + C(n - 2) + C(1)} \\
 &+ R \cdot 2^S \sum_{r=1}^{\lfloor (n-1)/2 \rfloor} \frac{p(r, n - r - 1)}{R \cdot 2^S + C(r) + C(n - r - 1)}. \tag{9}
 \end{aligned}$$

The function  $C(n)$  can be calculated by means of the partition probabilities of degree  $n$  and the functions  $C(r)$  for  $r < n$  [equation (7)]. The partition probabilities of degree  $(n + 1)$  can be calculated by means of the functions  $C(1), \dots, C(n)$  and the partition probabilities of degree  $n$  [equations (8) and (9)]. The start values of these functions are  $p(1, 1) = 1$  and  $C(1) = 1$ .

The functions  $I(\gamma | n)$  and  $T(\gamma | n)$  can also be expressed recursively and calculated explicitly once the partition probabilities are known.

$$T(\gamma | n) = \frac{1}{n} \sum_{r=1}^{\lfloor n/2 \rfloor} p(r, n - r) \cdot [rT(\gamma - 1 | r) + (n - r)T(\gamma - 1 | n - r)] \tag{10}$$

and

$$I(\gamma | n) = \frac{1}{n - 1} \sum_{r=1}^{\lfloor n/2 \rfloor} p(r, n - r) \cdot [(r - 1)I(\gamma - 1 | r) + (n - r - 1)I(\gamma - 1 | n - r)]$$

for  $0 < \gamma < n$ , while  $T(0 | 1) = 1$ ;  $I(0 | 1) = 0$  and  $T(0 | n) = 0$  and  $I(0 | n) = 1/(n - 1)$  if  $n > 1$ . Further we had  $I(n - 1 | n) = 0$  if  $n \geq 1$  [equation (1)].

### 3. Properties of the Model

*3.1 Partition probabilities.* The behavior of the partition probabilities depending on both parameters  $R$  and  $S$  is illustrated in Figs 1(a)–(c) displaying the  $(1, 6)$ -,  $(2, 5)$ - and  $(3, 4)$ -partition probabilities, respectively, for the parameter domain  $R < 10$  and  $-5 \leq S \leq 5$ . For certain values of the parameters  $R$  and  $S$ , the model has already been worked out analytically, namely for terminal growth  $(R, S) = (0, 0)$  and for segmental growth  $(R, S) = (1, 0)$

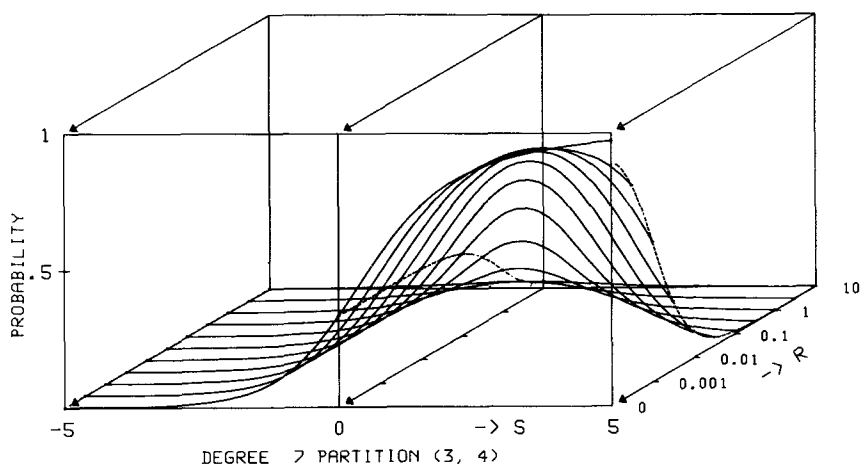
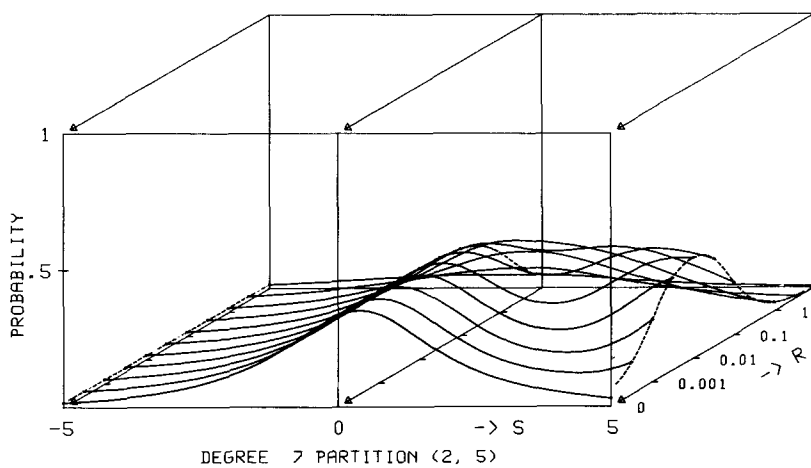
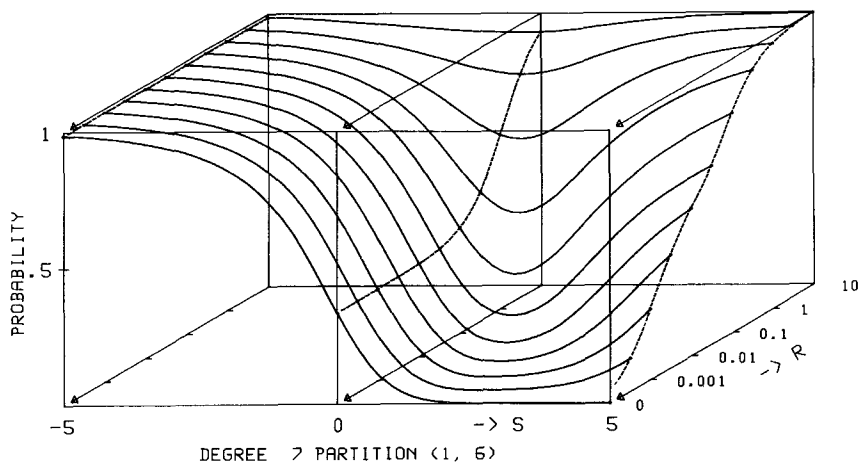


