

## GROWTH MODELS (INCLUDING TERMINAL AND SEGMENTAL BRANCHING) FOR TOPOLOGICAL BINARY TREES

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A growth model for topological trees is formulated as a generalization of the terminal and segmental growth model. For this parameterized growth model, expressions are derived for the partition probabilities (probabilities of subtree pairs of certain degrees). The probabilities of complete trees are easily derived from these partition probabilities.

*1. Introduction.* In the study of growth of branching patterns much attention has been paid to the so-called terminal and segmental growth models. These models differ in that segmental growth allows all segments to branch with equal probability, whereas terminal growth allows only terminal segments to branch with equal probability. In the field of neuroscience, where dendritic structures are frequently studied, the terminal growth model has often appeared to give a good fit to the experimental data (e.g. Berry *et al.* 1980; Meininger and Baudrimont, 1981; Uylings *et al.* 1983). However, deviations from the terminal model are also reported under normal growth conditions (e.g. Verwer and Van Pelt, 1983; Sadler and Berry, 1983) or under experimental conditions (McConnell and Berry, 1978, 1979). In the field of geomorphology, Dacey and Krumbein (1976) have calculated the probabilities of small two dimensional (2-D) stream channel networks for three growth models, viz. terminal growth, segmental growth and a model with fixed unequal non-zero branching probabilities for intermediate and terminal segments. The probabilities of these networks were obtained by enumerating all possible growth paths. They found that terminal growth did not fit any data set but that both other models were able to fit almost all the data. These examples show that (1) the terminal and segmental growth models are often able to describe experimental data, but also that (2) in many cases a better fit with the data should be expected if the branching probabilities of intermediate and terminal segments could be varied continuously. For this purpose, a growth model has been formulated mathematically which is provided with a parameter describing the ratio of branching probabilities of intermediate and terminal segments. For two particular

values of this ratio parameter the model corresponds to the terminal and segmental growth model, respectively.

As has been described in previous papers (Van Pelt and Verwer, 1983, 1984; Verwer and Van Pelt, 1983), the rules along which growth proceeds reflect themselves in characteristic probability distributions not only of tree types but also of the partitions in the trees. A partition is a pair of natural numbers denoting the degrees of a subtree pair, or in other words, the degree of a (sub)tree (number of terminal segments) is partitioned by its two next-order subtrees. Each bifurcation corresponds to a partition and as such, a tree can be decomposed in as many partitions as there are bifurcation points. If the partitions in a tree are mutually independent, then the tree-type probability can be calculated from the probabilities of all its constituting partitions including correction factors due to symmetrical partitions. As argued by Van Pelt and Verwer (1984), the partitions are independent as long as the branching probability of a segment is independent of the order of the segment (number of segments on the trajectory from the root of the tree up to the segment). The growth model described in this paper does meet this criterion and it has been elaborated for the partition probabilities. The probabilities of complete branching patterns are easily derived from these partition probabilities and examples for this calculation will be given.

*2. Partition Probabilities on a 2-D Matrix.* The partition probability  $p(r, s)$  is defined as the probability for a binary tree of degree  $n$  ( $n = r + s$ ) to have first-order subtrees of degree  $r$  and  $s$ . In the derivation of partition probabilities from hypothesized growth rules, a tree will be reduced to a root segment and a pair of subtrees identified by their degrees. In the first instance, the trees are assumed to be planar graphs, i.e. there is a left-right distinction at the bifurcation points and the partition probabilities are derived for these 2-D trees. The reason for this approach is (1) the expressions are symmetric with respect to both subtrees in 2-D and (2) the transition to a 3-D description is easy to make.

The growth process is assumed to consist of a series of branching events and each event means the addition of a new terminal segment to one of the existing segments. Since we assume the tree to remain binary, a new branching point arises also. In our simplified picture of a tree (root segment and two subtrees), the new segment is added somewhere in one of the two subtrees or to the root segment. A tree of the type  $(r, s)$  results in a  $(r + 1, s)$ -tree if the  $r$ -degree subtree branches somewhere, in a  $(r, s + 1)$ -tree if the  $s$ -degree subtree branches and in a  $(1, r + s)$ -tree or  $(r + s, 1)$ -tree if the root segment branches at the 'left' or 'right' side, respectively. As the tree is characterized by a pair of natural numbers ( $r$  and  $s$ ), it can be considered as a point in a coordinate system with natural numbers for the coordinates (Fig. 1).

