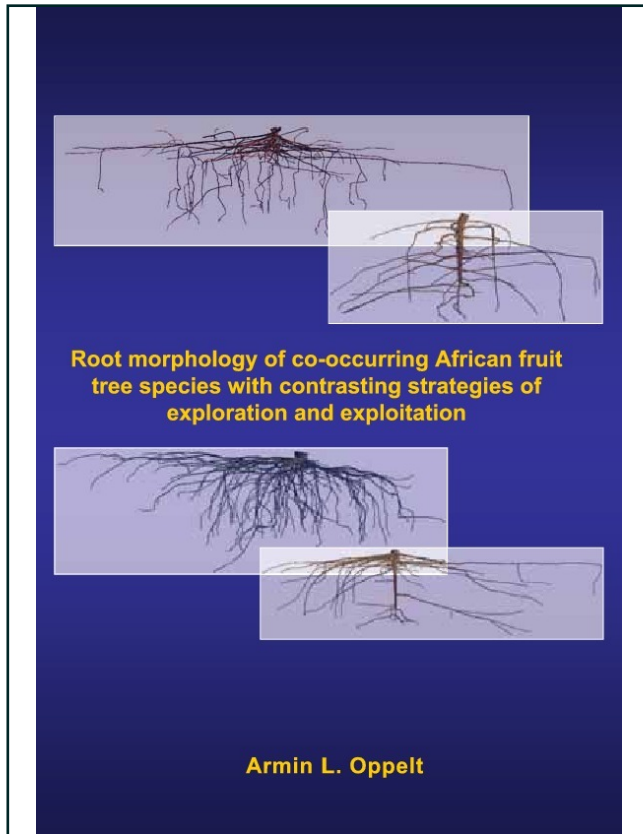Armin Oppelt (Autor)

# Root morphology of co-occurring African fruit tree species with contrasting strategies of exploration and exploitation



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# 1 Summary

Measurement of *in situ* grown and completely excavated coarse root systems (five individuals per species) from *Grewia flava* DC (Tiliaceae), *Strychnos cocculoides* BAK, *Strychnos spinosa* LAM (Loganiaceae) and *Vangueria infausta* BURCH (Rubiaceae) were used to derive several parameters describing *explorative* and *exploitative* features of the selected species. Additionally, systematic soil sampling was carried out to achieve information about morphological patterns of fine roots and data about spatial fine root distribution. Comparisons between fine root and coarse root characteristics are considered and correlations, concerning the spatial distribution of both entities, are calculated. Main focus was addressed to species-dependent architectural differences in order to select 'suitable', *i.e.* less competitive rooting patterns, sought-after for integration into sustainable agroforestry systems.

Each coarse root system was reconstructed with means of semi-automatic digitising in order to obtain 3-D models and to calculate the spatial distribution of root length density (*RLD*) and root volume density (*RVD*), respectively. With the aid of 3-D reconstruction it was possible to extract a large amount of information serving for various quantitative analysis. Apart from morphological and architectural distinctions, fractal characteristics, topological parameters, supplemented by link lengths analysis, dependencies between diameter and branching, as well as scaling relations were investigated, founded on a precise data basis. Furthermore, the spatial information was useful to quantify and assess several aspects of "*exploration*" and "*exploitation*", also including efficiency considerations, in order to estimate the potential competition of the selected species with agroforestry crops.

Measurements of fractal dimension *D* were conducted for comparison of space filling patterns and also to detect species-dependent differences. Discretisation of reconstructed spatial patterns, aided by the software GROGRA, made it possible to determine fractal *box counting dimension D* of complete, three-dimensional coarse root systems, thus bringing an improvement compared to recent literature where fractality was mostly investigated in small, herbaceous plants and using only 2D-projections. However, the *box counting dimension $D_{xy}$* of two-dimensional projections was also calculated, in order to compare both measurements with each other. Although the *box counting dimension* - for *D* and $D_{xy}$ - yields only very condensed information about spatial organization of the branching structure, results confirm different rooting strategies already obtained by visual inspection in the field and are also in accordance with other parameters obtained.

Going beyond the commonly used topological parameters, two new indices, $q_a$ and $q_b$, related to the well-known graph-theoretical *altitude a* and *mean topological depth*

Summary

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$b$, were developed. The introduction of these normed indices, confined to the interval [0;1], takes the different sizes of coarse root systems into account and ensures independence from planarity assumptions. Topological analysis was additionally complemented with analysis of external and internal link lengths. As topology also influences the source acquisition, the idea was born to compare architectural and topological features with the ability of *exploration* and *exploitation*. However, conscious that the used notions are normally not explicitly defined in the literature and also often used ambiguously, several quantitative methods, already established and applied in several investigations, were tested on the sample trees. An attempt was undertaken to clarify both notions and to apply already established parameters to the investigated coarse root systems and also to fine root samples.