Figure 1. Probabilities of (1, 6)-, (2, 5)- and (3, 4)-partitions plotted for the parameter domain  $-5 < S < 5$  and  $0 < R < 10$ . The intersection of the probability curves at  $S = -5, 0$  and  $5$  is indicated by the dashed curves.

by Van Pelt and Verwer (1983). The dashed curves in the midplanes at  $S = 0$  illustrate the partition probabilities if there is no order dependency in the branching probabilities of the segments. Then, these curves correspond to the ones predicted by the one-parameter model ( $R, S = 0$ ) (Van Pelt and Verwer, 1985). The probabilities in the latter paper are expressed not in terms of  $R$  but in terms of the parameter  $Q(Q = R/(R + 1))$ . As such the parameter domain  $R(0 \leq R)$  is mapped on  $Q(0 \leq Q \leq 1)$ .

*3.2 Partition asymmetry.* One of the reasons to develop a two-parameter model for growth was to be able to describe the formation of trees with more symmetry than may be predicted by the terminal growth model. Visual inspection of these figures [1(a)–(c)] shows clearly which parts of the parameter domain predict symmetrical trees [ $p(1, 6) \approx 0$  and  $p(3, 4) \approx 1$ ] and asymmetrical trees [ $p(1, 6) \approx 1$  and  $p(3, 4) \approx 0$ ]. In order to judge quantitatively whether this aim is satisfactorily fulfilled it is useful to introduce a measure for asymmetry in topological terms, i.e. in number of branching points in both subtrees of a bifurcation point.

As such we shall define the asymmetry  $A_p$  of a partition as the relative difference in number of branching points in both subtrees of the partition. A tree of degree  $n$  has  $n - 1$  branching points. For a partition of an  $n$ th-degree tree into two subtrees with  $r$  and  $n - r$  terminal segments, the asymmetry will be

$$A_p(r, n - r) = \frac{(n - r - 1) - (r - 1)}{(n - r - 1) + (r - 1)} = \frac{n - 2r}{n - 2}, \quad \text{if } r \leq n - r. \quad (11)$$

According to this definition the asymmetry ranges from a minimum value of 0 in case of a partition into equal-degree subtrees to the maximum value of 1 in case of a  $(1, n - 1)$ -partition. The asymmetry values of partitions of low degree are given in Table I. The mean asymmetry of partitions of the same degree predicted by the growth model can be defined as the mean value

$$\bar{A}_p = \sum_{r=1}^{\lfloor n/2 \rfloor} p(r, n - r) \cdot A_p(r, n - r) = \sum_{r=1}^{\lfloor n/2 \rfloor} p(r, n - r) \cdot \frac{n - 2r}{n - 2}. \quad (12)$$

