

Proximal root diameter as predictor of total root size for fractal branching models

II. Numerical model

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Abstract

If root systems have scale-independent branching rules, the total number of links in the root system can be predicted from the ratio of the largest and smallest root diameter. In Paper I we presented an algebraic model for a dichotomous pattern (the simplest form of proportionate branching forming two equal branches at each node) and a herringbone branching model (the simplest form of determinate branching rules). Here, we present a recursive computer model and its results to analyze intermediate patterns, derived from allotomous proportionate branching (with unequal branches). The numerical and algebraic model gave the same results when applied to the same situation and parameter values.

For practical applications of the relations found, a test is required on whether or not the underlying assumptions are met. To illustrate such a test, measurements of the branching pattern were made on Mondriaan's Red Tree painting. For patterns such as this tree a slight dependency of the proportionality factor on root diameter and random variability of several parameters may have to be included.

Introduction

In a fractal branching pattern the same rules govern branching at each subsequent level. The initial size (diameter) and the essential branching rules thus contain the information required to construct the whole pattern. If root branching patterns have fractal characteristics, measurement of the proximal root diameter at the stem base and the branching rules as observed anywhere in the root system, would be enough to predict total root length, root diameter distribution and root length per unit dry weight (specific root length).

An algebraic model was presented by Van Noordwijk et al. (1994) (Paper I) to derive the relation between total root system size and proximal root diameter for two extreme branching patterns: a dichotomous and a herringbone pattern, representing proportion-

ate and determinate branching patterns, respectively. The equations show that, to predict total root length from the proximal root diameter, at least information is needed on the minimum root diameter, the link ("internode") lengths as a function of root diameter and the proportionality factor between total cross sectional surface areas before and after branching. If this proportionality factor α differs from 1, the branching pattern (topology) affects the relation between total root length and proximal root diameter. Regardless of the value of α , further information on the branching pattern is needed to relate the proximal root diameter to the length of the longest root or the specific root length, as it is highest for determinate and proportionate branching rules, respectively. No general algebraic solution was formulated for intermediate cases, such

as allotomous proportionate branching with unequal branches.

A numerical model is presented here for various branching classes, including allotomous proportionate patterns. The model was used to investigate the shape of such branching systems and the relation between proximal root diameter, the number of links, diameter distribution and the diameter of root tips. Results will also be presented for the length of the longest root and for the specific root length (length per unit dry weight) and related parameters. Finally, a comparison will be made with the altitude and magnitude parameters, as defined by Fitter and Stickland (1991, 1992).

For practical applications of the fractal models we have to test whether two basic assumptions are met:

- 1) A test whether the decrease in root diameter in a branched root system can indeed be described with a constant proportionality factor α . The parameter α should be estimated at various levels of the branching pattern as the ratio of the squared root diameters before (1 axis) and after (sum of at least 2 axes) branching. Regression analysis of α on the main root diameter can show whether or not a single value for α can be used and if so, which.
- 2) For α of approximately 1.0 we need only the proximal root diameter D_0 , the minimum root diameter in the system D_m (or the average diameter of root tips) and the average link length; if link length is a function of branching order (or root diameter) a weighted average should be made,
- 3) For α differing from 1.0 we need other descriptors of branching, especially the allocation parameter q which can be estimated from the diameter ratio of main and branch roots at each branching point, or from the length of bare root tips (external links) relative to internal links. An example of a test of these assumptions for branched systems will be presented.

Methods

Numerical model

For different root branching patterns, total root length and other, corresponding parameter values were calculated, by the use of a recursive computer program (see appendix). Calculations were based on equation (1) in Van Noordwijk et al. (1994) (paper I). The notation is explained in paper I. In addition the following abbreviations are used: A_{rw} = specific root surface area (root

area per unit root dry weight), D'_m = actual mean diameter of external links (terminal root sections with a root tips), SSRRD = sum of square roots of root diameters times length.

If $D_0, D_{11}, D_{12} \dots D_{1k}$ indicate the diameter of a single root before and of k branch roots after the first branching, respectively, the fractal branching model is based on:

$$\frac{\pi D_0^2}{4} = \frac{\alpha \pi}{4} \sum_{i=1}^k D_{1i}^2$$

In a "true pipestem" model $\alpha = 1.0$. Root branching can proceed until a certain, chosen minimum value of the root diameter, D_m , has been reached.