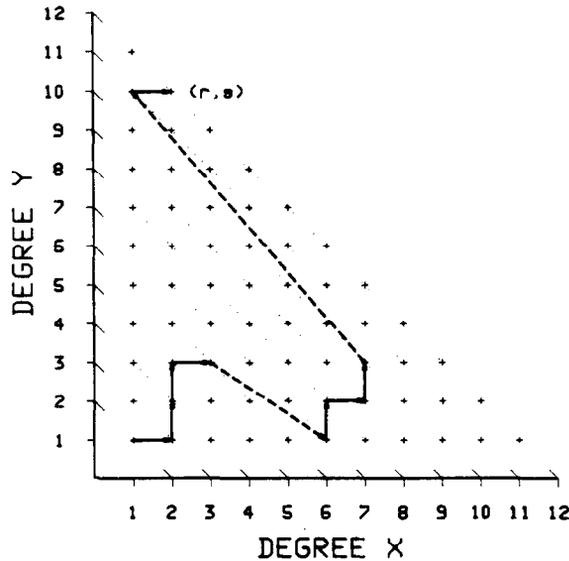


Figure 1. Matrix representation of partitions. A point  $(x, y)$  in the matrix denotes a tree of degree  $x + y$  with first-order subtrees of degrees  $x$  and  $y$ , respectively. All points on a dotted diagonal line are trees of the same degree as indicated by the intersection point of the diagonal line at each axis. The path in the matrix shows a growing tree. New branches can be formed in one of the two subtrees (unit steps in  $x$ - or  $y$ -direction) or at the root segment [dashed line from  $(3, 3)$  to  $(6, 1)$  and from  $(7, 3)$  to  $(1, 10)$ ].

All trees of the same degree  $n$  correspond to points  $(x, y)$  on the diagonal line  $n$  such that  $x + y = n$ . When a tree grows, its degree increments and the tree makes successive steps by crossing all diagonal lines. The tree starts at the point  $(1, 1)$ . A branching event in the 'left' or 'right' subtree corresponds to a unit step in  $x$ - or  $y$ -direction, respectively. Branching of the root segment, however, corresponds to a jump from the current point  $(x, y)$  on diagonal  $n$  to one of the extremes of the next diagonal line  $n + 1$ . The growth of a tree from partition  $(1, 1)$  to partition  $(r, s)$  can be represented as a path from point  $(1, 1)$  to point  $(r, s)$ . If bifurcations occur only within the subtrees, then the path is characterized as a series of unit steps in  $x$ - or  $y$ -direction. If branching of root segments occurs, then the path is interrupted by jumps to diagonal extremes. In Fig. 1 a path from partition  $(1, 1)$  to partition  $(2, 10)$  is shown. The tree with partition  $(3, 3)$  bifurcates on its root segment resulting in a jump to partition  $(6, 1)$  and there is a jump from  $(7, 3)$  to  $(1, 10)$ . All other steps represent bifurcations somewhere in the two subtrees. There are many paths from  $(1, 1)$  to  $(r, s)$ . In principle, each path represents a way in which a tree can grow.

The question of calculating the partition probability  $*p(r, s)$  (starred because of the 2-D description) can now be translated into the question of

calculating the probability that after  $(n - 2)$  steps the point  $(r, s)$  on diagonal line  $n$  is reached ( $n = r + s$ ). More specifically, the probability  $*p(r, s)$  is equal to the sum of the probabilities of all paths from  $(1, 1)$  to  $(r, s)$ . As we have seen, not all paths from  $(1, 1)$  to  $(r, s)$  are continuous on the matrix; jumps from a point on a diagonal to one of the two extremes of the next diagonal are allowed. In counting the number of different paths we can circumvent the jumps by restricting ourselves to continuous paths. We can account for all jumps by counting not only paths starting at  $(1, 1)$  but also paths which start at points  $(x, 1)$  or  $(1, y)$  for  $x > 1$  and  $y > 1$ . The entries to two of these points on a diagonal then represent all the jumps from the preceding diagonal and have together a probability equal to all these jump probabilities. This is illustrated in Fig. 2. The entries to the points  $(x, 1)$  and  $(1, y)$  for  $x > 1$  and  $y > 1$  are also indicated by dotted lines and can be interpreted as 'unit steps' from the  $x$ - or  $y$ -axis to these points. Point  $(r, s)$  can now be reached by all continuous paths, taken as a series of unit steps and starting from  $(1, 1)$  or from points on the  $x$ - or  $y$ -axis. A possible path from  $(4, 1)$  to  $(8, 4)$  is indicated. In the following we shall use the term 'path' for a continuous path on the matrix.

