Real and virtual root systems: Morphology, Leonardo's rule and L-systems

A. Oppelt[1], W. Kurth[2] & D. L. Godbold[3]

1: Universität Göttingen, Institut für Forstbotanik, Büsgenweg 2, D-37077 Göttingen, aoppelt1@gwdg.de
2: Universität Göttingen, Institut für Forstliche Biometrieund Informatik, Büsgenweg 4, D-37077 Göttingen, wkurth@gwdg.de
3: School of Agriculture and Forest Science, University of Wales, Bangor, Gwynedd LL57 2UW, d.l.godbold@bangor.ac.uk

Georg-August-Universität Göttingen

Institut für Forstliche Biometrie und Informatik
Institut für Forstbotanik

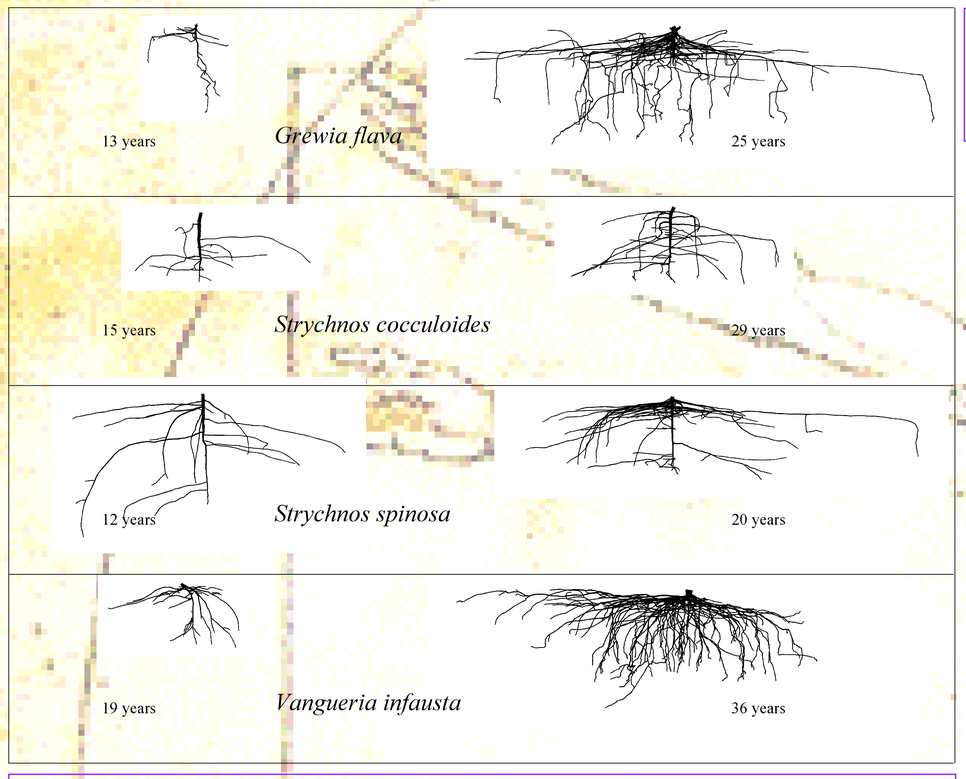
Introduction

Investigations of root structure of tropical tree species are few. However, information on the rooting structure of locally and economically important species can be of great benefits.
Special insights on diameter relations are shown. These informations are particularly relevant for hydraulic and morphological architecture of root systems as well as to explain survival strategies under extremely arid growth conditions.

Results and Discussion

Morphological reconstruction

A graphical output from GROGRA 3.2 shows the typical features of two root systems of each species with different ages (**Figure 1**).

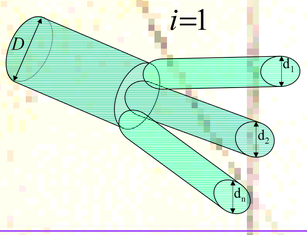


← **Figure 1:** Lateral view of coarse root systems in different age classes. Scale ≈1:60.