For herringbone branching (H) only the case where branch roots had a diameter D_m was considered. For dichotomous branching (D), situations with $D_{11} = D_{12}$ were considered, as well as situations with unequal partitioning (allotomy): $D_{12} = q D_{11}$, with $q = 2, 3$ or 4 (corresponding with angles β of $63.4, 71.6$ and 75.96° , respectively). Various values of the proportionality factor α , were used for dichotomous branching ($0.8 < \alpha < 2.0$).

For each branching pattern the number of links (theoretical and observable, Van Noordwijk et al., 1994, Paper 1) was determined. On the assumption that internal and external link lengths are equal and independent of diameter, the number of links is directly related to total root length (ΣL_i). The length of the longest root was determined for each branching pattern, as well as root surface area ($\pi \Sigma L_i D_i$), root volume ($\pi \Sigma L_i D_i^2$) and SSRRD "sum of square roots of root diameter" ($\Sigma(L_i D_i^{0.5})$). This SSRRD was included as effective diffusive transport to two root systems of different root diameter is approximately the same if their SSRRD (rather than their length or surface area) are equal (De Willigen and Van Noordwijk, 1987; Van Noordwijk and Brouwer, 1994). From these primary parameters the specific root length (L_{rw} = length per unit dry weight) and specific root surface area (A_{rw} = surface area per unit dry weight) were derived. Dry weight was taken as $0.1 \times$ volume.

Practical test of model assumptions

To demonstrate a practical method for testing some of the important model assumptions, an analysis was made of a reproduction of Piet Mondriaan's famous "Red Tree". For all the large diameter branchings and a selection of the small diameter ones, the diameters and link lengths were recorded, as would be done for

a real life aboveground tree or root system. For each branching we then calculated the apparent α .

Results

Root branching pattern

Root branching patterns derived by repeated application of the diameter² rule (equation 1, appendix 1) for herringbone-as well as proportionate branching with proximal diameters 4 and 8 are shown in Figure 1. Division characteristics are shown in this figure, but not the root diameters. With herringbone branching an oblong pattern occurs which may be effective in exploration of large volumes of soil, whereas with dichotomous branching the local root length density is much higher, which may lead to more intensive exploitation of a soil volume. Allotomous proportionate branching initially forms a main axis (a herringbone characteristic) and, with increase in proximal diameter side branches of increasing order (a dichotomous characteristic). The allotomous proportionate branching patterns thus are intermediate between herringbone and dichotomous branching. The longest root axes occur with the most unequal proportionate branching ($D_{i1} : D_{i2} = 1:4$). This is due to the formation of links with relatively large diameters at each (theoretical or observable) branching point. Therefore, link formation can progress longer to form longer axes. Meanwhile, fewer side axes are formed, as their diameter falls below the minimum diameter at a larger diameter of the main axis than in the dichotomous case, where always two links are formed at a branching point. The branching pattern of the main axis is repeated in the side axes, as is characteristic for fractal structures.

Number of links

Results of the recursive model (Fig. 2) agree with those for the algebraic solution (Fig. 4 in Van Noordwijk et al., 1994, Paper 1) for herringbone (H) and dichotomous (D) branching patterns, at the same parameter values. Figure 2 shows results for $\alpha = 1$. Figure 3 includes other values of α .

The algebraic solution suggested a continuous increase of number of links with increasing proximal root diameter D_0 ; in practice, however, the increase is discrete (step wise) (Fig. 2 and 3). This effect is strongest for a syntomous branching pattern because of the formation of equal branches at all root ends once the