For the two-parameter model these mean partition asymmetries are displayed in Fig. 2 for partitions of degree 7. The dashed curve in the midplane indicates the mean partition asymmetry if there is no order-dependency in the branching probabilities and the figure shows that positive values of  $S$  may indeed result in more symmetrical partitions. It illustrates that symmetrical partitions are only most probable for small values of the parameter  $R$ , while no part of the parameter domain predicts purely symmetric trees, i.e. the mean asymmetry does not attain a zero value. In Figs 3(a)–(b) contours are plotted of points in the parameter domain predicting equal



TABLE I

List of Asymmetry Value of Partitions ( $r, s$ ) with  $r = 1-10$  and  $s = 1-10$

$s \rightarrow$	1	2	3	4	5	6	7	8	9	10
$r$ ↓										
1	0	1	1	1	1	1	1	1	1	1
2		0	0.33	0.50	0.60	0.67	0.71	0.75	0.78	0.80
3			0	0.20	0.33	0.43	0.50	0.56	0.60	0.64
4				0	0.14	0.25	0.33	0.40	0.45	0.50
5					0	0.11	0.20	0.27	0.33	0.38
6						0	0.09	0.17	0.23	0.29
7							0	0.08	0.14	0.20
8								0	0.07	0.13
9									0	0.06
10										0

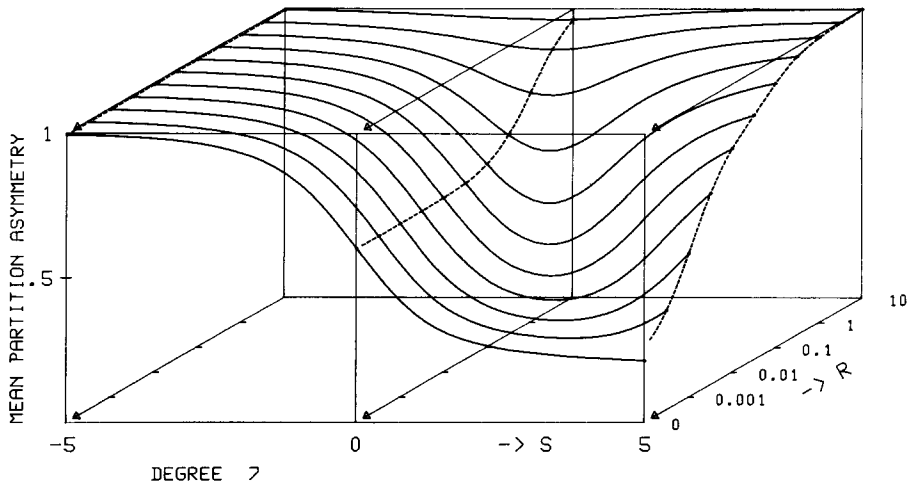


Figure 2. Mean asymmetry of partitions of degree 7 plotted for the parameter domain  $-5 < S < 5$  and  $0 < R < 10$ . The intersection of the asymmetry curves with the planes at  $S = -5, 0$  and  $5$  is indicated by dashed curves.

