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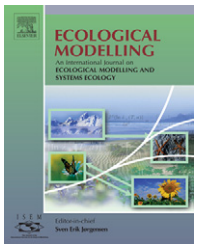

Short communication

Root tapering between branching points should be included in fractal root system analysis

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ABSTRACT

The proportionality factor (p) is a parameter used for fractal root system modelling. It describes tapering along root axes and is calculated by the ratio of total cross sectional area (CSA) before and after branching. The exact point where the area of the parent branch is measured is often not defined. By measurement of the CSA adjacent to a branching point tapering without branching is not included in factor p.

In this study p was measured on six tropical tree species (*Clethra revoluta*, *Graffenrieda emarginata*, *Vismia tomentosa*, *Weinmannia loxensis*, *Clusia* sp. and *Styrax foveolaria*). The measurement was conducted in three different ways, quantifying (i) tapering of roots by branching (p_{branch}), (ii) tapering without branching (p_{within}), and (iii) total root tapering (p_{total}). For five species p_{total} was significantly higher than p_{branch} ($p < 0.05$). For three species p_{within} contributed significantly more to p_{total} than p_{branch}. There was only a weak correlation between p and root segment diameter. The slope of the regression line was often higher for p_{within} than for p_{branch}. The results suggest that the exclusive use of p_{branch} in fractal branching models leads to an underestimation of total root system tapering and to an overestimation of total root system biomass and root length in fractal branching models. Furthermore in some species self-similarity decreases when tapering without branching is included in the proportionality factor p. This may imply that models should allow p to change with increasing diameter.

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1. Introduction

Leonardo da Vinci claimed in his notebook that the cross sectional area (CSA) of a tree trunk is equal to the sum of the CSA of branches at any higher level (Richter, 1970). In some cases, the assumption of area preserving branching was also confirmed for tree root systems even though variations between single branching points were large (Oppelt et al., 2001; Richardson and zu Dohna, 2003).

When branching at each subsequent level of a root system is governed by the same rules, the root system can be described as a self similar or fractal network (Spek and van Noordwijk, 1994; Richardson and zu Dohna, 2003). In fractal branching models tree specific scaling rules are assessed on the basis of easily observable parameters (Van Noordwijk and Mulia, 2002; Richardson and zu Dohna, 2003). The change of CSA during branching is often quantified by a proportionality factor (p) that is calculated as the ratio of total CSA before

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and after branching (Van Noordwijk and Mulia, 2002). Factor p affects the tapering of root systems and thus influences total root length and biomass at a given proximal diameter (Spek and van Noordwijk, 1994).

To test the assumption of the preservation of CSA or to quantify the rate of tapering along root axes for root system modelling, the exact point where the diameter of the parent branch is measured is often not defined (Ozier-Lafontaine et al., 1999; Oppelt et al., 2001). In other cases, branch diameters are measured adjacent to the branching point (Smith, 2001). This method may underestimate tapering along the root axes since tapering without branching is not included.

In this study the effect of the measuring point on factor p was tested on six different tree species growing in a tropical montane forest. It was hypothesized that the location of this point (at the beginning or at the end of the parent root segment) influences the predicted degree of root tapering.

2. Materials and methods

The study was performed at the Estacion Científica San Francisco (ECSF) near to the Podocarpus National Park in the South of Ecuador. The selected tree species grew at two different altitudes because measurements were part of another study. At the lower study site (1900 m a.s.l.; 03°58′S, 79°04′W) the species *Graffenrieda emarginata* (Ruiz & Pav.) Triana (Melastomataceae), *Clethra revoluta* (Ruiz & Pav.) Spreng. (Clethraceae) and *Vismia tomentosa* Ruiz & Pav. (Clusiaceae) were investigated. Here, average vegetation height was about 11 m. Soils were very acid, with an $pH_{(CaCl2)}$ about 3 and had an average depth of the forest floor of 0.15 m and a mineral soil >0.9 m depth.

