Topology, scaling relations and Leonardo's rule in root systems from African tree species

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Summary   Aspects of root architecture, including topology, link length, diameter and scaling relations, were analyzed in excavated coarse root systems of three field-grown fruit tree species (*Strychnos cocculoides* Bak., *Strychnos spinosa* Lam. and *Vangueria infausta* Burch) and the fruit-bearing shrub *Grewia flava* DC. We investigated the root systems using semi-automatic digitizing and computer-based 3-D reconstruction techniques. Topological analysis was carried out to investigate branching patterns as basic determinants of root architecture. New topological indices were developed and revealed significant differences among the species. The different architectural strategies can be explained in terms of cost–benefit relations and efficiency in soil resource exploration and exploitation. In addition, some well-known hypotheses about geometry and scaling, most of them previously unverified by empirical observations on root systems, were tested. For practical applications, the main emphasis is on the relationship between proximal root diameter, an easily determined parameter, and several parameters describing the size of the whole root system. We also tested the "pipe stem" theory, essentially dating back to Leonardo da Vinci, which underlies many models and which we found conformed to our measurement data with reasonable accuracy. A physiological consequence of the "constant cross-sectional area rule" may be a certain homogeneity of hydraulic architecture throughout root systems.

Keywords: architecture, branching pattern, cross-section area, Grewia flava, root diameter, root length, Strychnos cocculoides, Strychnos spinosa, Vangueria infausta.

Introduction

Investigation of tree roots is laborious and time consuming. Root systems of trees have, therefore, been much less frequently studied than aerial parts. In this paper, information about topology and geometrical scaling in coarse roots of fruit tree species native to southern Africa are presented. Root systems of the fruit trees *Strychnos cocculoides* Bak., *Strychnos spinosa* Lam. and *Vangueria infausta* Burch., as well as one shrubby species, *Grewia flava* DC., were investigated. Beside gathering information about these rarely investigated plants, we wanted to develop new techniques of root structural reconstruction and analysis. We also evaluated some well-known hypotheses about topology and scaling that might be of general interest in root system research, but are seldom tested empirically. We place this study in the context of functional and structural modeling of plants (Sievänen et al. 1997, Cruiziat 1998), topological analysis (Fitter et al. 1991, Berntson 1997) and the assessment of strategies for soil exploration and exploitation (Gandar and Hughes 1988, Hughes et al. 1995).

Topology

Topological properties of root systems have received considerable attention in the literature (Fitter 1985, 1986, 1987, Fitter and Stickland 1991, Spek and van Noordwijk 1994, Bert et al. 1998). They are believed to influence the efficiency and costs of resource exploitation in terms of carbon required for root segment construction (Fitter 1986, Fitter et al. 1991). One of the main goals of topological analysis is to find out whether habitat conditions lead to evolutionary adaptations in branching behavior and rooting strategy.

Various theoretical approaches to evaluating topology have been developed (Fitter 1985, 1986, van Noordwijk et al. 1994, Berntson 1997) and have been compared on theoretical grounds (Berntson 1995), but practical applications have, in most cases, been restricted to herbaceous plants (Fitter 1986, Fitter and Stickland 1991). Furthermore, some of the topological indices developed to compare root systems of different sizes show either an unstable oscillating behavior in random simulations (Berntson 1995) or are based on randomness assumptions that were originally developed for planar networks (see Werner and Smart 1973) and are inadequate for 3-D branching systems (Fitter 1986).

One of the most often cited topological distinctions is that between "dichotomous" and "herringbone" branching patterns (Fitter 1986, 1987, Fitter et al. 1991, van Noordwijk et al. 1994, Lynch 1995, Berntson 1997). We introduce two new indices to quantify branching patterns in the continuum between these extremes, and apply them to reveal species-specific characteristics of the root systems we investigated. This ap-

proach is complemented by the analysis of exterior and interior link lengths. These are metric values, but they are closely related to topological structure. The graph-theoretical background to our topological analysis is outlined in the Theory section below.

Diameter and branching

When examining metric properties of root systems, the question arises how the diameters before and after branching nodes are related to each other. Leonardo da Vinci claimed in his notebook that the cross-sectional area of a trunk or branch of a tree is equal to the sum of the cross-sectional areas of the branches at any higher level (Richter 1970). Locally, this means that in each branching node where n daughter branches emerge, the diameter d before the node is related to the diameters d_i ($i = 1, ..., n$) (Figure 1) of the daughter segments by:

$$d^2 = \sum_{i=1}^{n} d_i^2.$$ (1)

For a system of conducting tubes with negligible flow resistance, this condition enables equal flow rates throughout the system. Equation 1 was used in a large number of models of plant functioning and growth (e.g., Shinozaki et al. 1964, Perttunen et al. 1996) and was popularized under the names "pipe stem theory" (John Ruskin, see MacDonald 1983) or "pipe model." Examples of theoretical considerations building on Equation 1 are Mendès France (1981) and Long (1994).

Various generalizations of Equation 1 have been considered. One of them is:

$$d^\Delta = \sum_{i=1}^{n} d_i^\Delta,$$ (2)

where the parameter Δ is called the diameter exponent of the system (Mandelbrot 1983). Murray (1927) observed that in a number of aboveground tree branching systems that have been investigated, weight was approximately proportional to $d^{2.5}$, where d is the proximal diameter. From this he concluded (using additivity of weight in the branching nodes) that $\Delta = 2.5$ should hold constant. However, his argument was too simple, because weight is additive only if the contribution of the mother segment of the branches is neglected. Recalculating Δ,
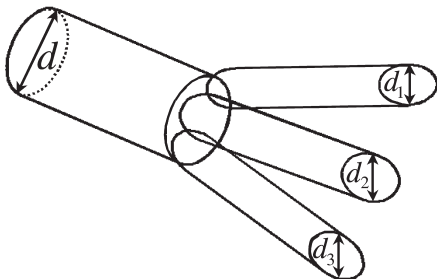

Figure 1. Principle of Leonardo's rule, which is expressed mathematically in Equation 1.

Mandelbrot (1978) obtained a value of 2, thus confirming Leonardo's rule.

Surprisingly, direct empirical estimations of Δ are rare. Mandelbrot (1983) mentioned a reexamination of data obtained by McMahon and Kronauer (1976) from three tree crowns, yielding a Δ near 2 or slightly below. An examination of three young *Picea abies* (L.) Karst. crowns (Anzola Jürgenson 1998) showed no significant deviation from $\Delta = 2$. We are unaware of corresponding investigations of root systems.

Another generalization of Equation 1, utilized by van Noordwijk et al. (1994) and Spek and van Noordwijk (1994) in theoretical studies, is:

$$d^2 = \alpha \sum_{i=1}^{n} d_i^2,$$ (3)

with a proportionality factor $\alpha > 0$. We checked Equations 2 and 3 with our root system data.

