

Root architecture in relation to tree-soil-crop interactions and shoot pruning in agroforestry

M. VAN NOORDWIJK and P. PURNOMOSIDHI
ICRAF-S.E. Asia, P.O. Box 161, Bogor 16001, Indonesia

Key words: competition, fractal, multipurpose trees, root methods, root pattern

Abstract. Desirable root architecture for trees differs between sequential and simultaneous agroforestry systems. In sequential systems extensive tree root development may enhance nutrient capture and transfer to subsequent crops via organic pools. In simultaneous systems tree root development in the crop root zone leads to competition for resources.

Fractal branching models provide relationships between proximal root diameter, close to the tree stem, and total root length or surface area. The main assumption is that a root branching proportionality factor is independent of root diameter. This was tested in a survey of 18 multipurpose trees growing on an acid soil in Lampung (Indonesia). The assumption appeared valid for all trees tested, for stems as well as roots. The proportionality factor showed a larger variability in roots than in stems and the effects of this variability should be further investigated. A simple index of tree root shallowness is proposed as indicator of tree root competitiveness, based on superficial roots and stem diameter.

Pruning trees is a major way to benefit from tree products and at the same time reduce above-ground competition between trees and crops. It may have negative effects, however, on root distribution and enhance below-ground competition. In an experiment with five tree species, a lower height of stem pruning led to a larger number of superficial roots of smaller diameter, but had no effect on shoot:root ratios or the relative importance of the tap root.

Introduction

Competition for below-ground resources between trees and food crops may mask or surpass many of the advantages trees may provide for the long term sustainability of agroforestry systems. Competition depends on above-ground demand for water and nutrients, as well as possibilities for uptake. Here initial tests of a new method to characterize the competitive strength of trees, as far as it is based on root distribution, are described.

Agroforestry systems can be biologically more productive than either pure crop or pure tree systems provided that trees and crops are at least partly complementary in the use of resources (above- and/or below-ground). If the tree and crop component represent approximately equal direct value to the farmer relative to the area occupied, a weak complementarity is sufficient to justify agroforestry; if trees have less or no direct value, the complementarity has to be pronounced [Van Noordwijk, in press].

Tree-(food) crop interactions in agroforestry can be spatial, temporal or both (Fig. 1). The lower left corner of Fig. 1 does not classify as agroforestry as the interactions are too weak, the upper right corner is only viable for shade-

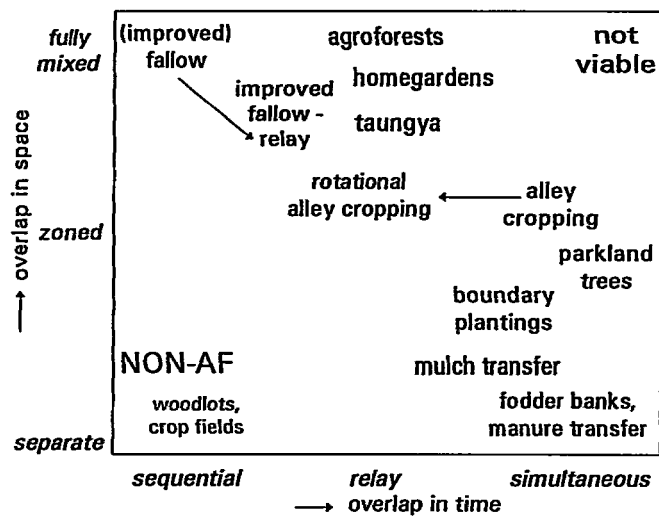


Fig. 1. Classification of agroforestry systems based on trees and food crops, by the degree of spatial and temporal overlap of trees and crops [Van Noordwijk, in press].

tolerant crops, as the interactions are strong [Van Noordwijk, in press]. Five main types of agroforestry systems based on trees and crops can be distinguished in this classification:

1. Upper left: *improved fallow* systems, where the trees and crops are completely separated in time, but spatially fully mixed;
2. Mid upper: *upper canopy tree* based systems, which allow for crop growth only in the early successional stages (taungya, homegarden, agroforests [sensu De Foresta and Michon, 1994];
3. Mid right: *hedgerow intercropping* systems or widely spaced upper canopy trees, which are spatially zoned, but where the tree and crop phase are fully integrated (e.g., coffee gardens with 'shade' trees);
4. Lower right: *mulch transfer* systems, where trees and crops are spatially separated;
5. The centre of the graph can be approached from upper left by improved fallow systems with relay cropping, or from mid right by rotational forms of hedgerow intercropping.