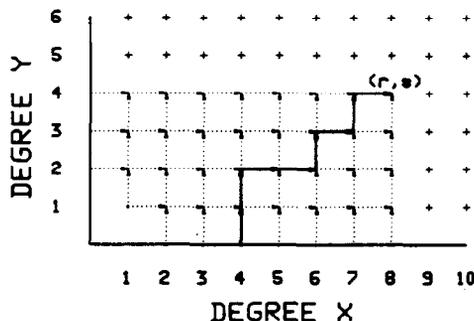


Figure 2. Display of all unit steps which can contribute to paths up to the partition  $(r, s)$ , here taken as  $(8, 4)$ . The paths on the matrix can start at point  $(1, 1)$  or at points  $(x, 1)$  or  $(1, y)$ ,  $x > 1$  and  $y > 1$ . If a path starts at  $(x, 1)$  or  $(1, y)$  it is indicated by a preceding unit step from the  $x$ - or  $y$ -axis. The probabilities to enter the matrix at the points  $(x, 1)$  or  $(1, y)$  are then associated with the unit steps from the axes to these points. A particular path is shown entering the matrix at partition  $(4, 1)$  up to partition  $(8, 4)$ .

*Number of paths.* In a path from  $(a, b)$  to  $(r, s)$ ,  $a \leq r$  and  $b \leq s$ , there are  $r + s - a - b$  steps of which  $r - a$  are in the  $x$ -direction and  $s - b$  in the  $y$ -direction. Each permutation in the  $r + s - a - b$  steps by interchanging an  $x$ - and  $y$ -step introduces a new path. As such, the total number of different paths from  $(a, b)$  to  $(r, s)$ ,  $N(a, b : r, s)$ , is equal to

$$N(a, b ; r, s) = \binom{r + s - a - b}{r - a} \tag{1}$$

(Feller, 1970).

*Probability of a path.* As indicated, each point in the coordinate system represents a tree. On branching there are four possible ways to proceed, i.e. two steps and two jumps. The probabilities of these four ways depend completely on the growth model. Under the assumption that there is no correlation between successive steps, the growth process is completely defined by the probabilities associated with all unit steps in the matrix and the entries from the  $x$ - and  $y$ -axis (Fig. 2). The probability of a continuous path from  $(a, b)$  to  $(r, s)$  ( $a \leq r ; b \leq s$ ) then is simply the product of all its unit-step probabilities.

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} P(z_i^j | x_i^j, y_i^j). \tag{2}$$

Here,  $j$  denotes a particular path and  $i$  identifies a step in this path. For convenience,  $i$  is taken as the degree of the growing tree (and equal to diagonal number) because for each step the degree increases with one. The path is defined by the sequence of steps  $z_i^j$  [ $i = a + b, \dots, (r + s - 1)$ ] where  $z$  denotes an  $x$ -step or an  $y$ -step. The probability of an  $x$ - or  $y$ -step in point  $(x_i^j, y_i^j)$  is given by  $P(x | x_i^j, y_i^j)$  and  $P(y | x_i^j, y_i^j)$ , respectively.

In the calculation of the partition probability  $*p(r, s)$  we have to calculate (1) the probabilities of all paths from  $(1, 1)$  to  $(r, s)$ , (2) the probabilities of all paths from points on the  $x$ -axis,  $x = 2, \dots, r$  to  $(r, s)$  and (3) the probabilities of all paths from points on the  $y$ -axis,  $y = 2, \dots, s$  to  $(r, s)$ . Let us first assume that both  $r > 1$  and  $s > 1$ . In formula we get

$$\begin{aligned} *p(r, s) &= \sum_{j=1}^{N(1,1:r,s)} P^j(1, 1 : r, s) \\ &+ \sum_{x=2}^r e(x, 1) \sum_{j=1}^{N(x,1:r,s)} P^j(x, 1 : r, s) \\ &+ \sum_{y=2}^s e(1, y) \sum_{j=1}^{N(1,y:r,s)} P^j(1, y : r, s). \end{aligned} \tag{3}$$

Here,  $j$  denotes the path number and  $e(x, 1)$  and  $e(1, y)$  denote the probabilities to enter the matrix from the  $x$ - or  $y$ -axis at the points  $(x, 1)$  or  $(1, y)$ , respectively.