The *exploration index* $E(0)$ and the *exploitation index* $E(\phi)$ were introduced and applied to coarse root systems as well as to fine root samples. In order to analyse potential competition of the coarse roots, the following parameters were additionally introduced: In an attempt to approximate soil volume explored by coarse roots, the parameter *number of explored cells NEC* was used. With the *exploration efficiency EE* and the new parameter *generalized efficiency of exploitation GEE($\phi$)*, efficiency aspects of *exploration* and *exploitation*, respectively, are also quantified. Thus, definitions from the literature, describing *explorative* and *exploitative* aspects, were further extended and generalized, in order to clarify commonly used notions.

Analysis of fine roots was carried out with digital image-analysis, using subsamples to measure the morphological parameters length, surface area, volume and average diameter of fine root samples, as well as the *planar box counting dimension $D_{xy}$*. Correlations between morphological parameters and *dry weight* (*Dwt*) were used to approximate whole fine root distribution and to evaluate species-specific differences in terms of competition.

The variation of ages and therefore different spatial extension of each single root system were taken into account by introducing an *individual soil volume ISV* adapted to each individual coarse root system. This volume was determined by the horizontal spread of the coarse roots and the coring depth of the fine root samples (80 cm). This accurate determination was beneficial, because a differing fine root distribution was detected inside and outside the *ISV*, and the considered rooting depth proved to adequately represent whole coarse root systems.

Clear distinctions arising from the analysis of the *box counting dimension D* have shown that coarse root systems from *Strychnos cocculoides*, with distinctively lowest values, were most contrasting with those from *Vangueria infausta*. In this regard *Grewia flava* and *Strychnos spinosa* have to be considered as intermediate species. Apparent evidence that $D$ values were well correlated with *RLD* are in agreement

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with the interpretation that the box counting dimension measures the tendency to fill space.

Findings from the topological assay, expressed as $q_a$ and $q_b$ values, resulted in evident differences, indicating that coarse root systems from *Strychnos cocculoides* were most of all approaching a "*herringbone*" branching pattern whereas *Vangueria infausta*, and *Grewia flava*, did more approximate a "*dichotomous*" configuration. *Strychnos spinosa* stands between both extremes. Results about *mean exterior link lengths* ($l_e$) are in close agreement with the above mentioned distinctions on branching patterns: samples from *Strychnos cocculoides*, representing the most *herringbone*-like type, and even *S. spinosa*, representing more intermediate patterns, were characterized by distinctively higher mean values, in contrast to the more *dichotomous* coarse root samples. Hence, the distinctive branching patterns are also correlated with the metric parameter $l_e$. In contrast, no species-specific differences were found for *mean interior link lengths $l_i$*. The empirical test of the theoretical assumption of Leonardo's rule, not yet tested on other coarse root systems, confirmed the "*pipe stem theory*" with reasonable accuracy. Furthermore, the relation between root collar diameter and total coarse root length respectively volume, often discussed but seldom applied to empirical data, yielded good correlations, independent of the considered species. However, analysis of a tapering rule, based on the theory of elastic similarity, did not show convincing results.

Comparing the values from the *exploration index $E(0)$* for a rooting depth between 0 and 80 cm, fine and coarse root distribution from *Strychnos cocculoides* turned out to be the least explorative species as opposed to the most competitive *Vangueria infausta*. Looking only at the fine roots, $E(0)$ values for both *Strychnos* species, were similarly low, indicating low competition levels, whereas a clearly transitional stage was assigned to *Grewia flava* samples. *Vangueria infausta*, as the most competitive representative, could be separated from all other species, and *Strychnos cocculoides* was still significantly different from the intermediate *Grewia flava*, For the coarse roots, variable and significant species-dependent differences were observed for $E(0)$, dependent on varying rooting depth. Considering a soil depth between 0 and 80 cm, *Strychnos spinosa* and *Grewia flava* were clearly standing between the most contrasting species *Strychnos cocculoides* and *Vangueria infausta*. Dependent on rooting depth, differences between the investigated species were even more pronounced for the upper soil layers. These differences lessened with increasing rooting depth. This can be explained by already decreasing values for $E(0)$ of coarse roots for *Grewia flava* and *Vangueria infausta* samples for a depth below 40 cm, whereas values of exploration indices were continuously increasing for both *Strychnos* species with increasing soil depths. In terms of *NEC*, *Grewia flava* and *Vangueria infausta*, with distinctively highest values, 'compete with each other' for a

superior position. But significant species-specific differences for *NEC* were only achieved when age was considered as a covariate. Looking at the *efficiency of exploration* (*EE*), compared with *E*(0) respectively *NEC*, it can be assumed that highly explorative species gain their outstanding status only with high efficiency, whereas those with low explorative ability do not reach this level of efficiency.