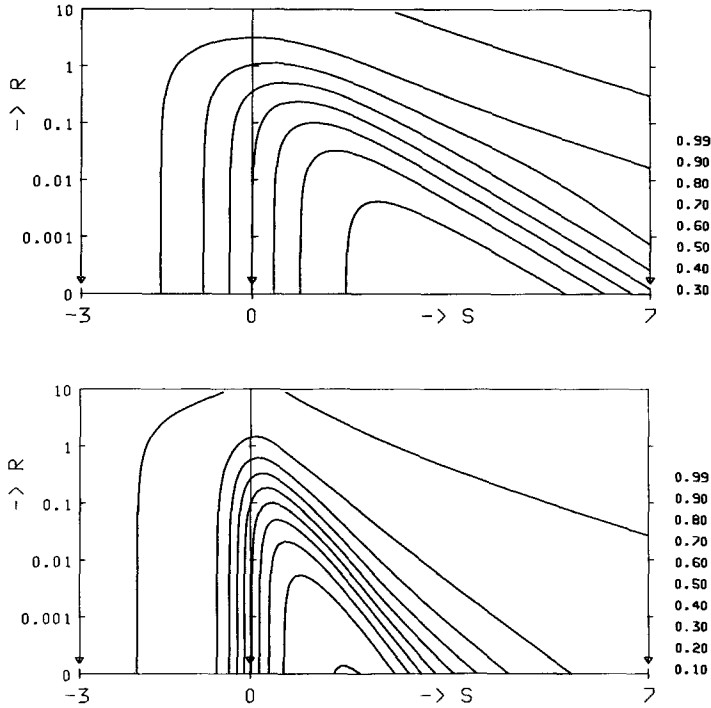


Figure 3. Contours of equal mean partition asymmetry plotted in the parameter domain for partitions of degree 7(a) and 40(b). The asymmetry values of the contours are displayed at the right side of the figure.

values for the mean partition asymmetries. Figures 2 and 3 show clearly that:

- (1) For each value of  $S$  the asymmetry increases for increasing values of  $R$ . Increasing values of  $R$  imply increasing probabilities for intermediate segments to branch with respect to terminal segments and as such increasing probabilities to get asymmetrical partitions.
- (2) For each value of  $R$ , there is one value of  $S$  with minimal mean asymmetry.

Large negative values of  $S$  imply high branching probabilities for high-order segments (most distal from the root) such that asymmetrical subtree pairs will become more asymmetrical on subsequent branching, irrespective of the value of  $R$ . Positive values of  $S$  imply high branching probabilities for low-order segments (most proximal to the root). The largest subtree in a pair will usually have its terminal segment at higher orders than in the smaller subtree. The number of terminal segments at low order may thus very well be larger in the smaller subtree. For  $R \rightarrow 0$  and  $S > 0$ , terminal segments are more likely to branch than intermediate segments and low-order segments

are more likely to branch than high-order segments. Under these conditions the smallest subtree in a pair will profit from having more low-order terminal segments than the larger subtree and will have a higher branching probability leading to a more symmetrical subtree pair. Comparison of the contour plots for different degrees [Figs 3(a)–(b)] reveals that at higher degree the contours are compressed in a direction parallel to the  $S$ -axis, such that with increasing degree symmetrical partitions are found in a more and more restricted area of the parameter domain.

*3.3 Distribution of the order of segments.* The range of symmetry values as predicted by different points in the parameter space is also reflected in the distributions of segments against the order  $I(\gamma | n)$  and  $T(\gamma | n)$  [equation (10)]. Trees consisting of mainly symmetric partitions will concentrate their segments at lowest orders. Highly asymmetric partitions will result in trees which extend their segments to high orders. Figures 4(a)–(c) show the order distributions for three points in the parameter space, namely  $(R, S) = (10, 0)$ ,  $(0, 0)$  and  $(0, 5)$ , respectively. In the first point [Fig. 4(a)], asymmetric partitions are highly probable and the corresponding distribution is clearly rather flat, i.e. about the same number of segments are expected for any order. The third point [Fig. 4(c)] gives rise to more symmetric partitions and trees have predominantly segments of low orders.

For a tree consisting of complete symmetric partitions the number of segments increases with order according to  $2^\gamma$  and this pattern is shown up to order 3 in Fig. 4(c). The second point [Fig. 4(b)] corresponds to the terminal growth model and the maximum number of segments for 10th degrees trees are expected at order 3. The mode for intermediate and terminal segments lies at order 2 and 4, respectively.

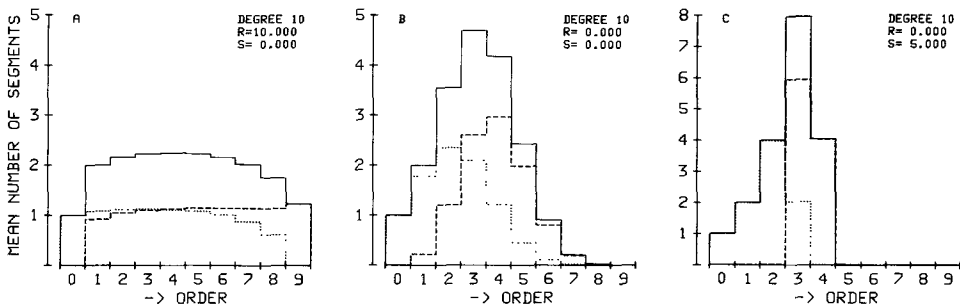


Figure 4. Segment vs order distributions for trees of degree 10 as predicted by three different growth models. Each figure displays the distribution of intermediate segments (dotted curve), terminal segments (dashed curve) and of both types of segments (full curve). (a)  $(R = 10, S = 0)$  results from trees with highly asymmetric partitions; (b)  $(R = 0, S = 0)$  shows the distribution for terminally grown trees; and (c)  $(R = 0, S = 5)$  results from trees which have a high probability of containing symmetric partitions.