3. *Growth Models.* For further evaluation of equation (3) the growth model must be specified in terms of step and jump probabilities. In this paper we shall define a growth model by a generalization of the terminal and segmental growth rules (Van Pelt and Verwer, 1983). In this generalization the distinction between terminal and intermediate segments is maintained but the relative probability of branching of segments of these two classes is parametrized. Assume that the growth model predicts a value  $R$  for the ratio of branching probabilities for intermediate ( $p_{is}$ ) and terminal segments ( $p_{ts}$ )

$$R = p_{is}/p_{ts}. \quad (4)$$

In a tree of degree  $n$  we have  $n$  terminal segments and  $(n - 1)$  intermediate segments. The probabilities  $p_{is}$  and  $p_{ts}$  must also obey the normalization

$$np_{ts} + (n - 1)p_{is} = 1 \quad (5)$$

as each time only one segment branches. Equations (4) and (5) result in the following values for  $p_{is}$  and  $p_{ts}$  in a tree of degree  $n$

$$p_{ts} = 1/\{n + (n - 1)R\}$$

and

$$p_{is} = R/\{n + (n - 1)R\}. \quad (6)$$

The probability that a branching event occurs in a subtree of degree  $r$  can be calculated by realizing that this subtree has  $r$  terminal and  $(r - 1)$  intermediate segments

$$P(r\text{-subtree}) = rp_{ts} + (r - 1)p_{is} = \frac{r + (r - 1)R}{n + (n - 1)R} = \frac{r - Q}{n - Q} \quad (7)$$

if  $Q$  denotes the ratio  $R/(R + 1)$  and is defined on the interval  $[0, 1]$ . In a tree of degree  $n$  with first-order subtrees of degree  $r$  and  $s$  ( $n = r + s$ ), the subtrees have probabilities  $(r - Q)/(n - Q)$  and  $(s - Q)/(n - Q)$  to branch somewhere, respectively. The branching probability of the root segment is equal to  $p_{is}$  which can be written as  $p_{is} = Q/(n - Q)$  [cf. equation (6)]. To apply this model to the schemes of Figs 1 and 2 we can interpret the subtree branching probabilities as the unit-step probabilities. To determine the jump probabilities we have to consider the 2-D description in the schemes of Figs 1 and 2. Our model is defined without specification on which side of a segment new branches are formed but for the 2-D description we have to specify it. Let us assume that there is no preference for one of the two sides. Jumps from a point on diagonal  $n$  to the extreme points of diagonal  $(n + 1)$  both have probability  $p_{is}/2$ , which is equal to  $Q/2(n - Q)$ . For the substitution in equations (2) and (3) we have

$$\begin{aligned}
 p(x \mid x_i^j, y_i^j) &= \frac{x_i^j - Q}{i - Q}, & p(y \mid x_i^j, y_i^j) &= \frac{y_i^j - Q}{i - Q}, \\
 e(x, 1) &= Q/2(x - Q) & \text{and} & & e(1, y) &= Q/2(y - Q).
 \end{aligned}
 \tag{8}$$

All three terms in equation (3) contain sums of path probabilities. Let us first evaluate the probability of a path  $j$  from  $(a, b)$  to  $(r, s)$ ,  $P^j(a, b : r, s)$ . The quantity  $z_i^j$  in equation (2) denotes a step in the  $x$ - or  $y$ -direction and we can write for equation (2)

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} \{P(x \mid x_i^j, y_i^j) \cdot \delta(x, z_i^j) + P(y \mid x_i^j, y_i^j) \cdot \delta(y, z_i^j)\}. \tag{9}$$

In this equation we have used the Kronecker delta symbol  $\delta_{kl}$  in a non-standard notation  $\delta(k, l)$  with

$$\delta(k, l) = \begin{cases} 1 & \text{if } k = l \\ 0 & \text{if } k \neq l. \end{cases} \tag{10}$$

By substituting the model probabilities of equation (8) in equation (9) we get

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} \left\{ \left( \frac{x_i^j - Q}{i - Q} \right) \cdot \delta(x, z_i^j) + \left( \frac{y_i^j - Q}{i - Q} \right) \cdot \delta(y, z_i^j) \right\}. \tag{11}$$

Because we have either an  $x$ -step  $\{\delta(x, z_i^j) = 1$  and  $\delta(y, z_i^j) = 0\}$  or a  $y$ -step  $\{\delta(x, z_i^j) = 0$  and  $\delta(y, z_i^j) = 1\}$ , the denominator in each term of the product has a value depending only on  $i$  such that we can write

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} \frac{(x_i^j - Q) \cdot \delta(x, z_i^j) + (y_i^j - Q) \cdot \delta(y, z_i^j)}{(i - Q)} \tag{12}$$

or

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} \frac{1}{i - Q} \cdot \prod_{i=a+b}^{r+s-1} \{(x_i^j - Q) \cdot \delta(x, z_i^j) + (y_i^j - Q) \cdot \delta(y, z_i^j)\}. \tag{13}$$

We can separate steps in  $x$ - or  $y$ -direction in the product series as follows