Scaling relations

There is much in the literature about scaling relationships and allometries of whole plants or plant organs; see, e.g., Niklas (1994) for a general overview. We were motivated to investigate the tapering of our roots by the work of McMahon and Kronauer (1976) on branch tapering in tree crowns. They related the diameter d of a segment, taken at some point in the branching system, to the average length L_p of all paths going from that segment distally to a branch tip.

From the theory of elastic similarity, they deduced a relationship of the form $d = \gamma (L_p + l_0)^\beta$, with constants γ, l_0 and β and with $\beta = 1.5$, which was confirmed by their empirical data. Because the mechanical argument does not apply to root systems, the question arose whether the same relationship with a possibly different value of β (or a different form of regression equation between d and L_p) holds for roots.

Another relationship, perhaps of greater practical significance, is that between the diameter d of a segment and the total length sum L of all roots distal to that segment. A tight correlation between these values, applied to the diameter at the root collar or to the diameters of the main roots near the collar, could be useful in estimating total root length. On the basis of self-similarity assumptions and Equation 3, van Noordwijk et al. (1994) and Spek and van Noordwijk (1994) obtained a proportionality between L and d^2 in artificially constructed branching patterns. However, they did not seek empirical confirmation of this relationship in the field.

Recently, West et al. (1997) derived scaling relations for vessel systems from the principle of minimal hydraulic resistance and from self-similarity assumptions. Their model coincided with empirical evidence from cardiovascular and respiratory systems of animals, and they claimed to have found "a general model for the origin of allometric scaling laws in biology." Applied to the mass m of the organism or organ to be fed and to the proximal diameter d of the supplying vessel, their model predicts the relation $d = \lambda m^\varepsilon$, where λ and ε are con-

stants and $\varepsilon = 3/8$. We checked this relationship on the root systems we studied by inserting the sum of the volumes of all root segments for m, assuming that this total volume is proportional to m, and root collar diameter for d.

Theory

Graphs of branching patterns

Topology studies the adjacency properties of objects, ignoring their metric sizes (e.g., lengths, angles, diameters). From the topological viewpoint, a root system is a graph in the sense of graph theory (e.g., Deo 1974), i.e., an object consisting of vertices and edges (links), each connecting two vertices. A graph is completely described by the information specifying which vertices are connected by an edge and which are not. Because we have found no anastomosis in our root systems, we can further restrict the class of graphs to so-called "trees," that is, graphs without cycles. The root collar, where the aboveground part of the plant begins, corresponds to a special vertex of the underlying graph, known in mathematical terminology as the root of the tree. However, to avoid confusion, we refer to the mathematical root, which in our application is the root collar or the shoot, as the base vertex. In our topological drawings the base vertex will be represented by an empty circle. The base vertex can serve to assign a unique direction to every link giving rise to a so-called directed tree. In our analyses, we assume a distal orientation of the system, biologically corresponding to the flow of assimilates from the shoot to the root tips (Figure 2 (the arrows are omitted in subsequent figures)).

Each link not emerging from the base vertex has indegree 1 (i.e., it is adjacent to one mother link in the proximal direction), and links can have various outdegrees, indicating the number of adjacent daughter links in the distal direction (Figure 2). We denote by v_k the number of links of outdegree k ($k = 0, 1, 2...$). When we omit the base vertex, we have an equal number $v = v_0 + v_1 + v_2 + ...$ of vertices and links.

In the literature, root systems are usually represented by binary trees, i.e., by trees where every link has outdegree 2 or 0,

and every vertex corresponds to a dichotomous branching node or to a root tip. However, in our field observations we found situations where two successive root segments had very different morphological characteristics, e.g., when an old axis had stopped apical growth but was the mother segment of a single, much younger reiterative root. In these cases we assigned a higher botanical order to the reiterative root, and we did not merge segments of different order to a single link. As a consequence, we obtained some links of outdegree 1 in our topological graphs. Furthermore, there were cases where several branches emerged from the same mother segment at nearly identical positions (distance of branching nodes < 5 mm), and we refrained from inserting artificial "mini-links" only to maintain the binary branching law. Hence we have some links of outdegree 3 or higher. This leads to a loss of mathematical elegance for the sake of realism. However, the number of these "exceptional" links remained limited, and binary branching can still be considered the normal case.

In binary trees, the number v_0 of exterior links (often referred to as the magnitude of the tree, e.g., Fitter 1986) determines the number v of all links:

$$v = 2v_0 - 1 \qquad (4)$$

(e.g., Deo 1974, Tucker 1980). In our general case, we must modify Equation 4 by a correction term or discrepancy (δ):

$$v = 2v_0 - 1 + \delta, \qquad (5)$$

with

$$\delta = \sum_{k=1}^{\infty}(2 - k)v_k. \qquad (6)$$

Only "exceptional" links contribute to δ (notice that v_2 makes no contribution in Equation 6), and, in contrast to v_1, all v_k with $k > 2$ have a negative coefficient.

Topological indices

The most obvious topologically extreme branching forms in the binary case occur, on the one hand, for the complete dichotomous pattern with 2^n exterior links of equal distance to the base, and on the other hand, for a single axis with only one exterior link emerging at each vertex ("herringbone pattern;" Fitter 1986, 1987, van Noordwijk et al. 1994). To quantify the position of an arbitrary binary tree between these extremes, it is necessary to define a topological equivalent of "rooting depth." The topological depth of an exterior link is the number of links in the unique directed path from the base vertex of the graph to the end vertex of the link in question (see Figure 2; terminology in accordance with the notion of "depth-first search" in computer science, e.g., Grimaldi 1989). The maximal topological depth or altitude (a) of a directed tree is the number of links in the (topologically) longest directed path. This parameter, which is in the binary case minimal for the complete dichotomous and maximal for the herringbone pattern, is named diameter (Fitter 1986) or altitude (Fitter 1987,
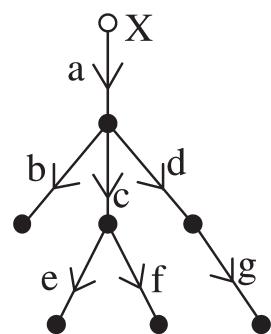

Figure 2. Example of a directed graph representing a root system topologically. Terminology: X is the base vertex, b, e, f, g are exterior links, a, c, d interior links, where a has outdegree 3, c outdegree 2, and d outdegree 1. The topological depth of b is 2 (measured always from X), that of e, f and g is 3.