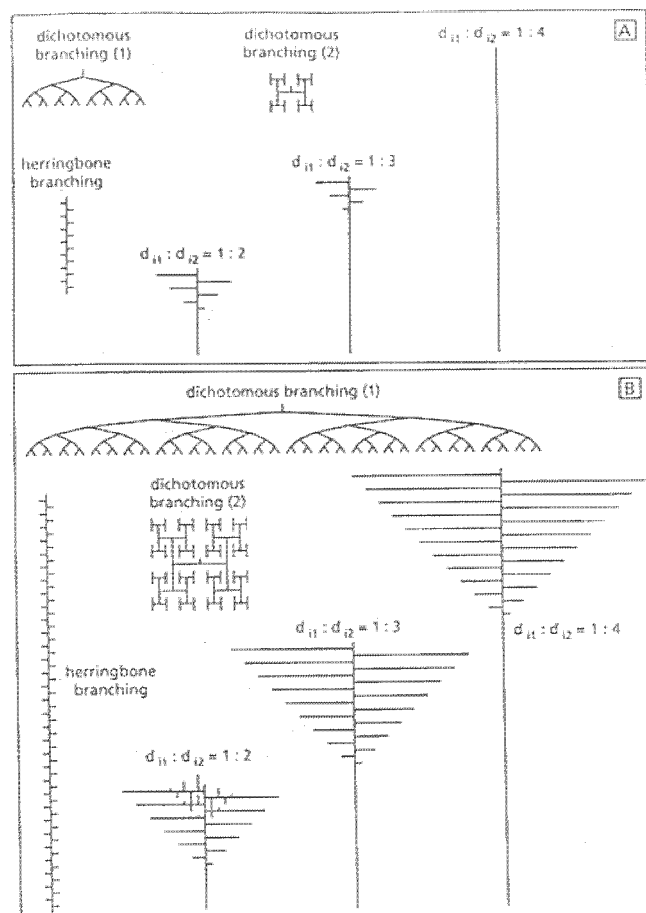


Fig. 1. Theoretical root patterns for herringbone branching and proportionate branching, derived from the (diameter)² rule. A) Proximal diameter = 4 and B) Proximal diameter = 8. Diameter values decline from the root basis towards the minimum value ($D_m = 1$), at each (branch) root tip (not shown in the figures). In the drawings, the longest axis of a 'root' pattern was placed vertically and the side branches perpendicular to them. Patterns are on scale of notation ($L_i = 1$), except for the third order branches of $D_{i1} : D_{i2} = 1 : 2$ in B, which are represented shorter for reasons of graphical representation. Proportionality factor $\alpha = 1$.

threshold value of D_m is reached for the branch roots. In a dichotomous pattern, the total number of links doubles for each increment of the proximal diameter by $2 \alpha D_m$. In allotomous proportionate branching patterns, links of different diameter are formed and this increases the possibility of link formation with increase of proximal root diameter; the increments in number of links are thus more gradual.

In Figure 2A the actual mean diameter of root tips, D'_m , was used for scaling the X-axis rather than the nominal minimum root diameter (D'_m , Fig. 2E). In fact, D'_m should be preferred as it is directly observable in real root systems, in contrast to D_m . The shift from D_m to D'_m reduced the distance between the lines

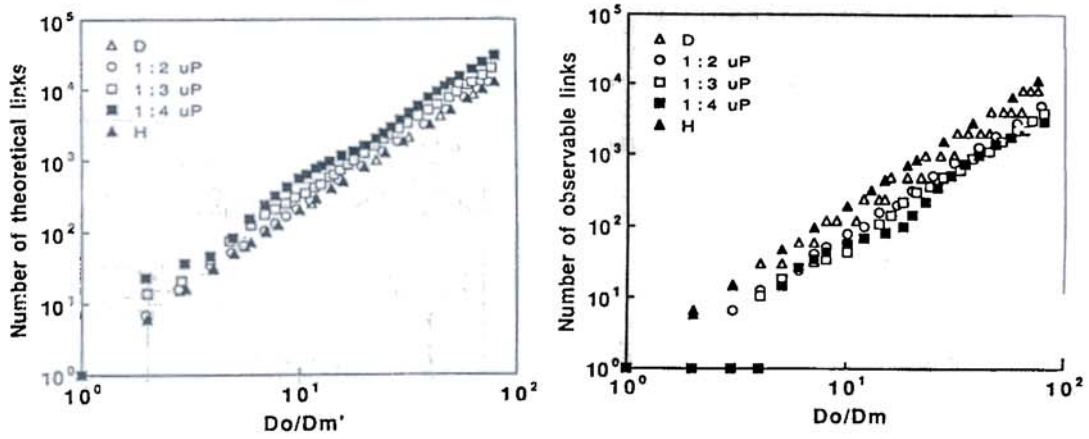


Fig. 2. Number of theoretical links (equivalent of total root length for $L_i = 1$) as a function of the proximal root diameter D_0 , for various branching patterns with $\alpha = 1.0$, calculated with the recursive model. D = dichotomous branching; uP = allotomous (= unequal) proportionate branching, with $D_{i1} : D_{i2} = 1 : 2, 1 : 3$ and $1 : 4$, respectively; H = herringbone pattern. In A. the actual mean value of the root tip diameters D'_m was used for scaling the x-axis; in B. the nominal minimum diameter D_m was used.