At the upper study site (3000 m a.s.l.; 04°06′S, 79°10′W) the species *Weinmannia loxensis* Harling (Cunoniaceae), *Clusia* sp. (Clusiacaea) and *Styrax foveolaria* Perkins (Styraceae) were investigated. Average vegetation height was about 4 m. The soils were often waterlogged and characterized by deep forest floors (average of 0.3 m), shallow mineral soils (average of 0.4 m) and pH about 3.

Three individuals of every species were investigated at the lower altitudes, four individuals each at 3000 m. The coarse root systems were excavated in a semicircle of 1 m radius at one side of the stem, parallel to slope direction. Additionally one primary root of every tree was excavated entirely. With a hedge clipper the organic layer was carefully removed, leaving all coarse roots (≥5 mm in diameter) intact as well as all roots with a diameter ≥2 mm that originated from those coarse roots. Because of the dense vegetation at 3000 m it was not always possible to conserve this procedure at this altitude. In this case, as many coarse roots of a tree as possible were excavated. The diameter at the beginning and at the end of every root segment was measured. With help of the WanFBA helpfile (Van Noordwijk and Mulia, 2002), factor p was calculated in three different ways:

$$p_{\text{branch}} = \frac{D^2_{\text{before branching dist}}}{\sum D^2_{\text{after branching prox}}} \quad (1)$$

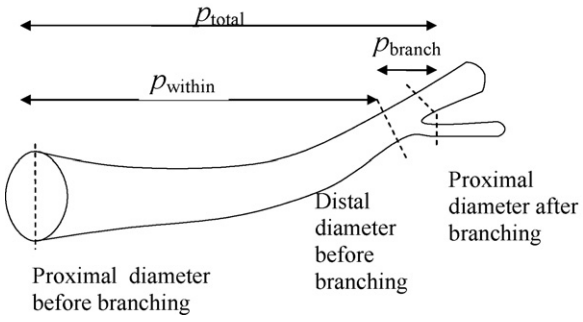

Fig. 1 – Measuring points of the parameters p_{total}, p_{within} and p_{branch}.

$$p_{\text{within}} = \frac{D^2_{\text{before branching prox}}}{D^2_{\text{before branching dist}}} \quad (2)$$

$$p_{\text{total}} = \frac{D^2_{\text{before branching prox}}}{\sum D^2_{\text{after branching prox}}} \quad (3)$$

where D is the diameter at the beginning (prox) or at the end (dist) of the respective root segment (Fig. 1).

2.1. Statistical analysis

Statistical analyses were realized with SPSS 11.0. For each species $p_{(\text{total})}$, $p_{(\text{within})}$, and $p_{(\text{branch})}$ values were compared pair wise by the nonparametric Wilcoxon-test.

3. Results

For the calculation of average p_{branch}, p_{within} and p_{total} 100 branching points per tree species were obtained randomly from all replicate observations, allowing a better comparability of standard errors between tree species than unequal numbers of replicates. Average data of p_{branch} ranged between 1.00 and 1.17 (Table 1). When tapering without branching was included (p_{total}) averages ranged from 1.12 to 1.50. Except for *G. emarginata* p_{total} was always significantly higher than p_{branch}. In three cases p_{within} was higher than p_{branch}. The p_{branch} of

Table 1 – Proportionality factor for different species measured by three different methods ($n = 100$)

Tree species	Proportionality factor		
	p_{branch}	p_{within}	p_{total}
C. revoluta	1.17 (0.04) a*	1.21 (0.09) a	1.38 (0.08) b
Clusia sp.	1.00 (0.02) a	1.13 (0.03) b	1.13 (0.04) b
G. emarginata	1.09 (0.04) a	1.02 (0.02) a	1.12 (0.04) a
S. foveolaria	1.16 (0.09) a	1.30 (0.12) a	1.50 (0.15) b
V. tomentosa	1.06 (0.02) a	1.31 (0.08) b	1.40 (0.09) c
W. loxensis	1.02 (0.03) a	1.13 (0.04) b	1.15 (0.05) b

* Data in parenthesis show standard error. Lower case letters (a, b, c) show differences between the methods at a 5% level (Wilcoxon Test).