Fitter et al. 1991, Berntson 1995) in the literature on root research and height in most textbooks on graph theory or discrete mathematics (e.g., Deo 1974, Liu 1977, Tucker 1980, Grimaldi 1989). Somewhat reluctantly, we continue to use the term altitude here. As a second parameter, we calculate the mean topological depth b of a directed tree as the average topological depth of all exterior links. Parameter b is of the same order of magnitude as a, and it is related to p_e, the sum of all pathlengths from the base to the exterior links, which is often used in the literature (exterior pathlength: Fitter 1986, total exterior pathlength: Fitter and Stickland 1991, total external path length: Berntson 1995, path length: Deo 1974), by:

$$b = p_e/v_0.$$

The range of possible values of a and b grows with the magnitude v_0 of the root system. To enable comparisons of branching patterns of different sizes, Fitter (1985) introduced indices based on expected values of a and p_e under a specific random model (Werner and Smart 1973). However, this model was derived for networks in geography and only makes sense for planar patterns. Unfortunately, the precise expected values and confidence intervals calculated by Berntson (1995) are also based on this planarity assumption and are therefore inappropriate for 3-D root branching patterns. We decided to avoid randomness assumptions; instead, we simply normed both parameters a and b by a linear transformation, making their minimal and maximal values for binary trees (given by Knuth 1973, Fitter 1986) 0 and 1, respectively. The explicit definitions of both resulting normed indices q_a and q_b, that are confined to the interval [0; 1] for binary trees (but can take values beyond these limits if $v_1 > 0$ or $v_3 > 0$), are:

$$q_a = \frac{a - 1 - \text{lb}\, v_0}{v_0 - 1 - \text{lb}\, v_0}, \quad q_b = \frac{b - 1 - \text{lb}\, v_0}{(v_0 + 1)/2 - v_0^{-1} - \text{lb}\, v_0},$$

where $\text{lb}\, v_0$ ($= \ln v_0/\ln 2$) is the binary logarithm.

The behavior of these indices is demonstrated in Figure 3 for the six possible binary trees for which one link emerges from the base. The pattern to the lower right is the herringbone type, corresponding to $q_a = q_b = 1$, whereas the value $q_a = q_b = 0$ would occur only for a perfectly dichotomous pattern.

The value of q_b follows a more continuous course between the extremes compared with q_a. Furthermore, Berntson (1995) identified the related parameter p_e in a series of growth simulations using the Monte-Carlo technique as that with the least erratic and most size-independent and stable behavior among several other topological indices. We therefore advocate the use of q_b, but in our empirical study we have also calculated a (and q_a) because of its simple definition.

Two further parameters related to topological structure are the mean lengths of exterior and interior links. Fitter (1986, 1987) and Fitter and Stickland (1991) intensively investigated these link lengths and their relation to water and nutrient supply.
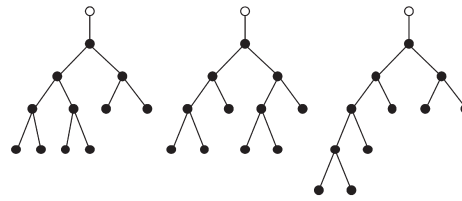
a	4	4	5
q_a	0.172	0.172	0.586
b	3.667	3.667	3.833
q_b	0.109	0.109	0.332
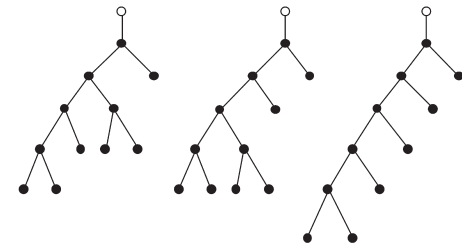
a	5	5	6
q_a	0.586	0.586	1.0
b	4.0	4.167	4.333
q_b	0.555	0.777	1.0

Figure 3. The six topologically distinct binary trees with $v_0 = 6$ distal edges (links), together with their respective altitude a, mean topological depth b and with the corresponding normed indices q_a and q_b. They represent the range from dichotomous to herringbone branching. The parameter b (or q_b) allows a better distinction between the types than parameter a, though both a and b fail to distinguish between the two upper leftmost types. Notice that the theoretical minimum $q_a = q_b = 0$ is not reached in this case because 6 is not of the form 2^n.

Materials and methods

The study site is located on sandveld near Mogorosi (Serowe Region, Central District, Botswana) between longitude 26°36.26′ and 26°36.70′ E and latitude from 22°25.09′ to 22°25.30′ S. For a more detailed site description see Oppelt et al. (2000).

The architecture of *in situ*-grown coarse root systems of the fruit tree species *Strychnos cocculoides* (Loganiaceae), *Strychnos spinosa* and *Vangueria infausta* (Rubiaceae), as well as the shrub *Grewia flava* (Tiliaceae) was studied. Coarse roots were defined as roots that exceed a threshold diameter of 3 mm. A reconstruction of spatial orientation and branching below that value was not possible.

Each species was represented by five coarse root systems, which were excavated by hand. Each exposed root was divided into segments of variable length, according to changes in growth direction or at positions where daughter roots were emerging, and marked with white ink. The spatial orientation (vertical and horizontal angle) as well as the length of each segment in its original position was determined with a digital compass (TECTRONIC 4000, Breithaupt, Kassel, Germany) and automatically recorded (L-file).

After spatial measurements, coarse roots were removed, the diameter of each segment measured with a digital caliper (PM

200, HHW Hommel, Switzerland), and the data recorded in a D-file corresponding to each L-file.

Both raw data sets (L- and D-files) were merged by self-authored interface software, creating the final code for reconstruction. As a basis for the topological description of the branching systems, a developmental botanical concept of branching order was applied: the order of the tap root (if it exists) is 0, and an nth order root has branches of order $n + 1$. The branching order was calculated for each segment automatically. For encoding the full geometrical and topological structure of the root systems (lengths, orientations and diameters of all segments and mother-segment linkages) we used the digital tree data format (dtd code, Kurth 1994). The dtd files, each representing a complete root system, were generated semi-automatically as described above.

The software GROGRA 3.2 (Kurth 1994) was used to reconstruct the architecture of individual root systems from the data files in the form of a linked list data structure. Lateral views of one example root system of each species, obtained from the software as graphical output, are shown in Figure 4.

The GROGRA software can extract different kinds of graphical and numerical information from the virtual 3-D structures. Metric information about each root segment and about the whole system was written into tabular files and processed with the SPSS data analysis software (SPSS 8.0, SPSS Inc., Chicago, IL) and Statistica v. 5 (StatSoft Inc., Tulsa, OK). Topological analysis was enabled using a transformation function in GROGRA, which was originally devised as an interface for a numerical water-flow simulator for tree crowns (Früh and Kurth 1999). It unifies each chain of subsequent unbranched root segments of the same botanical order into one link. Afterwards, the lengths of all links were artificially reduced to one to enable topological depth calculations with the same algorithms that had previously yielded the metric pathlengths.

Results

Coarse root systems from *Grewia flava* were characterized by an intensive shallow network of slowly tapering first-order laterals. Structural roots with higher branching orders developed mostly in a vertical direction, and exploited deeper soil layers. Functionally, these replaced the frequently absent taproot. An intensive development of adventitious roots, especially on older individuals, was observed.

In contrast to the other root systems investigated, both *Strychnos* species were characterized by a deep and prominent taproot, as a result of secondary growth. Branching intensity was low and branching orders did not normally exceed 2, so that they can be described as weakly exploiting root systems. Both species are distinguished by their vertical root distribution. *Strychnos cocculoides* showed the maximum amount and horizontal extent of first-order laterals in deeper subsoil layers, whereas *Strychnos spinosa* showed a greater horizontal extension of lateral roots with a high concentration in the topsoil.