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} \frac{1}{i - Q} \tag{14}$$

$$\times \prod_{i=a+b}^{r+s-1} \{1 + (x_i^j - Q - 1) \cdot \delta(x, z_i^j)\} \cdot \prod_{i=a+b}^{r+s-1} \{1 + (y_i^j - Q - 1) \cdot \delta(y, z_i^j)\}.$$

For instance, the product over the  $x$ -steps is actually a product of terms  $(x_i^j - Q)$  where  $x_i^j$  takes all values between  $a$  and  $(r - 1)$  such that we have

$$\prod_{i=a+b}^{r+s-1} \{1 + (x_i^j - Q - 1) \cdot \delta(x, z_i^j)\} = \prod_{i=a}^{r-1} (i - Q). \quad (15)$$

Equation (14) now results in

$$P^j(a, b : r, s) = \prod_{i=a+b}^{r+s-1} \frac{1}{i - Q} \cdot \prod_{i=a}^{r-1} (i - Q) \cdot \prod_{i=b}^{s-1} (i - Q). \quad (16)$$

It appears from equation (16) that all path probabilities are independent of the particular path  $j$ , but depend only on the beginning and the end-point. Thus

$$P(a, b : r, s) = P(1, 1 : r, s) / P(1, 1 : a, b) \quad (17)$$

while

$$P(1, 1 : r, s) = \prod_{i=2}^{r+s-1} \frac{1}{(i - Q)} \cdot \prod_{i=1}^{r-1} (i - Q) \cdot \prod_{i=1}^{s-1} (i - Q). \quad (18)$$

Further we have

$$P(1, 1 : 1, s) = (1 - Q) / (s - Q)$$

and

$$P(1, 1 : r, 1) = (1 - Q) / (r - Q) \quad (19)$$

and with equation (17) we get

$$P(1, b : r, s) = \frac{P(1, 1 : r, s)}{P(1, 1 : 1, b)} = \frac{b - Q}{1 - Q} P(1, 1 : r, s) \quad (20)$$

and

$$P(a, 1 : r, s) = \frac{P(1, 1 : r, s)}{P(1, 1 : a, 1)} = \frac{a - Q}{1 - Q} P(1, 1 : r, s).$$

The path probabilities of equations (19) and (20) can be substituted immediately into equation (3) and the summation over the number of different paths is easy to perform as they are independent of  $j$ .

$$\begin{aligned} *p(r, s ; Q) &= P(1, 1 : r, s) \cdot \left\{ N(1, 1 : r, s) \right. \\ &\quad \left. + \sum_{x=2}^r e(x, 1) \cdot N(x, 1 : r, s) \cdot \frac{x - Q}{1 - Q} + \sum_{y=2}^s e(1, y) \cdot N(1, y : r, s) \cdot \frac{y - Q}{1 - Q} \right\}. \end{aligned} \quad (21)$$

The number of different paths is given by equation (1) while  $e(x, 1)$  and  $e(1, y)$  can be substituted by means of equation (8) resulting in

$$*p(r, s; Q) = P(1, 1 : r, s) \times \left\{ \binom{n-2}{r-1} + \frac{Q}{2(1-Q)} \cdot \sum_{x=2}^r \binom{n-1-x}{s-1} + \frac{Q}{2(1-Q)} \cdot \sum_{y=2}^s \binom{n-1-y}{r-1} \right\}. \tag{22}$$

The sum over the combinatorial coefficients can be given explicitly according to Feller (1970)

$$*p(r, s; Q) = P(1, 1 : r, s) \cdot \left\{ \binom{n-2}{r-1} + \frac{Q}{2(1-Q)} \cdot \left[ \binom{n-2}{r} + \binom{n-2}{s} \right] \right\} \tag{23}$$

and finally after rearrangement of terms we get

$$*p(r, s; Q) = P(1, 1 : r, s) \cdot \binom{n-2}{r-1} \cdot \left\{ 1 + \frac{Q}{1-Q} \cdot \left[ \frac{n(n-1)}{2rs} - 1 \right] \right\}. \tag{24}$$

*4. Partition Probabilities in 3-D.* For the transition to a description in 3-D we simply ignore the distinction between ‘left’ and ‘right’ branches. The partition probability  $p(r, s; Q)$  with  $r \leq s$  is then the sum of  $*p(r, s; Q)$  and  $*p(s, r; Q)$ . Equation (24) shows that in 2-D the variables  $r$  and  $s$  occur symmetrically and thus  $*p(r, s; Q) = *p(s, r; Q)$ . In conclusion we can write

$$p(r, s; Q) = *p(r, s; Q) \cdot 2^{1-\delta(r, s)} \quad \text{for } r \leq s. \tag{25}$$

The Kronecker delta is used as there is only one term if  $r = s$ . Finally we have for the 3-D partition probability

$$p(r, s; Q) = P(1, 1 : r, s) \cdot \binom{n-2}{r-1} \cdot \left\{ 1 + \frac{Q}{1-Q} \cdot \left[ \frac{n(n-1)}{2rs} - 1 \right] \right\} \cdot 2^{1-\delta(r, s)} \tag{26}$$

while  $n = r + s$ ,  $r \leq s$  and  $P(1, 1 : r, s)$  given by equation (18).