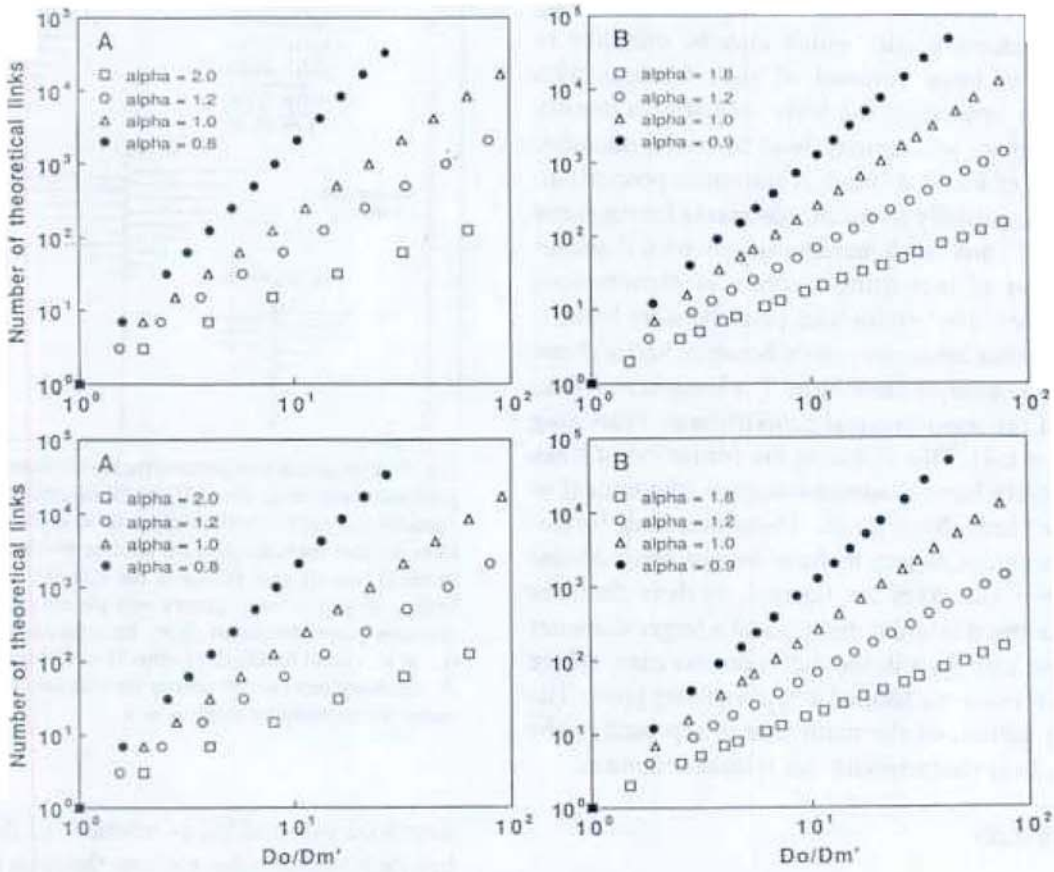


Fig. 3. Number of theoretical links as a function of proximal root diameter for different values of the proportionality factor α . A) Dichotomous branching, $D_{i1} : D_{i2} = 1 : 1$; B), C) and D) allotomous proportionate branching, with $D_{i1} : D_{i2} = 1 : 2, 1 : 3, 1 : 4$, respectively; the actual mean value of the root end diameters, D'_m , was used to scale the X-axis.

for different branching patterns and shifted all lines to the left, because D'_m can be larger than D_m . In Figure 2A the lines for herringbone and dichotomous

patterns are on the left (higher number of theoretical links at same D_0) of those for allotomous branching patterns; in Figure 2B they are found on the right hand

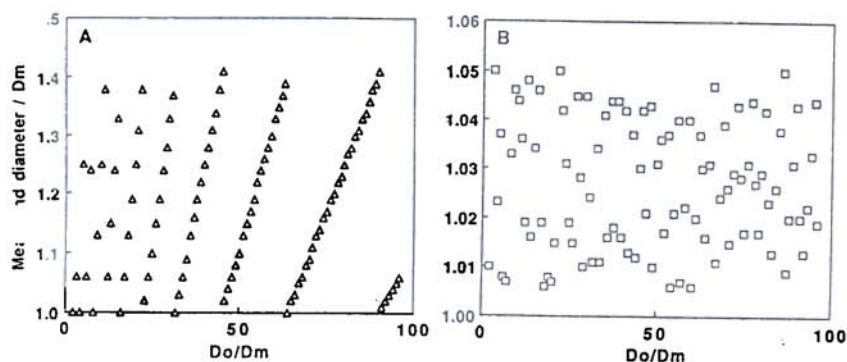


Fig. 4. Mean value of the actual root tip diameters as a function of proximal diameter. A) Purely dichotomous branching, B) Allotomous proportionate branching, $D_{11} : D_{12} = 1 : 3$. Proportionality factor $\alpha = 1$.