Table 2 – The impact of the proportionality factor on the biomass of a simulated root with a proximal diameter of 100 mm and a minimal diameter of 5 mm, using the WanFBA software (Van Noordwijk and Mulia, 2002)*

Tree species	Root weight (kg)	
	p_{branch}	p_{total}
C. revoluta	5.18	3.59
Clusia sp.	12.18	6.22
G. emarginata	7.41	6.62
S. foveolaria	5.49	3.21
V. tomentosa	8.26	3.61
W. loxensis	14.02	6.00

* Other important parameters were defined as follows: "Nsub": 2.04; "Range_p": 0.69; "Mean_q": 0.74; "Range_q": 0.48; continuous relationship between root diameter and the length of a root segment with "Intercept": 25 cm, "Slope": 10 cm and "Range_l": 0.2 cm; wood density: 0.14 g cm^3 (roots < 20 mm in diameter), 0.24 g cm^3 (roots 20–50 mm in diameter) and 0.34 g cm^3 (roots > 50 mm in diameter).

Clusia sp. and *W. loxensis* was close to 1. Here, tapering of the root system was predominantly caused by tapering without branching. In general, the contribution of p_{within} and p_{branch} to total tapering was highly dependent on tree species, but usually the impact of p_{within} was higher than the impact of p_{branch}.

The impact of p on root biomass was assessed using the WanFBAviz3a version of the WanFBA software for branching analysis (Van Noordwijk and Mulia, 2002). Proximal and minimal root diameter, wood density and all branching parameters except for p were taken for given (Table 2). The proportionality factor was modified according to Table 1. Calculated root weight was always lower when p_{total} was used instead of p_{branch} (Table 2). This was most pronounced for *V. tomentosa* and *W. loxensis* where root weight was decreased by 56 and 57% when tapering between branching points was considered.

For the determination of scale dependence p_{total} and p_{within} were plotted against the proximal root segment diameter of the parent root while p_{branch} was plotted against its distal root segment diameter. Stability indices showed no correlation between p and root segment diameter (Table 3). However, for *S. foveolaria*, *V. tometosa* and *W. loxensis* the slopes of the regression lines were markedly higher for p_{within} and p_{total} than for

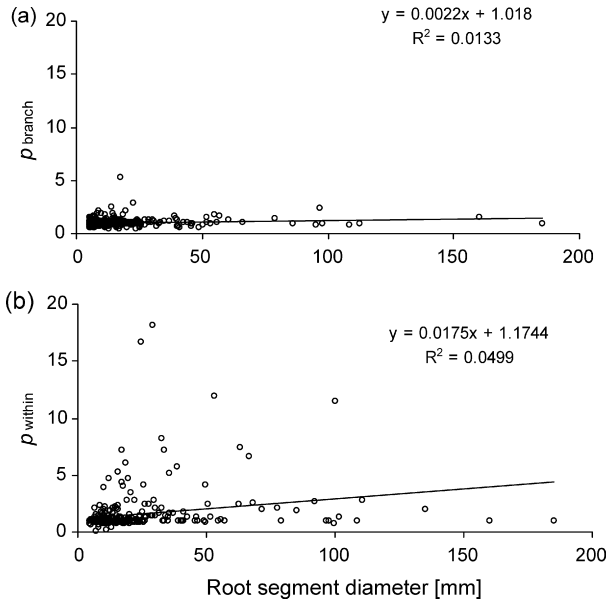

Fig. 2 – The impact of root segment diameter *D* on (a) tapering by branching and (b) tapering without branching from all root segments ($n = 345$) of *V. tomentosa*.

p_{branch}. Thus, p_{within} increased more with increasing diameter than p_{branch}. This is illustrated in Fig. 2 for *V. tomentosa* showing that tapering without branching occurred especially in the thick coarse roots while tapering by branching was more evenly distributed along the gradient of root segment diameters.