For complementarity of below-ground resource use, the major distinction is between simultaneous and sequential systems [Van Noordwijk et al., in press]. In sequential systems all biophysical interactions occur via soil conditions (i.e., its physical, chemical and biological fertility properties) at the end of the tree phase. On soils with sufficient nutrient reserves in the subsoil, deep rooted trees can act as 'nutrient pumps', bringing nutrients to the surface via litterfall. In simultaneous systems, competition for water and/or nutrients is of major importance, but if the tree roots occupy the zone just

underneath the crop roots, they can capture *current* losses from the crop root zone and can therefore act as 'safety-nets'. The safety net function is especially important for nutrients which, depending on rainfall surplus and apparent nutrient adsorption constant, leach so fast that they cannot be reached by a subsequent deep rooted (fallow) vegetation. Under high rainfall conditions the safety net function may yield at least as much N to companion crops as N fixation [Van Noordwijk et al., 1991a].

Rooting patterns that maximize root length density appear attractive for sequential (or spatially fully separated) agroforestry systems, as they probably increase nutrient capture by the tree and nutrient mobilization for the crop through organic residues. A dense tree root system probably also enhances biological formation of soil structure [Kooistra and Van Noordwijk, 1995]. Deep rooted trees in such systems may help to create the 'old tree root channels' which can help subsequent crops [Van Noordwijk et al., 1991a].

For simultaneous systems, which normally are spatially zoned, complementarity in root distribution between tree and crop is desirable to reduce competition. How effective the spatial zonation is in reducing below-ground interactions depends on the lateral spread of the (tree) root system. Trees which rely mainly on superficial root systems are probably highly competitive with shallow rooted crops, unless their above-ground phenology leads to reduced demand for water and nutrients in the period most critical for the crop.

The available evidence in the literature suggests that trees with a well-developed tap root but few laterals extending in the top soil will generally have slow initial growth [Coster, 1932; Van Noordwijk et al., in press]. The notion of 'fast-growing, non-competitive trees' may be a contradiction in terms, at least where the initial establishment phase is concerned. A further obstacle for managing simultaneous systems may be that above-ground pruning, to harvest tree biomass and/or to reduce shading, will have below-ground consequences. It probably enhances root turnover, which may be a positive effect, but may also induce death of root apices and formation of new adventitious roots which tend to grow in the upper soil layers. The latter effect was first described for *Peltophorum dasyrachis* [van Noordwijk et al., 1991b; erroneously identified as *P. pterocarpum* in the original publication]. As stem height left at pruning decreased, the number of proximal roots increased while their average diameter decreased. An experiment to test this effect for a range of tree species is described here.

Current root research methods on trees are laborious and cannot be directly related to farmers' criteria for selecting and judging the performance of trees. If root research stays in the domain of 'experts', it will not contribute to the development of agroforestry systems in the real world. The validity of generalizations about deep- or shallow-rooted trees, competitive and beneficial ones, is likely to be vastly overestimated, unless simple, non-destructive observation tools are developed that can be used to check root development for potentially any tree. As a first step in that direction, relations can be sought between the root diameter at the stem base (proximal roots) and functionally

important root parameters [Van Noordwijk and Brouwer, 1995] such as the total length or surface area of the fine roots. Soumaré et al. [1994] found in a study in Mali that for *Acacia seyal* and *Sclerocarya birrea* the root diameter at 1 m from the stem is a reasonable predictor of horizontal root spread.

In a 'fractal' branching pattern the same rules govern branching at each subsequent level [Fitter and Stickland, 1992; Van Noordwijk et al., 1994; Spek and Van Noordwijk, 1994]. The initial size (diameter) and the essential branching rules thus contain the information required to construct the whole pattern [Prusinkiewicz and Lindenmayer, 1990]. If root branching patterns have fractal characteristics, measurement of the proximal root diameter at the stem base and the branching rules as observed anywhere in the root system, would be enough to predict total root length, root diameter distribution and root length per unit dry weight (specific root length). Leonardo da Vinci claimed that the cross sectional area of a tree's main stem is equal to the sum of the cross sectional areas of its branches [Mandelbrot, 1983]. The same rule might apply to rivers, and may be based on the approximately constant volume of water passing through the river system from the sum of all sources to the final sink. A constant sum of squared diameters in trees might indicate a constant resistance to longitudinal water flow, if individual xylem cells have a constant diameter (the maximum of which is determined by the risk of forming air bubbles in large cells). For tree stems, stability and strength requirements [Coutts, 1983] may be as relevant as water transport capacities in determining stem diameters. The 'constant cross sectional area' or 'pipe-stem model' [Shinozaki et al., 1964] at least forms a valuable point of reference in studying the above-ground architecture of actual trees. A similar rule might apply to roots, but this assumption requires testing. For realistic representations of above-ground tree architecture many parameters are needed which go beyond the pipestem model [De Reffye et al., this volume]. Empirical relationships between stem diameter and root biomass [Kuiper et al., 1990] may be re-interpreted in the light of the pipe-stem model.