Side. This shift in relative position is caused by the larger difference between D'_m and D_m for syntomous branching patterns (see next section). As Y-axis we chose for presenting the number of “theoretical” rather than “observable” links (compare paper I). In combination with the assumption of constant link length, the use of “theoretical” links may lead to a larger “observable” link length for external links in allotomous patterns. For the herringbone and the dico-syntomous pattern the number of observable and theoretical links are equal.

The total number of links (reflecting total root length) strongly decreases with increase in α , at given proximal root diameter D_0 in all proportionate branching patterns (Fig. 3). With further decrease in α a value will be reached where one of the branch roots is larger than the main root before branching, and the branching will continue without bounds (compare the algebraic restrictions on α given in paper I). With increasing inequality of the branches, the effects of a change in α become more dramatic. In Figure 3 C and D a “wave-like” increment in the number of theoretical links is apparent for allotomous branching patterns, especially for low values of α .

Root tip diameters

With increasing proximal root diameter, the mean diameter of root tips increases until a new branch can be formed and the mean end diameter is decreased. With a dico-syntomous branching pattern, the mean root tip diameter is exactly D_m when a new branching level is reached and a saw-tooth pattern is obtained (Fig. 4A; note that the X-axis is linear, rather than logarithmic as in Figs. 2 and 3). In Figure 4A the Y axis covers the range 1–1.42 ($2^{0.5}$); in Figure 4B no values above 1.05 were found. In the dico-syntomous pattern

a doubling of the proximal root diameter is needed for each new branching order, the width of the saw teeth is increasing by a factor 2 for each step.

With allotomous proportionate branching (Fig. 4B), a rather chaotic picture emerges, as new opportunities for branching arise more gradually when the proximal root diameter increases and links with different diameters are formed at each branching step. Only in exceptional cases will the mean root tip diameter be equal to the nominal D_m value (if this occurs at all).

Length of longest root (altitude)

Figure 5 shows the length of the longest chain of theoretical links in each branching pattern (altitude), as a function of proximal root diameter, which may be interpreted as the length of the longest root. For the herringbone pattern, the length of the longest root increases linearly with increasing squared proximal root diameter (compare equation 30 in Van Noordwijk et al., 1994; Paper I; the slope of the log-log plot in Fig. 5 is 2). For the dico-syntomous pattern the length of the longest root increases proportional to the logarithm of the proximal root diameter (compare equation 44 in *idem*).

At small D_0 the allotomous patterns have the greatest length, when theoretical links are supposed to have the same length as observable ones. Curves for allotomous proportionate branching are flattening off to parallel the line for a syntomous pattern at larger proximal root diameters, as soon as side branches are formed. The curves for allotomous proportionate branching intersect the straight line for herringbone branching in Figure 5.

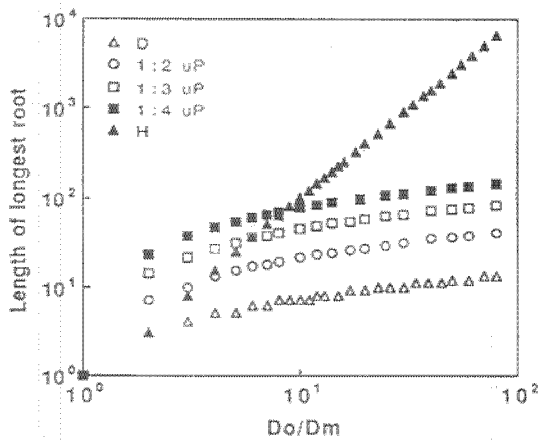


Fig. 5. Length of the longest root (number of theoretical links) within a root branching pattern in dependence on the proximal root diameter, for herringbone branching and proportionate branching. Proportionality factor $\alpha = 1$.

Total root surface area and root volume

Root diameter values are incorporated in calculations of total root surface area and volume (Fig. 6). In both a herringbone and a dichotomous branching pattern, (slightly more than) half of the links are external ones (compare equation 1 in Paper 1) and thus have a diameter close to or equal (just after the step wise increment as shown in Fig. 3) to D_m . In the herringbone pattern the main axis only gradually decreases towards D_m , while in the dichotomous pattern this decrease is rapid. This leads to a larger average diameter for the H pattern, at the same numbers of links as D, and thus to a larger total root surface area and root volume at the same proximal root diameter. Results for the allotomous proportionate branching patterns are intermediate between H and D at larger proximal root diameters, but initially the allotomous proportionate branching leads to larger root area and root volume, at least if the theoretical rather than the observable number of links is used for the calculations.