Substitution of equation (18) into equation (26) and rewriting the factorials results in

$$p(r, n-r; Q) = 2^{1-\delta(r, n-r)} \times \left\{ 1 + Q \left( \frac{n(n-1)}{2r(n-r)} - 2 \right) \right\} \cdot \frac{1}{n-1-Q} \cdot \prod_{i=1}^{r-1} \frac{1-Q/i}{1-Q/(i+n-r-1)}. \quad (27)$$

Equation (26) is derived under the condition  $r > 1$  and  $s > 1$ . The calculation of  $p(1, n-1; Q)$  proceeds in the same, but considerably simplified way. Equation (26) appears to be also valid for  $r = 1$  and results in the strikingly simple expression for the partition probability  $p(1, n-1; Q)$

$$p(1, n-1; Q) = \frac{2 + Q(n-4)}{n-1-Q} \quad (28)$$

with the additional property

$$\lim_{n \rightarrow \infty} p(1, n-1; Q) = Q.$$

The asymptotic behavior of the  $(r, n-r)$  partition probability can be derived from equation (27) and results for finite values of  $r$  in

$$\lim_{n \rightarrow \infty} p(r, n-r; Q) = \frac{Q}{r!} \prod_{i=1}^{r-1} (i-Q). \quad (29)$$

In Fig. 3 the cumulative probabilities are displayed for the partitions of degree 10 against parameter  $Q$ . The asymptotic behavior of the  $(1, n-1)$  partition probability for large values of  $n$  is clearly shown in Fig. 4, where several curves are plotted for  $Q = 0.2$  and  $Q = 0.5$ . In the limit for  $Q \rightarrow 1$  ( $R \rightarrow \infty$ ), only intermediate segments are allowed to branch and the partition probabilities converge asymptotically to

$$p(1, n-1; 1) = 1$$

according to equation (28) while

$$p(r, n-r; 1) = 0 \quad \text{if } r \neq 1$$

which can be derived from equation (27). Due to the first term of the product ( $i = 1$ ) these partition probabilities are all zero.

In a previous paper (Van Pelt and Verwer, 1983) the partition probabilities have been calculated for the terminal and segmental growth model. It is easily verified that, if  $Q = 0$  ( $R = 0$ ) for the terminal growth model, equation (26) also results in

$$p(r, n-r; 0) = \frac{1}{n-1} \cdot 2^{1-\delta(r, n-r)} \quad (31)$$

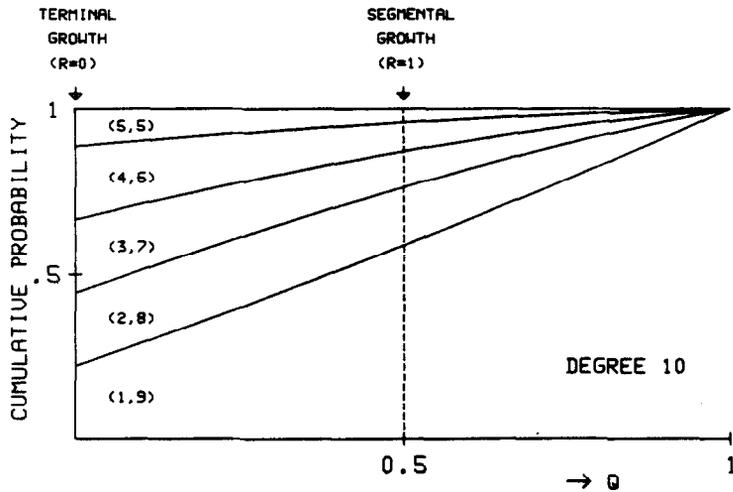


Figure 3. Partition probabilities for trees of degree 10 vs parameter  $Q$ . The curves are plotted cumulatively, i.e. the difference between two curves is the contribution of the indicated partition. The probabilities at  $Q = 0$  and  $Q = 0.5$  correspond to the terminal and the segmental growth model, respectively.