In contrast, root systems of *Vangueria infausta* showed higher branching intensity. First-order laterals were distinctly shorter and branched rapidly into higher orders. Most laterals initiated in the horizontal plane, but changed with time to a more vertical orientation. If present, taproots tapered rapidly, never reaching great depth (Figure 4, see also Oppelt et al. 2000).

Quantitative characteristics of all the root systems investigated are given in Tables 1 and 2.

Topological indices

Figure 5 shows the results of the calculation of the topological indices q_a and q_b (numerical values given in Table 1), grouped according to species.

Both indices are closely correlated with each other (Pearson's $r = 0.92$). A one-factorial ANOVA with species as factor showed a highly significant effect on q_a ($F = 11.2$, $P =$
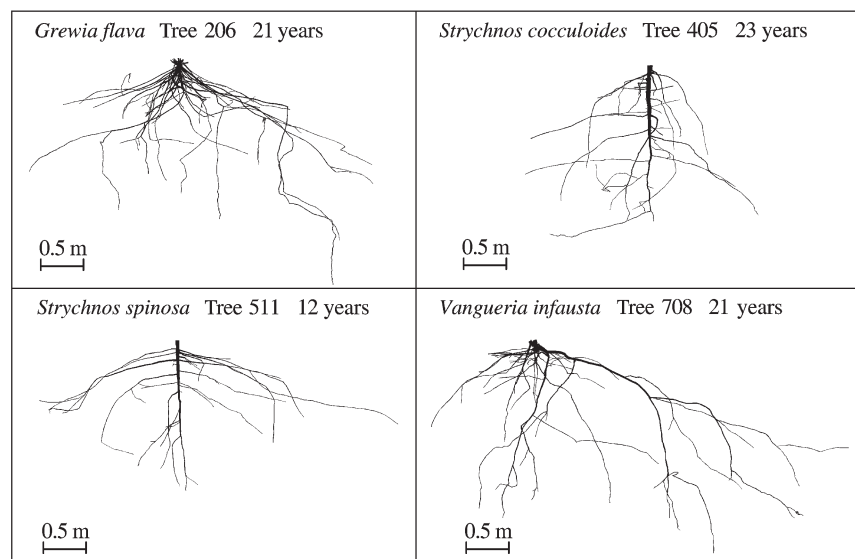

Figure 4. Lateral view of four reconstructed root systems (graphical output from GROGRA). The age of each tree is also indicated.

Table 1. Topological parameters of the root systems of each sample tree.

Species	Tree	Age	v[1]	v_0[2]	δ[3]	a[4]	b[5]	q_a[6]	q_b[6]
Grewia flava	203	25	252	138	−23	23	9.41	0.11	0.02
	206	21	127	78	−28	10	4.09	0.04	−0.10
	213	18	100	54	−7	16	8.09	0.20	0.06
	214	14	47	23	2	11	4.74	0.31	−0.11
	215	13	37	20	−2	13	6.45	0.52	0.18
Mean		18.2	112.6	63.0	−12.4	14.6	6.56	0.24	0.013
SD		5.0	86.3	49.2	14.15	5.22	2.23	0.19	0.12
Strychnos cocculoides	405	23	92	50	−7	31	13.62	0.58	0.36
	409	15	39	20	0	16	9.90	0.73	0.75
	412	17	25	13	0	12	7.62	0.88	0.90
	425	29	76	38	1	23	12.58	0.53	0.45
	426	13	28	14	1	12	7.79	0.78	0.82
Mean		19.4	52.0	26.8	−0.6	18.8	10.30	0.70	0.66
SD		6.5	30.2	16.0	2.51	8.17	2.73	0.14	0.24
Strychnos spinosa	501	20	127	73	−18	33	18.21	0.39	0.36
	508	12	48	26	−3	15	8.08	0.46	0.27
	509	17	16	9	−1	5	3.89	0.17	−0.16
	510	15	86	48	−9	27	13.08	0.49	0.34
	511	12	67	35	−2	22	11.77	0.55	0.44
Mean		15.2	68.8	38.2	−6.6	20.4	11.01	0.41	0.25
SD		3.4	41.6	24.1	7.09	10.85	5.38	0.15	0.24
Vangueria infausta	703	36	371	188	−4	18	11.02	0.05	0.03
	708	21	114	61	−7	16	9.36	0.17	0.10
	711	19	75	35	6	16	8.63	0.34	0.19
	712	25	92	48	−3	19	10.04	0.30	0.18
	713	25	123	60	4	17	10.77	0.19	0.16
Mean		25.2	155.0	79.4	−2.8	17.2	9.96	0.21	0.13
SD		6.6	122.2	64.4	8.17	1.30	0.99	0.11	0.07

[1] v = Number of links.
[2] v_0 = Number of exterior links.
[3] δ = Discrepancy (see Introduction).
[4] a = Altitude (maximal topological depth).
[5] b = Mean topological depth.
[6] q_a, q_b = Normed values corresponding to parameters a and b.

0.00033) and q_b ($F = 11.7$, $P = 0.00026$). This effect was even more pronounced when the age of the tree was considered as a covariate (q_a: $F = 20.5$, $P = 1.4 \times 10^{-5}$; q_b: $F = 14.7$, $P = 9.8 \times 10^{-5}$). The root system of Tree 509, a *Strychnos spinosa* specimen with clear reiterative growth because of damage and an unusual growth habit, had atypically low topological indices compared with the other four *S. spinosa* root systems. When this abnormal specimen was omitted from the analysis of covariance, the significance of the species effect was further enhanced (q_a: $F = 27.3$, $P = 4 \times 10^{-6}$; q_b: $F = 24.7$, $P = 7 \times 10^{-6}$). A closer look at the numbers (least significant difference test) showed that all species (except *Grewia flava versus Vangueria infausta*) could be separated from one another at the 5% level using either q_a or q_b (Tree 509 removed; Statistica *post hoc* tests). In particular, the two *Strychnos* species, tending to a herringbone structure, differed markedly from the two other species. Figure 6 demonstrates this difference in topological architecture in *Strychnos cocculoides* (Tree 412; upper part of figure) and *Vangueria infausta* (Tree 711; lower part)

root systems, both shown in their metrical (left) and topological (right) reconstruction. The age of the corresponding trees was 17 and 19 years, respectively. Both topological indices had a tendency to decrease slightly with age ($R(q_a$, age$) = −0.50$, $R(q_b$, age$) = −0.28$).

As an alternative topological index, Fitter (1985, 1986, 1987) investigated the slope that a collective of root systems exhibits in a diagram where altitude a is plotted against magnitude v_0. We performed this type of analysis for the subset of the *Strychnos* samples contrasted to the other species (diagram not shown) and obtained a difference corroborating our finding that the two *Strychnos* species differed considerably in root system topology from the *Grewia* and *Vangueria* specimens that were investigated.

Link lengths

The same distinction emerges for the metric parameter mean exterior link length (l_e) (empty bars in Figure 7, cf. Table 2). An ANOVA with species as single factor yields a highly sig-

Table 2. Geometrical parameters of the root systems of each sample tree.