Specific root length and surface area

In all branching patterns total root volume and thus root weight (taken to be $0.1 \times$ volume) increases faster than total root length with increasing proximal root diameter, as the number of links with large root diameters increases. This means that the specific root length L_{rw} , specific root surface area A_{rw} and SSRRD all decrease with increasing proximal root diameter (Fig. 7) for all branching patterns. The decrease is faster for the H pattern (and approximately linear on a log-log plot)

than for D, as the H pattern has a relatively large total root volume at given proximal root diameter. Results for L_{rw} , A_{rw} and SSRRD for allotomous proportionate branching are very close to the ones for a dichotomous pattern.

Altitude and magnitude

Figure 8 shows the relationship between the number of observable links of the longest root axis (altitude) and the number of growing points of the root system (magnitude). The parameters altitude and magnitude were used here, as defined by Fitter and Stickland (1991, 1992). The deviation from the curve for herringbone branching by the curves for proportionate branching indicates the branching of branch roots. This occurs at larger D_0 for a higher inequality in the branching pattern.

Test of model assumptions

Application of the theoretical results to real root systems, is only possible when the underlying assumptions of the method are (largely) met. Figure 9 shows results of a test on the constancy of α and link length within a branched structure. For this particular example, the α values were found to have an approximately normal distribution within the range 0.69 to 1.20, with an average value of 0.92 and a standard deviation of 0.141. All except one branching displayed were bifurcate ($N_k = 2$), but for the only trifurcated ($N_k = 3$) one the α was not exceptional. The values of α tended to decrease with decreasing diameter, although a linear regression line explained only 28% of the variation. For a more refined modelling of such a tree this dependency may be relevant. The figure also shows that link length is virtually independent of diameter, but that it has a considerable variability, with a coefficient of variability (standard deviation divided by mean) of 0.55.

Discussion

The algebraic model and the recursive computer program gave the same results when used for the same situations and parameter values. The recursive program can be used for exploring more complex patterns, such as the allotomous proportionate branching rules and can in future be used for introducing (random) variability in parameters such as q , α and D_m and/or deviations

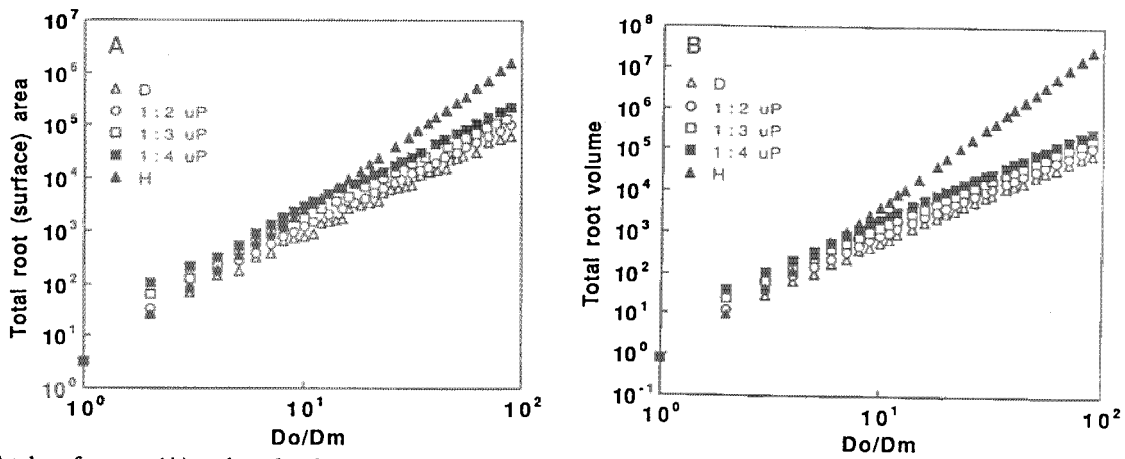


Fig. 6. Total surface area (A) and total volume (B) of herringbone branching and proportionate branching in dependence on the proximal diameter. Proportionality factor $\alpha = 1$.