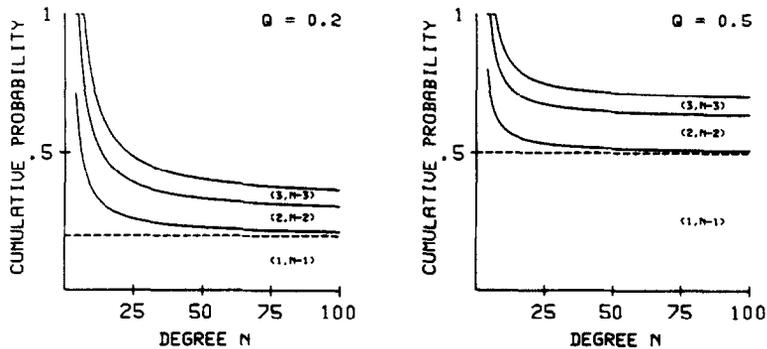


Figure 4. Partition probabilities plotted against the degree  $n$  for the parameter values  $Q = 0.2$  and  $Q = 0.5$ . The curves are plotted cumulatively, i.e. the difference between two curves is the contribution of the indicated partition. Only the first three partition curves are plotted. Note that for instance the area of partition  $(3, n - 3)$  starts at degree  $n = 6$ . The asymptotic value of the  $(1, n - 1)$  partition probability for large  $n$  is equal to the parameter value  $Q$  and is clearly shown in both figures.

and, if  $Q = 1/2$  ( $R = 1$ ) for the segmental growth model, in

$$p(r, n-r; 0.5) = \frac{N_r^r \cdot N_r^{n-r}}{N_r^n} \cdot 2^{1-\delta(r, n-r)}$$

if (32)

$$N_r^n = \binom{2n-1}{n} \cdot \frac{1}{2n-1}.$$

Note for this verification that  $\prod_{i=1}^n (i - 0.5)$  can be written as

$$\prod_{i=1}^n (i - 0.5) = \frac{2n!}{2^{2n} \cdot n!}.$$
(33)

*5. Ambilateral Type Probabilities.* The probability of occurrence of a particular tree of degree  $n$  within the set of  $n$ th-degree trees can easily be calculated from the partition probabilities. A tree will be characterized by its ambilateral type  $\alpha_i^n$  indicating the degree  $n$  ( $n$  terminal segments) and the rank number  $i$  within the set of  $n$ th-degree trees. In a slightly different notation, Van Pelt and Verwer (1983) have expressed the probability of a tree type  $\alpha_i^n$  into the probabilities of its two first-order subtrees  $\alpha_j^r$  and  $\alpha_k^s$  as

$$P(\alpha_i^n; Q) = p(r, s; Q) \cdot P(\alpha_j^r, \alpha_k^s; Q) \quad \text{for } n = r + s, \quad (34)$$

by separating the partition probability  $p(r, s; Q)$  from the probability of the joint occurrence of both first-order subtrees conditioned on the degrees  $P(\alpha_j^r, \alpha_k^s; Q)$ . This joint occurrence probability could further be expressed as

$$P(\alpha_j^r, \alpha_k^s; Q) = 2^{\delta(r, s)} \cdot 2^{-\delta(r, s) \cdot \delta(j, k)} \cdot P(\alpha_j^r; Q) \cdot P(\alpha_k^s; Q). \quad (35)$$

Here,  $\delta(r, s) = 1$  if both subtrees are of equal degree and  $\delta(r, s) \cdot \delta(j, k) = 1$  if in addition both subtrees are of the same ambilateral type. All ambilateral types of equal degree constitute an ambilateral set. Pairing trees from different sets results in unique combinations. However, if trees from the same set are paired, then all combinations occur twice except combinations of identical trees (of equal type). For instance, pairing trees from the set  $\{\alpha, \beta, \gamma\}$  results in the combinations  $\alpha\alpha, \beta\beta, \gamma\gamma, 2 \times \alpha\beta, 2 \times \alpha\gamma$  and  $2 \times \beta\gamma$ . The subtrees in their turn can be expressed again in terms of probabilities of their subtrees. Finally, the probability of a tree is expressed in a product of partitions and factors which correct for subtree pairs of equal degree and of unequal type. This will be illustrated in the following examples. Take a tree with branching code 8(3 5(1 4(1 3))). A decomposition results in the partitions (3, 5), (1, 4) and (1, 3). The probabilities of these partitions for

$Q = 0.2$  are  $p(3, 5) = 0.2221$ ,  $p(1, 4) = 0.5790$  and  $p(1, 3) = 0.7143$ . The probability of the complete tree is equal to the product of all its partitions and thus equal to  $p(\text{tree}, Q = 0.2) = 0.0919$ . No correction factors are needed as there are no equal-degree, unequal-type pairs. The probability of the tree  $16(8(4(1\ 3)4(2\ 2))\ 8(4(1\ 3)4(1\ 3)))$ , however, is equal to  $p(8, 8) \cdot p(4, 4) \cdot p(1, 3) \cdot p(2, 2) \cdot p(4, 4) \cdot p(1, 3) \cdot p(1, 3) \cdot 2 \cdot 2$ . The correction factor 4 accounts for the two partitions of equal degree and unequal type, viz.  $4(1\ 3)4(2\ 2)$  and  $8(4(1\ 3)4(2\ 2))8(4(1\ 3)4(1\ 3))$ .