Leonardo's rule

According to Richter (1970), in Leonardo da Vinci's notebooks the following principle of construction of tree branching systems is sketched: In every branching node, the sum of the cross-section areas of the outgoing conducting elements balances the cross-section area of the mother element (**Figure 2**). Provided constant conductivities, this would imply equal velocities of flow throughout the branching system and is used as an assumption in numerous models (e.g. Shinozaki et al. 1964).

$$D^2 = \sum_{i=1}^{n} d_i^2$$



← **Figure 2**: Principle of Leonardo's rule.

species	slope (b)		intercept (c)		R^2	
	mean	std	mean	std	mean	std
Grewia flava	**0.9563**	*0.0426*	**0.3376**	*2.5061*	**0.9085**	*0.1160*
Strychnos cocculoides	**0.9971**	*0.0212*	**-2.5333**	*0.7530*	**0.9789**	*0.0104*
Strychnos spinosa	**0.9750**	*0.0189*	**-1.0718**	*1.7420*	**0.9613**	*0.0477*
Vangueria infausta	**1.0977**	*0.2061*	**-4.9107**	*7.7547*	**0.8785**	*0.0883*

↑ **Table 2**: Statistical fit of Leonardo's rule: $\Sigma d_i^2 = bD^2+c$.

In **Figure 3** one example from our population was chosen to show the relationship between the squared mother segment diameter (D^2) and the corresponding sum (S) extended over all daughter segments. Our statistical results in Table 2 show a very strong species-independent correlation between the two values with a regression coefficient (b) very close to 1.0, i.e. Leonardo's rule holds with great precision in our investigaed root samples.

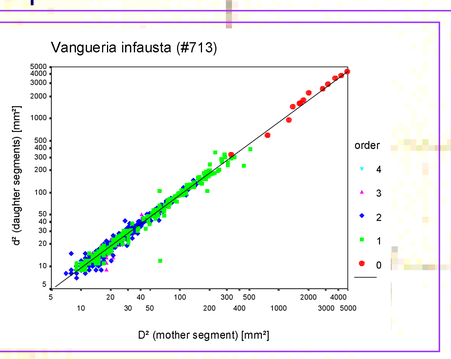


Figure 3: Correlation between D^2 and Σd_i^2.

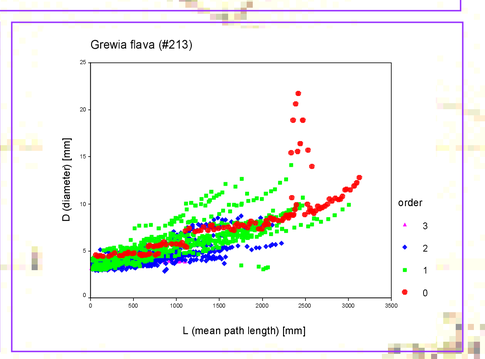


Figure 5: Diameter-pathlength-relation.

Methods

The architecture of *in situ* grown coarse root systems from *Grewia flava* [Tiliaceae], *Strychnos cocculoides*, *S. spinosa* [Loganiaceae] and *Vangueria infausta* [Rubiaceae] was studied in natural habitats.
The investigation site is located on sandveld near Mogorosi (Serowe Region, Central District, Botswana).
Each species was represented by five replicates, which were excavated by manual digging. According to their vertical and horizontal changes in growth direction, roots (> 3 mm) were devided into segments of different lengths, and their positions were recorded with a digital compass (TECTRONIC 4000). The diameters of the segments were measured with a digital calliper (MP 200).
The root systems were semi-automatically encoded, using the *dtd* coding system (digital tree data format, Kurth 1994). Subsequently, for 3-D reconstruction, topological and geometrical analysis of the root architecture and further morphological studies, the software GROGRA 3.2 (Kurth, 1994) was used. For more information, see Oppelt et al. (1999).

Global root system parameters

In **Table 1** global parameters from analysis of all excavated root systems are summarised.