An algebraic model has been developed [Van Noordwijk et al., 1994] to derive the relation between total root system size and proximal root diameter for two extreme branching patterns: a dichotomous and a herringbone pattern. These patterns represent the wider classes of proportionate and determinate branching, respectively. The equations show that to predict total root length from proximal root diameter, information is needed on at least the minimum root diameter, the link ('internode') lengths as a function of root diameter and the proportionality factor α between total cross sectional areas before and after branching (Fig. 2). A further parameter, q , is defined as the ratio of the largest root diameter to the sum of all branch root diameters; in dichotomous systems q is 0.5, in herringbone patterns it gradually decreases from nearly 1 to 0.5. The parameter q is important for the length of the longest root and for the specific root length. Spek and Van Noordwijk [1994] presented an algorithm which can be used to explore these relationships for branching patterns intermediate between dichotomous and herringbone patterns. Here

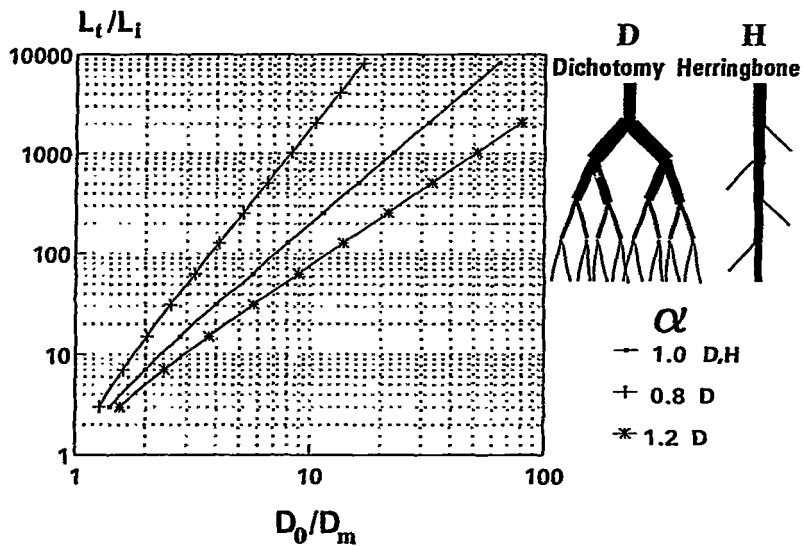


Fig. 2. Relation between the ratio of proximal (D_0) and minimum root (D_{min}) diameter and the number of links in a branched system (L_t/L_i , or the ratio of total and average link length) for a dichotomous (D) and herringbone (H) pattern, for various values of the proportionality factor α [Van Noordwijk et al., 1994].

initial tests of the validity of the main assumptions underlying these methods are described.

Material and methods

Site

Observations were made in North Lampung ($4^{\circ} 31' S$, $104^{\circ} 55' E$) on a gross-arenic kandiuult; soils are well drained, (very) low in CEC ($4-10 \text{ cm}_c \text{ kg}^{-1}$) and with a $\text{pH}(\text{H}_2\text{O})$ of 4.5–5.0 and a $\text{pH}(1 \text{ M KCl})$ of 3.8–4.2. Al toxicity is common, especially below a depth of 15 cm. Typical soil organic matter contents in the topsoil are 1.7–1.9%, root development is possible down to a plinthic layer at 1–1.5 m depth. Annual rainfall is about 2200 mm on average, with 1–4 months having less than 50 mm of rainfall. Further site description is given by Van Noordwijk et al. [1992].

Root survey

A number of multipurpose/fruit trees (see list in Table 1, one or two trees per species) were selected for a root survey from a homegarden close to the site of a long term soil fertility experiment, and the neighbouring village. Most trees were about six years old. The basal part of the roots at the stem base

Table 1. Root patterns of multipurpose trees on acid soil, North Lampung (Indonesia); preliminary survey of five to seven-year-old trees (mostly in homegardens).