Species	Tree	cd[1]	r_{max}[2]	L[3]	L_p[4]	V[5]	l_e[6]	l_i[7]
Grewia flava	203	97	5708	190509	2568	8304	851	641
	206	65	3267	73076	1257	2884	652	454
	213	58	3349	58991	1906	1769	614	562
	214	32	1603	19723	1078	522	538	306
	215	27	1506	8419	587	274	305	136
Mean		55.8	3087	70144	1479	2751	592.0	419.8
SD		28	1708	72410	770	3276	198	202
Strychnos cocculoides	405	56	2480	38247	1430	2443	644	144
	409	67	4385	24595	2238	2932	920	326
	412	48	3880	18930	2495	1599	1113	372
	425	68	3417	50814	2428	4248	976	361
	426	44	3020	20849	2282	1407	876	613
Mean		56.6	3436	30687	2175	2526	905.8	363.2
SD		11	739	13550	429	1146	171	167
Strychnos spinosa	501	72	5990	113735	2279	5682	1345	288
	508	60	4230	42970	2737	3643	1262	462
	509	40	1447	10545	1863	1011	769	517
	510	64	2758	49307	1569	2983	901	160
	511	44	2738	34700	1594	1487	768	245
Mean		56.0	3433	50251	2008	2961	1009.0	334.4
SD		14	1736	38414	498	1860	276	150
Vangueria infausta	703	140	5070	207137	2526	12440	718	394
	708	86	3642	51750	1929	2989	580	309
	711	48	1708	24645	1442	1282	412	255
	712	60	1247	24825	895	1084	366	164
	713	70	1547	34910	1058	1496	361	210
Mean		80.8	2643	68653	1570	3858	487.4	266.4
SD		36	1652	78198	667	4856	157	89

[1] cd = Root collar diameter (mm).
[2] r_{max} = Maximal radial extension of the system (mm).
[3] L = Total coarse root length (mm).
[4] L_p = Mean path length (mm).
[5] V = Total coarse root volume (cm^3).
[6] l_e = Mean exterior link length (mm).
[7] l_i = Mean interior link length (mm).

nificant effect on l_e ($F = 7.31$, $P = 0.0027$) that becomes even more pronounced when age is included as a covariate ($F = 8.44$, $P = 0.0016$). A *post hoc* test enabled a statistical separation of all species from each other at the 5% level, except for the two pairs *Grewia flava* versus *Vangueria infausta* and *Strychnos cocculoides* versus *S. spinosa*. In contrast, mean interior link length (l_i; black bars in Figure 7) showed no difference between species, regardless of whether age was included as covariate ($F = 0.97$ and 0.82, respectively; $P > 0.4$).

Leonardo's rule

We estimated the diameter exponent Δ from Equation 2 for each root system separately and for the whole population of branching nodes, by nonlinear regression analysis (iterative Hooke-Jeeves coordinate search, independent control with quasi-Newton method; Statistica 5). The iteration converged in all cases and explained a large part of the variance (see left half of Table 3). Because the oldest and largest root segments

were potentially linked to rotten parts of the system that could not be measured, we also conducted the analysis for the subsample of branching nodes where the mother segment did not exceed a threshold diameter of 20 mm (right-hand half of Table 3), thus focusing on the younger parts of the system. Generally, the resulting average best-fit exponent (2.29 and 2.18 for the unresticted and restricted samples, respectively) did not contradict the theoretical assumption of Leonardo's rule ($\Delta = 2$).

Adopting this value for Δ, we checked linear regressions between d^2 and $\sum_{i=1}^{n} d_i^2$ for all branching nodes. These gave tight fits for all individual root systems. Statistically, it was not possible to prove or disprove that the proportionality factor α (cf. Equation 3) is 1 and the intercept 0. However, no systematic deviation from these values was detected (see Table 4).

Length and diameter

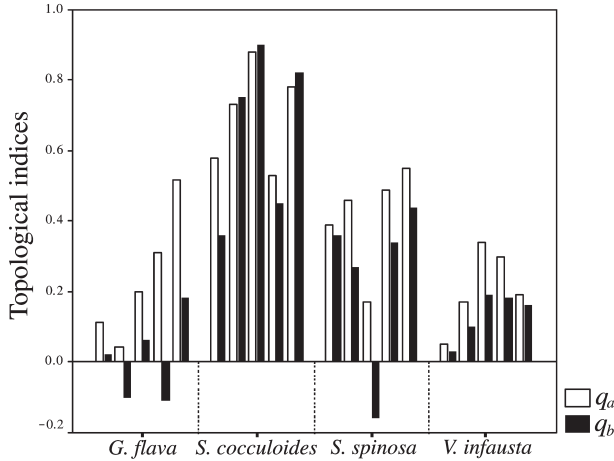At the level of whole root systems, we related the root collar

Figure 5. The topological indices q_a (empty bars) and q_b (black bars) of the root systems investigated.

Figure 7. Mean exterior link length l_e (empty bars) and mean interior link length l_i (black bars) for each of the root systems investigated.

diameters cd to the total length, L, of the measured roots. The value of L was obtained by adding the lengths of all root segments. The linear regression of log cd (independent variable) versus log L (dependent) yielded a slope of 1.95 (intercept 1.15, $r^2 = 0.75$, $n = 20$; see Figure 8). This is close to the allometric exponent 2 proposed by van Noordwijk et al. (1994) for the relationship between base diameter and total length.

Diameter can also be related to root size in topological terms. Replacing total length L by the number of links v, we compared log cd with log v (*cf*. Spek and van Noordwijk 1994). The resulting regression was somewhat less tight (slope 1.61, intercept -0.98, $r^2 = 0.62$) than in the case of log L.

The relationship between diameter and length can also be studied at the level of individual root segments within a system. Besides the total length L distal to a given segment, we used GROGRA to calculate the mean distal pathlength L_p (values in Table 2) and maximal distal pathlength L_{max} (not shown). Both L_p and L_{max} typically exhibited a broad scattering when plotted against root segment diameter. Tentative nonlinear fitting of the equation $d = \gamma(L_p + l_0)^\beta$ from McMahon and Kronauer (1976) yielded generally unconvincing results

Table 3. Nonlinear regression results for the diameter exponent Δ. Abbreviation: CD = coefficient of determination.