species	id[1])	Age [yr]	rcd[2]) [mm]	trl[3]) [m]	r_{max}[4]) [m]	z_{max}[5]) [m]	b_{max}[6])	ibd[7]) [mm]	rld[8]) [cm/dm³]	δ [cm³/cm³]	rvd[9])
Grewia flava	**203**	25	97	191	5.7	2.3	3+ad	656	0.0806	0.0035	
	206	21	65	73	3.3	2.6	3+ad	459	0.0842	0.0033	
	213	18	58	59	3.3	3.2	3	554	0.0522	0.0016	
	214	14	32	20	1.6	2.0	3+ad	183	0.1219	0.0032	
	215	13	27	8	1.5	2.0	2+ad	33	0.0579	0.0019	
mean		**18**	**56**	**70**	**3.1**	**2.4**		**377**	**0.08**	**0.003**	
std		*5.0*	*28.2*	*72.4*	*1.7*	*0.5*		*174.1*	*0.03*	*0.00*	
median		**18**	**58**	**59**	**3.3**	**2.3**		**459**	**0.08**	**0.003**	
Strychnos cocc.	**405**	23	56	38	2.5	2.0	3	23	0.1011	0.0065	
	409	15	67	25	4.4	1.5	2	97	0.0263	0.0031	
	412	17	48	19	3.9	1.9	2	161	0.0207	0.0018	
	425	29	68	51	3.4	1.7	3	406	0.0814	0.0068	
	426	13	44	21	3.0	1.8	2	103	0.0403	0.0027	
mean		**19**	**57**	**31**	**3.4**	**1.8**		**158**	**0.05**	**0.004**	
std		*6.5*	*10.9*	*13.5*	*0.74*	*0.2*		*71.4*	*0.04*	*0.00*	
median		**17**	**56**	**25**	**3.4**	**1.8**		**103**	**0.04**	**0.003**	
Strychnos spinosa	**501**	20	72	114	6.0	1.7	2	426	0.0577	0.0029	
	508	12	60	43	4.2	3.1	2	396	0.0248	0.0021	
	509	17	40	11	1.4	2.1	2	39	0.0764	0.0073	
	510	15	64	49	2.8	1.3	2	138	0.1595	0.0096	
	511	12	44	35	2.7	1.7	2	194	0.0880	0.0038	
mean		**15**	**56**	**50**	**3.4**	**2.0**		**239**	**0.08**	**0.005**	
std		*3.4*	*13.6*	*38.4*	*1.8*	*0.7*		*194.1*	*0.05*	*0.00*	
median		**15**	**60**	**43**	**2.8**	**1.7**		**194**	**0.08**	**0.004**	
Vangueria infausta	**706**	36	140	207	5.1	2.5	5	309	0.1032	0.0062	
	708	21	86	52	3.6	2.4	4	178	0.0520	0.0030	
	711	19	48	25	1.7	1.3	5	142	0.2037	0.0106	
	712	25	60	25	1.2	1.8	4	120	0.2817	0.0123	
	713	25	70	35	1.5	1.1	4	252	0.4132	0.0177	
mean		**25**	**81**	**69**	**2.6**	**1.8**		**200**	**0.21**	**0.010**	
std		*6.6*	*35.9*	*78.2*	*1.7*	*0.6*		*70.1*	*0.14*	*0.01*	
Median		**25**	**70**	**35**	**1.7**	**1.8**		**178**	**0.20**	**0.011**	

1) identifying number of individual
2) root collar diameter
3) total root length
4) maximal radius of the whole root system
5) maximal depth of the whole root system
6) branching order; ad: adventitious roots
7) inter branching distance (mean of all branching orders)
8) root length density (rld = trl/$\pi r_{max}^2 z_{max}$)
9) root volume density (rvd = total root volume/$\pi r_{max}^2 z_{max}$)

↑ **Table 1:** Global prameters from excavated root systems in different age classes.

Tapering analysis

For tree crowns, McMahon & Kronauer (1976) proposed a simple power law describing branch tapering. Their model relates the local diameter (D) to the mean length (L) of all paths extending to the periphery (**Figure 4**).

In our data, the *D vs. L*-plot shows marked patterns corresponding to different branching orders (**Figure 5**). No global model seemed appropriate to describe these relationships. Hence, McMahon's and Kronauer's model cannot be applied directly to these below-ground systems.

Simulation

How can we check how good we have understood the characteristic architectural development of the root system of a species? One way is to *simulate* the growth of the root system in 3D space. Several approaches are possible. We have decided to use a *discrete* model: The basic elements are discrete entities (internally homogeneous), the root *segments* and root *tips*, which form together a branched network, representing the root system. New segments and tips are formed in fixed time steps according to a prescribed set of *rules*.

A formalism developed by the biologist Aristid Lindenmayer allows the representation of rules and branched structures in the form of simple character strings which can be manipulated with ease (L-systems, **Figure 6**). Such L-systems were already used to describe branching rules of above-ground plant parts in a very precise and reproducible way (Prusinkiewicz et al. 1994; Kurth 1999). They can be extended by *sensitive* rules allowing an interaction of plant organs with the environment (Kurth & Sloboda 1999). The translation of sensitive L-systems into time series of virtual shoot or root systems is done by the software GROGRA 3.2 (Growth Grammar Interpreter, Kurth 1994).
In our example (**Table 3**), sensitivity is restricted to the ability of root tips to sense their depth and gravicentric orientation. Parameters (fixed and stochastic) of the model are given in 9 declarations. Growth and architectural development is governed by 11 rules (+ 2 additional rules for graphical interpretation), and by a procedurally implemented method ensuring the persistence of cross-section area in each higher-order branching node.