Regarding exploitation by fine roots, clear species-dependent differences (expressed as *k* values) occurred: *Vangueria infausta*, with highest value of *exploitation*, could be significantly distinguished from all other investigated species. Less distinct results were attained for the *exploitation index* for the coarse roots. $E(\phi)$ did not induce a clear ranking between the species. In contrast, for the parameter $GEE(\phi)$, also only applied to coarse roots, estimating the *efficiency of exploitation*, showed clear distinctions between the species, independent of considered $\phi$ values. *Strychnos cocculoides* was assigned the lowest mean value as opposed to *Grewia flava*. Ranking between the species was similar to that from *EE*, indicating that *efficiency of exploration* and *efficiency of exploitation* are closely related with each other.

In general, the results presented here do not support the frequently discussed hypothesis that a clear trade-off between *exploration* and *exploitation* exists. In the majority of cases, *Strychnos cocculoides* was always most contrasting with *Vangueria infausta*. Depending on the considered parameters *Grewia flava* and *Strychnos spinosa* were assigned intermediate patterns with more or less affinity to one of both extremes. These trends were well associated with topological distinctions, indicating a more *herringbone* configuration for both *Strychnos* species. Hence, features that clearly favour low competitive attitudes (deep rooting with pronounced tap root, associated with weakly branched laterals and even weak development of fine roots). In most instances, either *Grewia flava* or *Vangueria infausta* were most contrasting to *Strychnos cocculoides*. Comparing these results with the output from topological analysis, the observations coincide with a *dichotomous* branching configuration, associated with an intensive and dense network of roots, especially in topsoil layers. Hence, among the investigated species *Strychnos cocculoides* can be clearly favoured for the integration into simultaneous agroforestry systems. Whereas shallow rooting architecture, additionally associated with high explorative and exploitative potential and also with an intensive fine root development, contributes to a high potential competition with agroforestry crops. Samples from *Strychnos spinosa* stand between both extremes, but here, too, dependent on the considered parameters, the species can express a more or less competitive potential. Some tentative conclusions, concerning the general construction plans of coarse root systems, can be drawn: topological distinctions seem to be obviously associated with different morphological and/or architectural patterns, features that clearly affect *explorative* and *exploitative* behaviour. This also

determines the extend of species-dependent potential belowground competition. Whether this is a general construction plan also inherent to other species, can be elucidated only with further investigation. Comparison between coarse and fine root characteristics confirmed a tendency towards a 'common strategy'. For example, intensity of fine root development, easily obtained in the field, seem to be suitable to predict certain architectural features of their coarse root systems (and vice versa). These patterns can be used to estimate *explorative* and/or competitive ability of the species. The existence of contrasting branching patterns of co-occurring species can be interpreted as an effective means of spatial and/or temporal sharing of soil-derived sources. These distinctive features might be exceptionally important in arid and nutrient-poor habitats. Although it cannot be concluded which branching pattern is definitely more advantageous, the information gained supports decisions for the selection of 'suitable' species with low competition for simultaneous agroforestry systems.

The present work demonstrates that complete excavation combined with systematic core sampling can be a suitable method to obtain detailed information about the composition of whole root systems and to distinguish species-related differences. With the help of this approach it was possible to confirm the theory of contrasting rooting patterns in the same habitat. With the data obtained, species could be classified according to their potential competition with agroforestry crops.

## 2 General Introduction

The main focus of the present work was to distinguish rooting patterns of *in situ* grown species, *Strychnos cocculoides* Bak, *S. spinosa* Lam (Loganiaceae), *Grewia flava* DC (Tiliaceae) and *Vangueria infausta* Burch (Rubiaceae). These indigenous fruit trees are an important food source, especially for people practising subsistence dryland farming, because they yield crops even when arable agriculture fails, improving food security for rural households. Therefore, their suitability for integration into simultaneous agroforestry systems is of vital interest. In order to ensure sustainable yield benefits, a combination between trees and crops is necessary where spatial and temporal sharing between soil-derived resources is possible (Cannell et al. 1996). But for a possible co-existence with annual crops their rooting patterns must be 'suitable' in terms of competition. For integration of potential perennials into agricultural systems it is recommended that competition between trees and crops can be reduced by selecting species with limited lateral root extension and/or deep rooting species. Therefore, species-dependent rooting patterns were analysed, in order to evaluate the suitability of the investigated species for simultaneous agroforestry systems.

But, the key question appeared: May co-occurring species develop only similar or even contrasting rooting patterns when grown in the same habitat? Proceeding from the assumption that distinctive patterns of rooting architecture might occur, different parameters were tested, aiming at quantitative methods, mainly discussed under the aspect of competition.

Several agroforestry research efforts, however with contrasting results, have not yet managed to conclude which factors, either above or belowground, are more important for a successful co-existence of perennials and annual crops (e.g. Singh et al. 1989, Ong et al. 1991, Rao et al. 1991, De Costa and Chandrapala 2000a, 2000b). But results tend to indicate that belowground competition increases with severe drought conditions (Ong et al. 1991).

Main attention is turned to the investigation of whole root systems, including information on fine root distribution as well as architectural aspects of entire coarse root systems. But thought has also been given to aspects of complementarity considering potential soil conservation.