Tree	All		$d \leq 20$	
	Δ	CD	Δ	CD
203	3.02	0.96	3.23	0.92
206	1.98	0.91	2.58	0.68
213	1.61	0.96	2.48	0.89
214	1.43	0.51	2.58	0.68
215	1.65	0.56	2.58	0.68
405	6.27	0.91	2.65	0.96
409	1.70	0.96	1.51	0.93
412	1.81	0.96	3.07	0.93
425	1.98	0.99	1.69	0.90
426	1.58	0.97	1.43	0.83
501	2.39	0.98	1.84	0.92
508	2.11	0.98	2.56	0.90
509	1.84	0.87	1.23	0.87
510	2.38	0.97	1.91	0.96
511	2.04	0.98	1.64	0.95
706	2.08	0.98	2.48	0.92
708	2.74	0.66	2.08	0.92
711	3.65	0.95	2.21	0.89
712	1.81	0.98	1.89	0.97
713	1.77	0.99	1.96	0.92
Mean	2.29	0.90	2.18	0.88
SD	1.08	0.15	0.55	0.09

Figure 6. Examples of two contrasting root systems in their metric view (left side) and in the form of a topologically equivalent pattern with approximately equal link lengths (right side). Upper part: A *Strychnos cocculoides* (Tree 412) with nearly herringbone topology, lower part: A *Vangueria infausta* (Tree 711) with intensive dichotomous branching in some parts of the system.
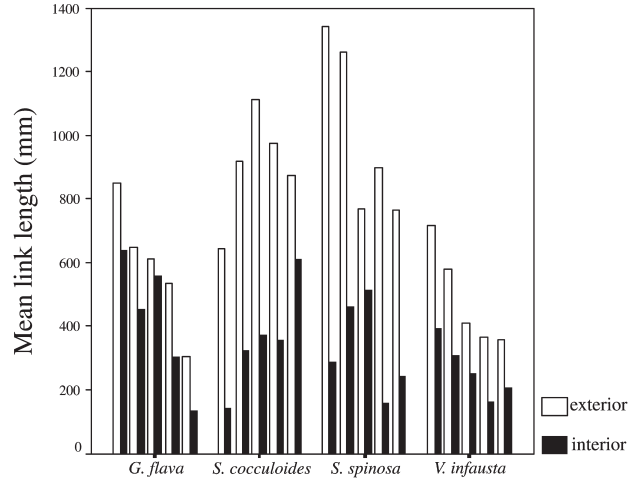
Table 4. Results of regression for Leonardo's rule. Dependent variable: d^2, independent: sum of d^2 of all daughter segments.

Species	Slope	Intercept	r^2
Grewia flava	1.13	−29.4	0.89
Strychnos cocculoides	1.00	17.9	0.90
Strychnos spinosa	1.02	−5.7	0.97
Vangueria infausta	0.92	46.4	0.94
Mean	1.02	7.3	0.93
SD	0.09	32.4	0.04
Total population	0.99	28.0	0.92

(slow convergence; and the shape of the scatterplot was poorly reflected by the regression curve). Total distal root length L showed a better correlation to segment diameter, particularly when only small diameters were considered (e.g., Figure 9).

Correlation was not improved when d was replaced by d^2 in the linear regression approach for L. Only for the largest and oldest segments was the fit better in the quadratic case.

Root volume and diameter

At the level of whole root systems, we found a good correlation between log (root collar diameter) and log (total coarse root volume), shown in Figure 10 (slope 2.19, intercept 2.47, $r^2 = 0.84$, $n = 20$). The slope of the regression lines (ω in the relation $V = \theta d^\omega$) was relatively stable among the four species investigated.

Discussion

In a methodological sense, our study—together with earlier results from the same data (Oppelt et al. 2000)—demonstrates the large amount of information that can be extracted from one architectural database by means of 3-D reconstruction and analysis. Until now, the advantages of detailed 3-D recon-
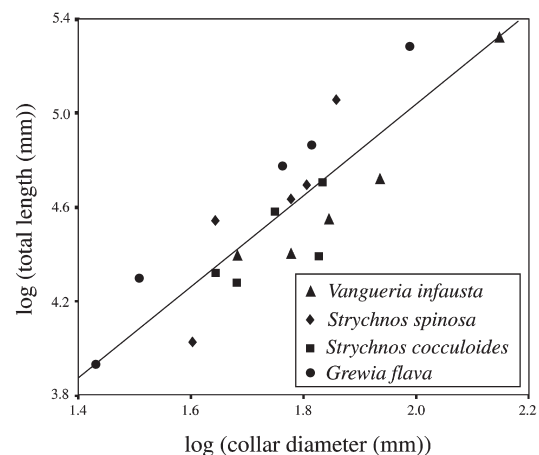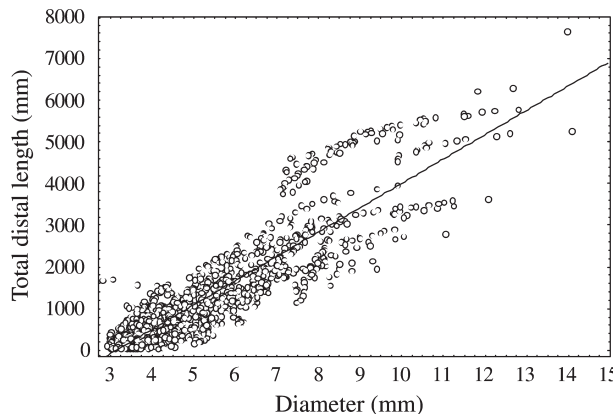

Figure 9. Diameter d and total distal root length L of all segments with $3 < d < 15$ mm from a *Grewia flava* coarse root system (Tree 213). Shown also is the linear regression $L = -1823 + 583\,d$ ($r^2 = 0.81$, $n = 1323$) for this individual root system.

struction of branching structures have mainly been appreciated in studies of aboveground plant architecture (Sinoquet and Rivet 1997, Godin et al. 1999). The diverse pieces of information are like a puzzle from which a picture, giving better insight into structural and functional aspects of plant architecture, can emerge. Furthermore, the architectural data can be the basis for simulation studies (e.g., Früh and Kurth 1999 for aboveground structures).

When our data are compared with results from the literature, our restriction to coarse roots ($d \geq 3$ mm) has to be taken into account. Most published studies on root system topology consider small seedlings in which all roots, including the finest, were measured. The topology of fine root branching could differ from the patterns found at the coarse root scale. The differences that we identified in our root systems between fractal
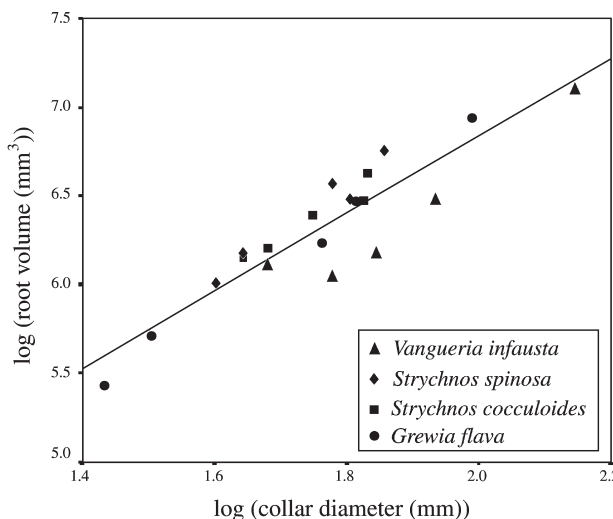

Figure 8. Logarithms of root collar diameter (*cd*) and total coarse root length (*L*) of all 20 investigated root systems, together with the best-fit regression line (see text).