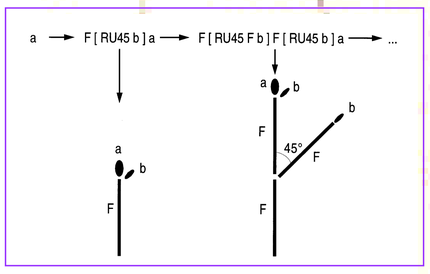


Figure 6: Application of the simple L-system $a \rightarrow$ F [RU45 b] a, $b \rightarrow$ F b.

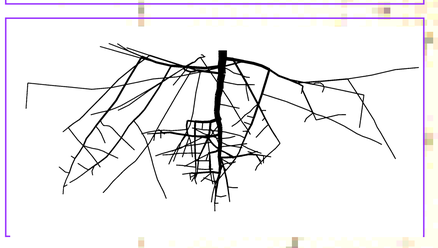


Figure 7: Artificial root system, resulting from the application of the L-system shown in **Table 3**, obtained with GROGRA after 20 simulated growth periods.

This L-system does not yet model a certain species, though its results (e.g. **Figure 7**) show already some resemblance to *Strychnos* root systems. We are currently in the process of modifying the rules and inserting measured root parameters to obtain a better resemblance. In this way, we can learn about the significance of certain architectural parameters for the overall structure of the root systems.

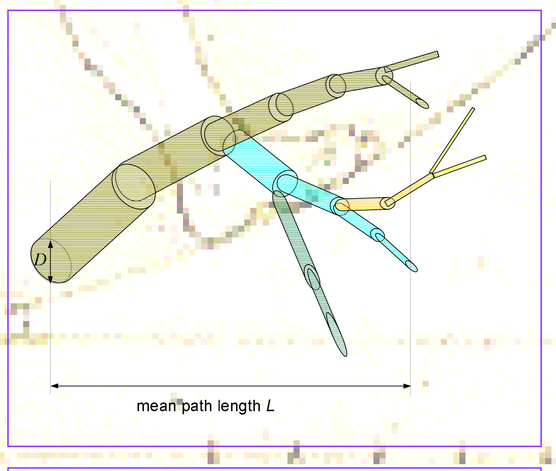


Figure 4: Principle of McMahon's and Kronauer's tapering rule.

```
/* declarations of model parameters: */
\const lb 10,                   /* basic length unit, pseudoshoot length (mm) */
\const l0 3,                    /* length unit for taproot (order 0)  */
\var devi normal 0 60,          /* deviation angle inside axis */
\var angle normal 85 20,        /* branching angle */
\var rr uniform 0 360,          /* random rotation angle */
\var z zcoordinate,             /* -depth */
\var elangle function 7 0,      /* elevation angle, relative to z axis */
\var diam diameter,             /* diameter from previous step */
\const di 0.2,                  /* initial diameter */
\askrandomseed,

/* start rule with method M2 to enforce Leonardo's diameter rule: */
* → RG tip(0, 0) M2,

/* generative rules for apical root growth and branching: */

(z>0.1) tip(t, o) → ,      /* root can't grow above ground */
/* taproot: */
(o=0) tip(t, o) → segment(0, o, di, l0) RG RL(devi) RH(rr) tip(t+1, o) ?0.3,
(o=0) tip(t, o) → segment(0, o, di, l0) RG RL(devi) RH(rr)
                  [ RU(angle) tip(0, o+1) ] tip(t+1, o) ?0.7, /* branching */
/* higher order roots: */
(o>1) tip(t, o) → ,        /* maximal branching order can't be exceeded  */
(elangle < ?0) tip(t, o) → ,   /* inhibition to grow upwards */
(o>0) tip(t, o) → segment(0, o, di, if(z>-20,lb,lb*0.3)) RU(devi) RH(rr)
                  tip(t+1, o) ?0.3,  /* length diminished below z = -20 */
(o>0) tip(t, o) → segment(0, o, di, if(z>-20,lb,lb*0.3)) RU(devi) RH(rr)
                  [ RU(angle) tip(0, o+1) ] tip(t+1, o) ?0.6, /* branching */
(o>0) tip(t, o) → ?0.1,    /* mortality of root tips */
(o>0) segment(t, o, d, l) → segment(t+1, o, d+0.15, l),  /* segment ageing */
segment(t, o, d, l) → segment(t+1, o, diam, l),

/* Interpretive rules: */
segment(t, o, d, l) ⇒  Dl(d) Pl(o+2) Ll(l) F,
tip(t, o) ⇒  Dl(di) Pl(0) Ll(0.1) F
```

Table 3: Exemplary L-system for root system development.

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