3.4 *Probabilities of ambilateral types.* Up till now we only have derived the probabilities of partitions. Since the model involves independency for the partitions in a tree, the probability of a tree is easy to calculate being the product of the probabilities of all the partitions in the tree. An extra factor of 2 is required for each occurrence of an equal-degree, unequal-type subtree pair (Van Pelt and Verwer, 1985).

4. *Applications.* The results presented above enable comparison of the model with samples of observed trees, i.e. to find the most likely parameter values of the model with respect to the observed trees. To find an optimal parameter set, the likelihood of the observed sample is calculated for several discrete points in the parameter domain and the point of maximum likelihood is taken, eventually followed by a local search on a finer grid, etc. As an example we have applied this procedure with data of basal dendrites of pyramidal cells from rat neocortex, obtained from Dr Uylings of our institute. As mentioned above, these data have also been used by Verwer and Van Pelt (1983) for testing against the terminal and segmental growth model. Contours of equal likelihood of the whole sample are shown in Fig. 5. The maximum likelihood is obtained for the parameter values  $R = 0.013$  and  $S = 0.40$ . From these values one can conclude that branching occurs mainly at terminal segments and that segments proximal to the cell body have a higher probability of branching than distal segments. The partition probabilities associated with these parameter values are displayed in cumulative distributions in Fig. 6 for degree 4–11 along with those for terminal and segmental growth. These figures clearly show a very good agreement between model and observations. In particular, because the model succeeds in predicting symmetrical partitions with high probability, the fit is considerably

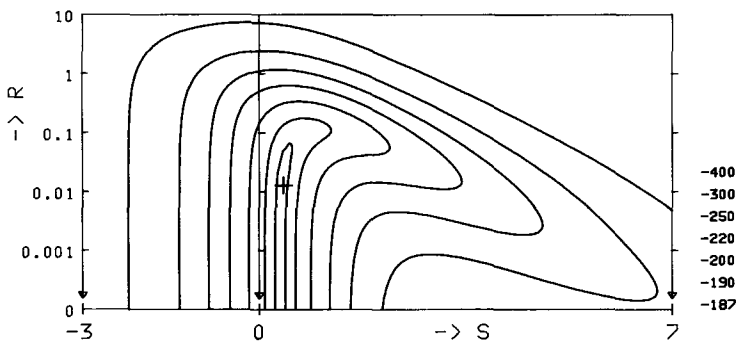


Figure 5. Contours of equal likelihood for the total sample of observed partitions as given in the columns 'Obs' of Fig. 6. The log-likelihood takes its maximum value of  $-186.6$  at the parameter values  $R = 0.013$  and  $S = 0.40$ , indicated with a cross. The log-likelihood values of the contours are displayed at the right side of the figure.