Figure 10. Logarithms of root collar diameter (*cd*) and of total root volume (*V*) of all 20 root systems investigated, together with the best-fit regression line (see text).

dimensions at coarse root and fine root scales (Oppelt et al. 2000) indicate that such a structural gap between the two scales might exist for topology as well.

The large values of average exterior and interior link lengths in our study (ranging from 14 cm to 1.3 m), which lie almost one order of magnitude greater than values reported by Fitter (1987) for a number of herbaceous plants and tree seedlings, are probably also due to our omission of roots < 3 mm.

In a qualitative sense, it is well known that a deep taproot with little lateral growth is adapted to dry environments (Epstein 1973). In quantitative simulation studies, Fitter et al. (1991) found that herringbone root systems have a higher exploitation efficiency in terms of soil volume accessed, but require more carbon for construction compared with dichotomous patterns of equal magnitude. Hence the herringbone pattern is likely to be favored when soil resources limit growth. We conjecture that in the case of our sample trees—all grown under arid conditions—the two *Strychnos* species are more specifically adapted to extreme drought than the other two species investigated. This is consistent with the observation that both *Strychnos* species exhibit a distinct xeromorphic habit in their leaf morphology, whereas *Grevia flava* and *Vangueria infausta* show less pronounced xeromorphic crown features. Root system topology and exterior link lengths thus appear to be indicators of ecophysiological differences in drought adaptation.

Because the root systems considered in this study have also been investigated for their fractal dimension D (see Oppelt et al. 2000), the question arises whether D is related to topological parameters. In fact, the topological index q_a is negatively correlated with D ($r = -0.56$): the more a root system conforms to the herringbone pattern, the lower its space-filling potential and its fractal dimension. However, our findings also show that a considerable amount of variance of D cannot be explained by purely topological properties (all other parameters calculated in this study showed a weaker correlation with D than that obtained for q_a). Hence the fractal dimension D remains a characteristic in its own right, integrating topological and geometrical properties of a whole root system (Fitter and Stickland 1992).

The diameter exponent of most of the root systems we investigated was close to the ideal value of 2, indicating preservation of cross-sectional area in the branching nodes. Thus, application of Leonardo's rule in models of secondary growth and hydraulic function, which is quite common in the literature, is corroborated—at least for coarse roots. Given the high hydraulic conductivity of coarse roots (Riedl 1937, Fahn 1964, Lafolie et al. 1991), this amounts to a homogeneity of flow velocity throughout the system, provided there is a constant proportion of functional xylem in all coarse roots.

Van Noordwijk et al. (1994) and, more generally, West et al. (1997) derived several scaling laws from the theoretical assumptions of self-similarity and preservation of flow. These laws were confirmed quite well when we checked them at the level of whole root systems. Total length of coarse roots is roughly proportional to cross-sectional area of the root collar,

as predicted by van Noordwijk et al. (1994), and a particularly stable fit was found between total volume of coarse roots and collar diameter (Figure 10), although the exponent of the diameter in this relation, 2.19, deviates slightly from the theoretical value of 2.67 predicted by West et al. (1997). Our number of replicates was too small for statistical security at the whole-system level, but nevertheless it seems possible to use root collar diameter as a predictor of total coarse root length and biomass on the basis of these scaling relations.

However, the picture becomes more complex when the lengths and diameters inside the root system are considered. Our exemplary Figure 9 shows considerable variance, but also some traces of structured patterns in the data. Simple power laws like those proposed by McMahon and Kronauer (1976) or van Noordwijk et al. (1994) seem inadequate to describe these structures. The distribution of link lengths in the root system is much more complicated than these authors assumed in their self-similar models. Crawford and Young (1990) suggested that, in branching systems of higher plants, a spectrum of scale factors, which itself has a fractal signature, may operate. Our data do not contradict this assumption. Our topological results suggest that the architecture of the sample systems has features that do not fit into the standard self-similar branching models. Morphological features like developmental axes, reiteration or functional differentiation of root segments may contribute to this internal complexity.

Conclusions

The architectural comparison of four species has revealed significant differences, resulting in a coherent picture: the two *Strychnos* species tend to have a root system topology conforming nearly to the herringbone pattern and large unbranched zones at the distal ends of their root axes. This is in accordance with the general appearance of these root systems (Figure 4; see also Oppelt et al. 2000) and indicates an explorative strategy of root system architectural development, whereas *Grevia flava* and *Vangueria infausta*, have a topology tending to dichotomous or intermediate patterns and shorter exterior links that may possibly exploit smaller volumes of soil more thoroughly.

It will be necessary, however, to complement our study by investigations of fine root distribution, because the diameter threshold of 3 mm prevented a direct calculation of exploited soil and total root biomass. Nevertheless, the pattern of coarse roots sets structural constraints on the extent and locations of fine root development, and thus has implications for resource capture and efficiency of growth.

Our empirical test of cross-sectional area preservation supported the pipe stem theory, justifying the use of this simple rule in simulation models.

Likewise, some scaling laws deduced from theoretical considerations, particularly that of West et al. (1997), were confirmed by our data and can be used to predict parameters of whole coarse root systems from root collar diameter. However, a closer consideration of the inner structure of the root

systems revealed more complicated patterns that could not be expressed in simple allometric relations.

Generally, we believe that further improvements in our understanding of root system architecture, beyond the characteristics described in this study, can be obtained only if ontogenetic development is taken into account (Colin-Belgrand et al. 1989, Raimbault 1991). Root architecture results from an interplay between endogenous growth laws and opportunistic reactions (Atger 1991). Dynamic studies of growing root systems are, however, difficult and rare, particularly in the case of large trees; therefore, it makes sense to extract as much information as possible from the static data at our disposal.

References

Anzola Jürgenson, G.A. 1998. Auswertung und Modellierung der Morphologie junger Fichten (*Picea abies* (L.) Karst.) in Abhängigkeit von Licht und Wuchsdichte. Diploma Thesis, Universität Göttingen, 72 p.

Atger, C. 1991. L'architecture racinaire—est-elle influencée par le milieu? *In* L'arbre. Biologie et Développement. Ed. C. Edelin. Naturalia Monspeliensia, Montpellier, pp 71–84.

Berntson, G.M. 1995. The characterization of topology: a comparison of four topological indices for rooted binary trees. J. Theor. Biol. 177:271–281.

Berntson, G.M. 1997. Topological scaling and plant root system architecture: developmental and functional hierarchies. New Phytol. 135:621–634.

Bert, D., F. Danjon, D. Loustau, A. Porté, P. Trichet, I. Champion and C. Godin. 1998. Topology and geometry measurement of root and shoot architecture of *Pinus pinaster*. Second International Workshop on Functional-Structural Tree Models (Clermont-Ferrand, France, 12-15 Oct. 1998), Abstract Volume. INRA, Clermont-Ferrand, pp 7–8.

Colin-Belgrand, M., L. Pagès, E. Dreyer and H. Joannes. 1989. Analysis and simulation of the architecture of a growing root system: application to a comparative study of several tree seedlings. Ann. Sci. For. 46 (Suppl.):288s–293s.