4. Discussion

Means of p_{branch} were consistent with those of tree root systems from other studies, which lay between 1.09 and 1.33 (Van Noordwijk and Purnomosidhi, 1995; Ozier-Lafontaine et al., 1999; Smith, 2001). Also the broad scattering of single p values is in accordance with these studies.

By including tapering without branching (p_{total}) means obtained in this study were often higher than p_{branch} (Table 1). With increasing deviation of p from 1 the assumption of area

Table 3 – Equation for the regression (R.E.) of p_{total} against the proximal link diameter D_{prox} (mm) and of p_{branch} against distal link diameter D_{dist} (mm) for different tree species and stability index (R^2)

Tree species	D_{dist} against p_{branch}		D_{prox} against p_{within}		D_{prox} against p_{total}		n
	R.E.	R^2	R.E.	R^2	R.E.	R^2	
C. revoluta	$Y = 0.0022x + 1.12$*	0.0256	$Y = 0.0010x + 1.23$	0.0012	$Y = 0.0012x + 1.36$	0.0017	317
Clusia sp.	$Y = 0.0023x + 0.96$	0.0078	$Y = 0.0031x + 1.08$	0.0146	$Y = 0.0045x + 1.03$	0.0196	295
G. emarginata	$Y = 0.0030x + 1.07$	0.0092	$Y = 0.0000x + 1.04$	0.0003	$Y = 0.0027x + 1.12$	0.0060	953
S. foveolaria	$Y = 0.0077x + 0.98$	0.0268	$Y = 0.0179x + 0.88$	0.0910	$Y = 0.0232x + 0.92$	0.1027	133
V. tomentosa	$Y = 0.0022x + 1.02$	0.0133	$Y = 0.0175x + 1.17$	0.0499	$Y = 0.0188x + 1.18$	0.0636	344
W. loxensis	$Y = 0.0044x + 0.97$	0.0299	$Y = 0.0103x + 1.01$	0.0614	$Y = 0.0149x + 0.98$	0.0755	268

* Y = link diameter and x = proportionality factor.

preservation looses its validity. Thus, even if area preservation may be true for the average of single branching points expressed by p_{branch} (Richardson and zu Dohna, 2003) it is not necessarily true for the entire root system.

Scaling rules for tree biomass (Y) normally follow the equation $Y = aD^b$ (Van Noordwijk and Mulia, 2002). In our example the variation between p_{branch} and p_{total} influenced both the constants a and b. The smaller p, the higher a and b and the more branching events were needed until the defined minimum diameter was reached (unpublished data). This had considerable consequences for the calculated root biomass (Table 2). Thus, when p_{branch} is much lower than p_{total}, the exclusive use of p_{branch} in fractal branching models may overestimate root system biomass. This might be of practical relevance for root related functions such as carbon storage (Brown et al., 2007). Richardson and zu Dohna (2003) included a separate factor for the rate of tapering between two branching points (the inverse of p_{within}) in their model, but in other models tapering without branching was neglected (Ozier-Lafontaine et al., 1999; Van Noordwijk and Mulia, 2002).

The lack of correlation between p and root segment diameter is in accordance with other studies (Van Noordwijk and Purnomosidhi, 1995; Smith, 2001). However, in the present study the slope of the regression line p against root diameter was often higher for p_{total} than for p_{branch}. If the dependence of the factor p on root size is pronounced, models have to be modified to allow p to change with root diameter (Van Noordwijk and Mulia, 2002; Richardson and zu Dohna, 2003). From a functional point of view a dependence of p from root diameter means that flow velocity or the proportion of xylem to total CSA may vary with root diameter (Van Noordwijk et al., 1994; Oppelt et al., 2001). The possible decrease in self similarity when using p_{total} instead of p_{branch} should be taken into account for root system modelling.

5. Conclusions

Depending on tree species root tapering without branching can have a great impact on total root system tapering. Thus, verification of fractal branching models is important especially for those tree species which differ considerably in p_{branch} and p_{total}. Self similarity of p_{total} is often lower than of p_{branch}. The use of several p values for different root diameter classes might be necessary when using p_{total}.

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