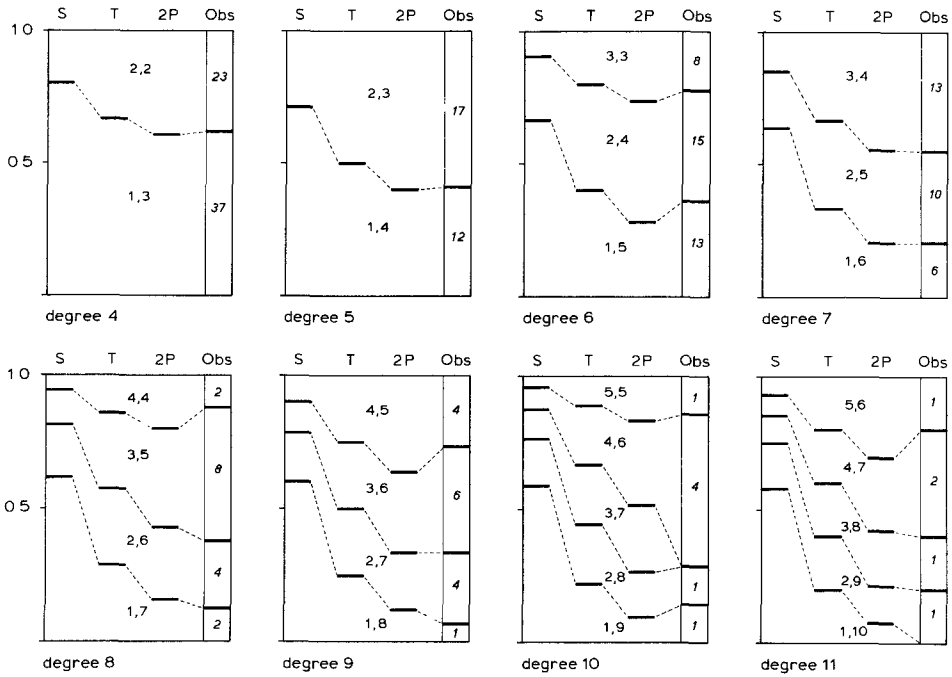


Figure 6. Cumulative probability distributions of partitions of degree 4-11 for segmental growth (S), terminal growth (T) and the two-parameter model (2P), compared with the corresponding observed frequencies of partitions (Obs). The data are from basal dendrites of pyramidal cells from rat neo-cortex, obtained from Dr Uylings. The number pairs denote the partitions.

better than in the case of terminal growth. However, the quality of the fit is difficult to calculate from the likelihood value itself. Therefore we have applied the Kolmogorov goodness-of-fit test for all separate distributions against the model with the most likely parameter set. Table II shows the attained levels of significance. These values, however, are conservative because the parameters were estimated from the same data. Nevertheless, a comparison can be made with both primary models and all the outcomes confirm a good agreement between the observations and the hypothetical model which is better than for the terminal growth model in all but one case.

6. Discussion. Without order dependency the present model reduces to a one-parameter model described by Van Pelt and Verwer (1985). Whereas the partition probabilities for this one-parameter model could be formulated in closed, analytical expressions, this was unfortunately not possible for the two-parameter model and the probabilities must be obtained by a somewhat more laborious algorithm. The main reason for the present study was to obtain a description of the frequency distributions of topological types of

TABLE II  
The Levels of Significance Obtained by the Kolmogorov Goodness-of-fit Test for Discrete Distributions of the Data Shown in Fig. 6

Degree	No. of obs.	Level of significance		
		Segmental growth	Terminal growth	$R = 0.013$ $S = 0.40$
4	60	$8 \times 10^{-4}$	0.43-0.49	0.70-0.90
5	29	$7 \times 10^{-4}$	0.41-0.45	0.75-1.00
6	36	$2 \times 10^{-4}$	0.73-0.96	0.45-0.51
7	29	$3 \times 10^{-6}$	0.27-0.29	0.86-1.00
8	16	$2 \times 10^{-4}$	0.30-0.37	0.74-0.98
9	15	$1 \times 10^{-5}$	0.33-0.36	0.66-0.84
10	7	$3 \times 10^{-3}$	0.09	0.39-0.43
11	5	0.01	0.82-1.00	0.83-1.00

observed dendritic trees, better than was possible with the one-parameter model, including terminal growth. For this purpose it was necessary that the model should be able to grow symmetrical trees with higher probability. The incorporation of an order dependency in the branching probability is an answer to this question and the calculations and figures in this paper demonstrate that for certain areas in the parameter domain this aim is indeed fulfilled. Especially at small values for  $R$ , the relative frequency of more symmetrical tree types increases for moderate positive values of  $S$  and for  $R = 0$  it increases continuously for increasing values of parameter  $S$ . The usefulness of the model is further supported by the results obtained during fitting of the model to observed branching patterns. It appeared that in all cases where the one-parameter model ( $S = 0$ ) failed to find a maximum for the likelihood function in the defined interval for  $R$  ( $0 \leq R$ ), the two-parameter model indeed yielded a good fit for a nonzero value of  $S$ .

The model will, of course, not be able to describe any possible distribution of topological types. We think that the model will suffice in most practical cases, since, apart from the withdrawal of branches, it accounts for biological reasonable features such as branching from any segment, distinction between terminal and intermediate segments and the distance of a segment from the soma.

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