Crawford, J.W. and I.M. Young. 1990. A multiple scaled fractal tree. J. Theor. Biol. 145:199–206.

Cruiziat, P. 1998. Structural-functional tree models (SFTms): where should we go? *In* Second International Workshop on Functional-Structural Tree Models, Abstract Vol., INRA, Clermont-Ferrand (France), p 94.

Deo, N. 1974. Graph theory with applications to engineering and computer science. Prentice-Hall, Englewood Cliffs, NJ, 478 p.

Epstein, E. 1973. Roots. Sci. Am. 228:48–58.

Fahn, A. 1964. Some anatomical adaptations of desert plants. Phytomorphology 14:93–102.

Fitter, A.H. 1985. Functional significance of root morphology and root system architecture. *In* Ecological Interactions in Soil. Eds. A.H. Fitter, D. Atkinson, D.J. Read and M.B. Usher. Blackwell, Oxford, pp 87–106.

Fitter, A.H. 1986. The topology and geometry of plant root systems: influence of watering rate on root system topology in *Trifolium pratense*. Ann. Bot. 58:91–101.

Fitter, A.H. 1987. An architectural approach to the comparative ecology of plant root systems. New Phytol. 106 (Suppl.):61–77.

Fitter, A.H. and T.R. Stickland. 1991. Architectural analysis of plant root systems. 2. Influence of nutrient supply on architecture in contrasting plant species. New Phytol. 118:383–389.

Fitter, A.H. and T.R. Stickland. 1992. Fractal characterization of root system architecture. Funct. Ecol. 6:632–635.

Fitter, A.H., T.R. Stickland, M.L. Harvey and G.W. Wilson. 1991. Architectural analysis of plant root systems. 1. Architectural correlates of exploitation efficiency. New Phytol. 118:375–382.

Früh, T. and W. Kurth. 1999. The hydraulic system of trees: theoretical framework and numerical simulation. J. Theor. Biol. 201:251–270.

Gandar, P.W. and K.A. Hughes. 1988. Kiwifruit root systems. 1. Root-length densities. N.Z. J. Exp. Agric. 16:35–46.

Godin, C., Y. Guédon and E. Costes. 1999. Exploration of a plant architecture database with the AMAPmod software illustrated on an apple tree hybrid family. Agronomie 19:163–184.

Grimaldi, R.P. 1989. Discrete and combinatorial mathematics. An applied introduction. 2nd Edn. Addison-Wesley, Reading, MA, 722 p.

Hughes, K.A., P.W. Gandar and H.N. de Silva. 1995. Exploration and exploitation of soil by apple, kiwifruit, peach, Asian pear and grape roots. Plant Soil 175:301–309.

Knuth, D.E. 1973. The art of computer programming. Vol. 1. Fundamental Algorithms. 2nd Edn. Addison-Wesley, Reading, MA, 634 p.

Kurth, W. 1994. Growth grammar interpreter GROGRA 2.4. Berichte des Forschungszentrums Waldökosysteme, Vol. B 38. Universität Göttingen, 192 p.

Lafolie, F., L. Bruckler and F. Tardieu. 1991. Modeling root water potential and soil-root water transport: I. Model presentation. Soil Sci. Soc. Am. J. 55:1203–1212.

Liu, C.L. 1977. Elements of discrete mathematics. McGraw-Hill, New York, 294 p.

Long, C.A. 1994. Leonardo da Vinci's rule and fractal complexity in dichotomous trees. J. Theor. Biol. 167:107–113.

Lynch, J. 1995. Root architecture and plant productivity. Plant Physiol. 109:7–13.

MacDonald, N. 1983. Trees and networks in biological models. Wiley, Chichester, U.K., 215 p.

Mandelbrot, B.B. 1978. The fractal geometry of trees and other natural phenomena. *In* Geometric Problems and Biological Structures. Lect. Notes Biomath. 23:235–248.

Mandelbrot, B.B. 1983. The fractal geometry of nature. W.H. Freeman, New York, 468 p.

McMahon, T.A. and R.E. Kronauer. 1976. Tree structures: deducing the principle of mechanical design. J. Theor. Biol. 59:443–466.

Mendès France, M. 1981. De l'arbre de Leonardo da Vinci à la théorie de la dimension. Revue du Palais de la Découverte 10:52–60.

Murray, C.D. 1927. A relationship between circumference and weight in trees and its bearing on branching angles. J. Gen. Physiol. 10:725–729.

Niklas, K.J. 1994. Plant allometry. The scaling of form and process. Univ. Chicago Press, Chicago, 395 p.

Oppelt, A.L., W. Kurth, H. Dzierzon, G. Jentschke and D.L. Godbold. 2000. Structure and fractal dimensions of root systems of four co-occurring fruit tree species from Botswana. Ann. For. Sci. 57: 463–475.

Perttunen, J., R. Sievänen, E. Nikinmaa, H. Salminen, H. Saarenmaa and J. Väkevä. 1996. LIGNUM: a tree model based on simple structural units. Ann. Bot. 77:87–98.

Raimbault, P. 1991. Quelques observations sur les systèmes racinaires des arbres de parcs et d'alignements: diversité architecturale et convergence dans le développement. *In* L'arbre. Biologie et Développement. Ed. C. Edelin. Naturalia Monspeliensia, Montpellier, pp 85–96.

Richter, J.P. 1970. The notebooks of Leonardo da Vinci (1452–1519), compiled and edited from the original manuscripts. Dover, New York (Reprint of a work originally published by Sampson Low, Marston Searle and Rivington, London 1883), 367 p.

Riedl, H. 1937. Bau und Leistungen des Wurzelholzes. Jb. Wiss. Bot. 85:1–75.

Shinozaki, K., K. Yoda, K. Hozumi and T. Kira. 1964. A quantitative analysis of plant form—the pipe model theory. I. Basic analyses. Jap. J. Ecol. 14:97–103.

Sievänen, R., A. Mäkelä, E. Nikinmaa and E. Korpilahti. 1997. Preface. Special Issue on Functional-Structural Tree Models, Silva Fenn. 31:237–238.

Sinoquet, H. and P. Rivet. 1997. Measurement and visualization of the architecture of an adult tree based on a three-dimensional digitising device. Trees 11:265–270.

Spek, L.Y. and M. van Noordwijk. 1994. Proximal root diameter as predictor of total root size for fractal branching models. II. Numerical model. Plant Soil 164:119–127.

Tucker, A. 1980. Applied Combinatorics. Wiley, New York, 462 p.

van Noordwijk, M., L.Y. Spek and P. de Willigen. 1994. Proximal root diameter as predictor of total root size for fractal branching models. I. Theory. Plant Soil 164:107–117.

Werner, C. and J.S. Smart. 1973. Some new methods of topologic classification of channel networks. Geogr. Anal. 5:271–295.

West, G.B., J.H. Brown and B.J. Enquist. 1997. A general model for the origin of allometric scaling laws in biology. Science 276: 122–126.