Species	Root _{vert} :ΣRoot basal area ratio, A	Stem:ΣRoot basal area ratio, B	Index of shallow-rootedness (1-A)/B
<i>Leucaena leucocephala</i>	0.17	0.39	2.13
<i>Parkia speciosa</i>	0.23	0.46	1.67
<i>Annona muricata</i>	0.28	0.44	1.64
<i>Perunema canescens</i>	0.04	0.78	1.23
<i>Psidium guajava</i>	0.11	0.74	1.20
<i>Nephelium lappaceum</i>	0.15	0.77	1.10
<i>Pithecolobium jiringa</i>	0.10	1.00	0.90
<i>Gliricidia sepium</i>	0.18	0.94	0.87
<i>Paraserianthes falcataria</i>	0.17	0.86	0.97
<i>Eugenia aquea</i>	0.17	1.43	0.58
<i>Ceiba pentandra</i>	0.45	0.95	0.58
<i>Gnetum gnemon</i>	0.15	1.53	0.56
<i>Anacardium occidentale</i>	0.45	1.20	0.46
<i>Calliandra calothyrsus</i>	0.75	0.64	0.39
<i>Peltophorum dasyrachis</i>	0.74	0.69	0.38
<i>Artocarpus heterophyllus</i>	0.69	0.89	0.35
<i>Durio zibethinus</i>	0.75	1.14	0.22
<i>Artocarpus integer</i>	0.84	0.86	0.19
<i>Mangifera indica</i>	0.85	1.04	0.14

was carefully excavated, in a half sphere of 0.5–1 m radius. Root diameter and angle from a horizontal plane were measured for all proximal roots, i.e., roots originating from the stem base or as laterals from the top part of the tap root. Stem diameter D_{stem} was measured at breast height, or as ‘root collar’ diameter for pruned trees; stem basal area was calculated as πD_{stem}^2 . The basal area of roots with an angle from the horizontal plane of less than 45° was calculated as $\pi \Sigma D_{hor}^2$, and for those with vertical orientation as $\pi \Sigma D_{vert}^2$. An *index of root shallowness* was calculated as $\Sigma D_{hor}^2 / D_{stem}^2$, or as ratio of basal area of all horizontally oriented roots and the stem.

Test of fractal branching

To test the independence of branching rules from root diameter (a key assumption for the fractal model), parts of the root system were exposed, by tracing roots from the stem base. For each branching point where both the previous and subsequent ‘links’ had been exposed, root diameter before and after the branching point was recorded and the α parameter calculated as $D_{before}^2 / \Sigma D_{after}^2$. The allocation parameter q was calculated as $\max(D_{after}^2) / \Sigma D_{after}^2$. Regression of α , q and link length on root diameter was analyzed per tree with linear and non-linear models in Genstat-V. The null-hypothesis of ‘no relation’ was tested with a 5% probability level. Similar measurements were made on above-ground branching patterns of the same tree.

Effects of tree pruning height on root distribution

For five tree species (*Calliandra calothyrsus*, *Senna (Cassia) siamea*, *Gliricidia sepium*, *Paraserianthes (Albizia) falcataria* and *Peltophorum dasyrachis*) the effects of repeated tree pruning at 0.5, 0.75 or 1 m height on proximal root diameter and orientation were studied. Tree species were used as main plots, pruning height as a split-plot factor. Trees were planted at a distance of 2×0.5 m and were not intercropped. Pruning consisted of removing all above-ground biomass except for the stem, to the height indicated, at three-month intervals for two years. Observations were made on six trees for each pruning height. Further details of the experiment are given by Hairiah et al. [1992]; proximal root data were re-analyzed for this publication.

Results

Proportionality factors α and q in relation to diameter

In none of the 29 trees tested was a significant regression of α or q on D found, for stems or roots. When data for all tree roots and stems were combined ($n = 4607$ and 5112 branching points, respectively), again no significant regression was found.