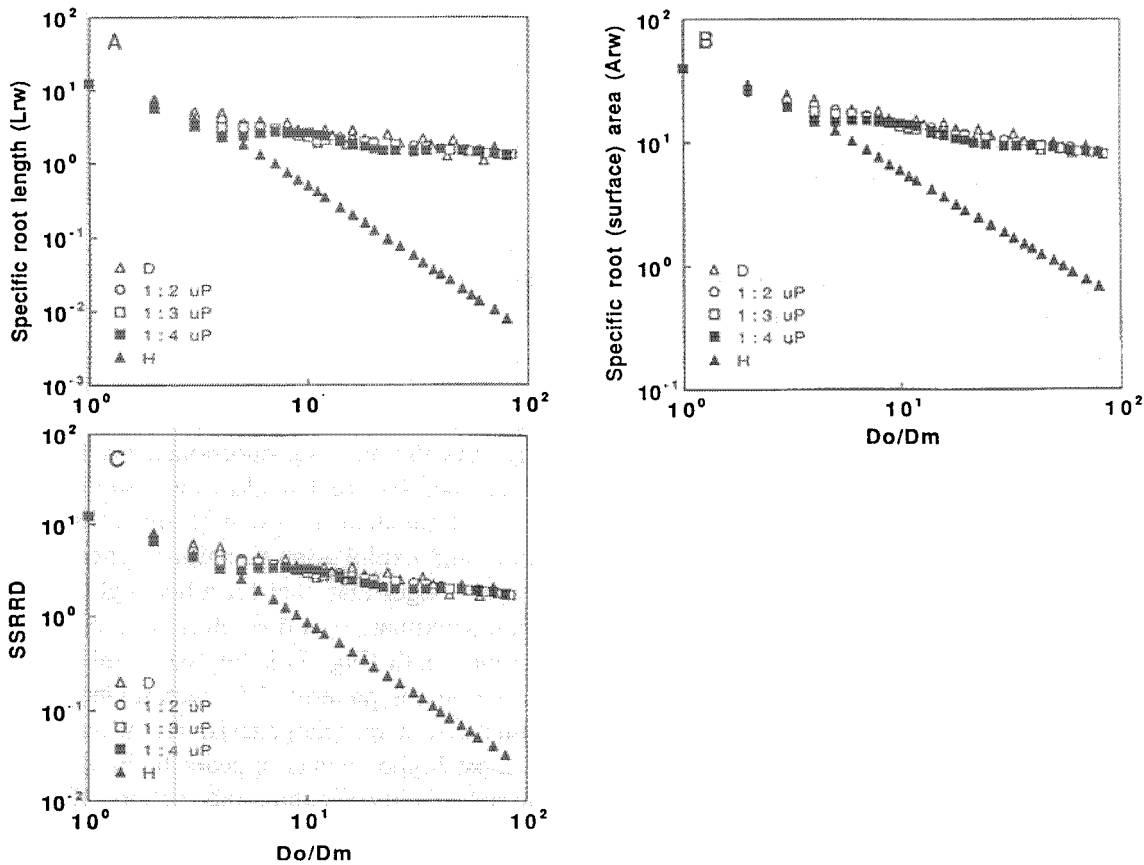


Fig. 7. Specific root length L_{rw} (A), specific root (surface) area A_{rw} (B) and $SSRRD = \sum (L_i \times \text{SQRT}d_{i2}) / (0.1 \times \text{volume})$ (C) in dependence of the proximal diameter, for herringbone branching and proportionate branching. Proportionality factor $\alpha = 1$.

from the scale-independence (e.g. a relation between α and link diameter).

In general, the allotomous proportional branching patterns are intermediate between the dichotomous and herringbone patterns studied algebraically (paper 1) and support the conclusion that the number of links

can be predicted from the proximal root diameter and the mean root tip diameter, provided that α is (approximately) 1.0. Whether or not the total number of observable links is a good estimator of total root length should be checked carefully, however. The allotomous proportionate branching patterns which look like real world

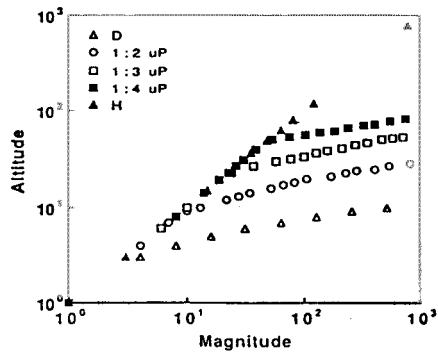


Fig. 8. Relationship between the number of observable links of the longest axis (altitude) and the number of growing points (magnitude), for herringbone branching and proportionate branching patterns.

root systems if the theoretical number of links is equated with root length, point at a probable difference in length between 'external' and 'internal' links.