6. *Discussion.* In this paper a mathematical description of a one-parameter growth model is given for binary topological trees. This model is a generalization of the terminal and segmental growth model. It maintains the distinction between intermediate and terminal segments but allows for variation of the branching-probability ratio for both types of segments. In addition, the model defines equal branching probabilities for segments of equal type. Within this model, we have derived closed expressions for the partition probabilities, i.e. the probabilities of occurrence of pairs of subtrees of particular degrees. The probability of occurrence of a tree of particular degree within the set of trees of the same degree is equal to the product of the probabilities of all the partitions in the tree, corrected for equal-degree, unequal-type subtree pairs. This parameterized growth model offers the possibility to test the partition frequencies in a set of experimentally observed trees against a wider range of growth models than is used in the literature on tree analysis, viz. terminal and segmental growth model. Conversely, it enables the search of that value of the parameter  $Q$ , for which the model optimally predicts the experimentally observed frequencies of partitions or ambilateral types.

Equation (30) shows that for  $Q = 1$  only partitions occur of the type  $(1, n - 1)$ , i.e. the tree is most asymmetrical if asymmetry is interpreted in terms of the difference in degree between both subtrees in a partition. This property is also shown in Fig. 3. From this notion of asymmetry the most symmetrical tree would only consist of partitions in subtrees of equal degrees. From Fig. 3 it can already be concluded that for the range  $0 \leq Q \leq 1$  the least asymmetrical trees have highest probability at  $Q = 0$  (terminal growth). For this value of  $Q$ , the  $(n/2, n/2)$  partition occurs with half the probability of each other partition.

The probabilities of occurrence of channel networks as calculated by Dacey and Krumbein (1976) by enumerating only small networks (up to degree 6) are readily obtained from the present equations. Model C in their paper then corresponds to a branching-probability ratio of intermediate and terminal segments of  $R = 2$  ( $Q = 2/3$ ). However, our results enable calculations up to any degree and any value of  $Q$ .

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## LITERATURE

- Berry, M., P. McConnell and J. Sievers. 1980. "Dendritic Growth and the Control of Neuronal Form." In *Current Topics in Developmental Biology*, Ed. R. K. Hunt, Vol. 15, pp. 67-101. New York: Academic Press.
- Dacey, M. F. and W. C. Krumbein. 1976. "Three Growth Models for Stream Channel Networks." *J. Geol.* **84**, 153-163.
- Feller, W. 1970. *An Introduction to Probability Theory and its Applications*, Vol. 1. New York: J. Wiley.
- McConnell, P. and M. Berry. 1978. "The Effects of Undernutrition on Purkinje Cell Dendritic Growth in the Rat." *J. comp. Neurol.* **177**, 159-172.
- and —. 1979. "The Effects of Postnatal Lead Exposure on Purkinje Cell Dendritic Development in the Rat." *Neuropathol. appl. Neurobiol.* **5**, 115-132.
- Meininger, V. and M. Baudrimont. 1981. "Postnatal Modifications of the Dendritic Tree of Cells in the Inferior Colliculus of the Cat. A Quantitative Golgi Analysis." *J. comp. Neurol.* **200**, 339-355.
- Sadler, M. and M. Berry. 1983. "Morphometric Study of the Development of Purkinje Cell Dendritic Trees in the Mouse Using Vertex Analysis." *J. Microsc.* **131**, 341-354.
- Uylings, H. B. M., R. W. H. Verwer, J. Van Pelt and J. G. Parnavelas. 1983. "Topological Analysis of Dendritic Growth at Various Stages of Cerebral Development." *Acta stereol.* **2**, 55-62.
- Van Pelt, J. and R. W. H. Verwer. 1983. "The Exact Probabilities of Branching Patterns Under Terminal and Segmental Growth Hypotheses." *Bull. math. Biol.* **45**, 269-285.
- and —. 1984. "New Classification Methods of Branching Patterns." *J. Microsc.* **136**, 23-34.
- Verwer, R. W. H. and J. Van Pelt. 1983. "A New Method for the Topological Analysis of Neuronal Tree Structures." *J. Neurosci. Meth.* **8**, 335-351.

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