In descriptive models of a maize root system, Pages and coworkers (Pages and Aries, 1988; Pages and Kervella, 1990) put emphasis on the different branching rules for each order of branching. The degree of geotropism (or the preferred angle of roots) definitely depends on the order of branching, but also parameters such as the length of the bare root tip and the distance between branch roots. As their model systems look realistic for maize, careful checking is needed to which extent fractal models (with scale-invariant rules) can be used for particular plant species. One complication which could be relatively easily incorporated would be to describe link length and α as function of diameter and of 'branching order' (as Pages c.s. do). Further comparison of the two model approaches is needed.

The example with Mondriaan's tree shows that the main underlying assumptions of our models can be tested relatively easily. We have started on applying these tests to real tree root systems. These tests, just like the example given here, show that considerable variability occurs around the average parameter values occur, even when scale independence is confirmed, and that effects of such variability should be studied. The recursive model used here can be adapted to study such effects.

Apart from the possible practical applications, the present study of branching patterns allows some conclusions on the possible plant strategies in root branching patterns. A herringbone pattern has a much longer main root axis than a dichotomous pattern with the same proximal root diameter (Fig. 5); to a lesser degree this advantage is maintained when compared at the

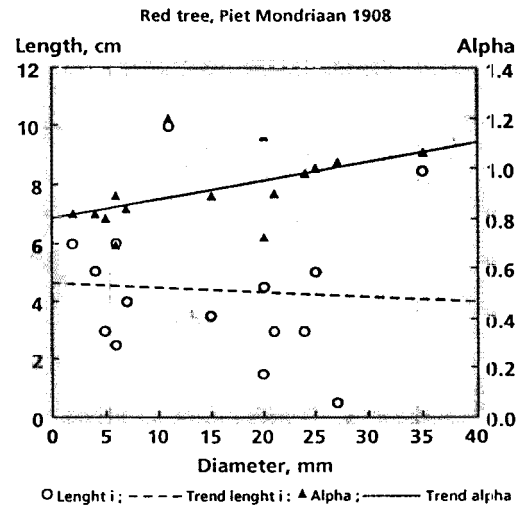


Fig. 9. Example of a test of two underlying assumptions of the fractal model. Relation between branch diameter, link length (circles, left Y axis) and α parameter (triangles, right Y axis) for the 'Red Tree' painted by Piet Mondriaan in 1908 on the basis of an apple tree in Winterswijk, which is on display at the Gemeentemuseum, The Hague, The Netherlands (for copyright reasons the tree cannot be depicted here).

same total root weight) and is the superior pattern if exploration of new soil layers or zones with increasing vertical or horizontal distance to the tree stem is required. When a high uptake efficiency (exploitation) is required, the dichotomous pattern with its relatively high specific root length (L_{rw}) is superior. Interestingly, the allotomous proportionate branching patterns which look like real-world root systems are superior to or intermediate between H and D in both exploration and exploitation functions. Their longest axis is even longer than that for a herringbone pattern for small proximate root diameters (Fig. 5); their specific root length (Fig. 7) is approximately equal to that of symtomous patterns. So, even under rigidly deterministic root morphogenesis, the allotomous pattern of most higher plants appears to be superior to the more "primitive" symtomous pattern. In real world plants, the response of branch root development may actually depend on the local circumstances and the choice between "exploration" and "exploitation" type roots does not only depend on a genetic program. The delayed response of branch root formation from secondary meristems gives the plant more possibilities to react to local soil conditions than possible in a purely dichotomous pattern.

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Appendix: Recursive computer program

Basic form of a Pascal program for root branching according to the diameter² rule. Abbreviations used: d = root diameter, dmin = minimum root diameter, n = counter, ni = the number of 'theoretical' links, a/x and b/x = partition factors, α = proportionality factor.

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program branching (input,output);
var d, dmin, ni: real; i, n: integer;
function branch(d, dmin: real; n: integer): real;
begin
  if d < dmin then branch:=0 else
    for herringbone branching:
      branch:=1+branch(SQRT((d**2)/ $\alpha$ )-(dmin**),dmin,n+1)+:
    for dichotomous branching:
      branch:=1 + branch(SQRT((a/x)*(d**2)/ $\alpha$ ),dmin,n+1)
        +branch(SQRT((b/x)*(d**2)/ $\alpha$ ),dmin,n+1);
end;
begin
  for i:=y to z do
    begin
      d:=0; dmin:=1; n:=0; ni:=branch(d, dmin, n); writeln(ni, i);
    end;
end.

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