Figure 3 shows that the α values for shoots were mostly in the 0.85–1.05

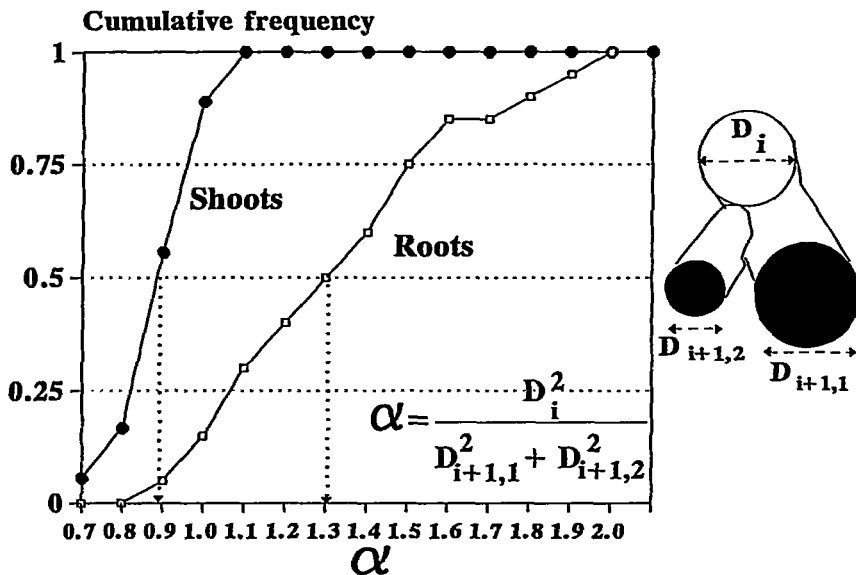


Fig. 3. Cumulative frequency of the α parameter of shoots and roots (averaged per tree) for multipurpose trees in Lampung.

range, while for roots the mean α per tree ranged from 0.9–2.0. The overall mean value for α for roots in the combined-data set was 1.328 with a standard deviation of 0.5377. The α of shoots cannot be used to predict the α of roots (Fig. 4).

The allocation parameter q (by definition restricted to the range 0.5–1) had a mean of 0.765 for the stems of all trees combined (5112 branching points), with a standard deviation of 0.144, with an even spread over the 0.5–1 interval (Fig. 5). For roots the mean value was 0.8552, with a standard deviation of 0.1475, and a clear over-abundance of values in the range 0.9–1 (Fig. 5).

Link length was not correlated with diameter for the roots; above ground a weak relationship was found, mostly based on the unbranched portion of the main stem.

Stem basal area at breast height was 40–150% of the total root basal area (Fig. 6). The contribution of vertically oriented roots to the total root basal area ranged from 0.11–0.85. The values obtained for the 'index of tree root shallowness' ranged from 0.14–2.13 (Table 1), with the highest value for the shallow rooted *Leucaena leucocephala* and the lowest value for the relatively deep rooted *Mangifera indica*.

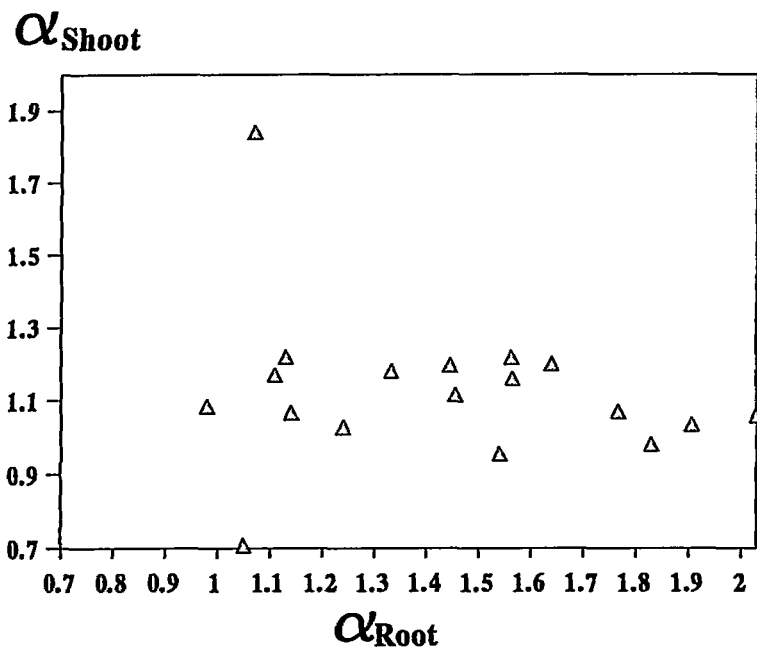


Fig. 4. Relation between average α of shoots and roots per tree; no statistically significant regression was obtained.

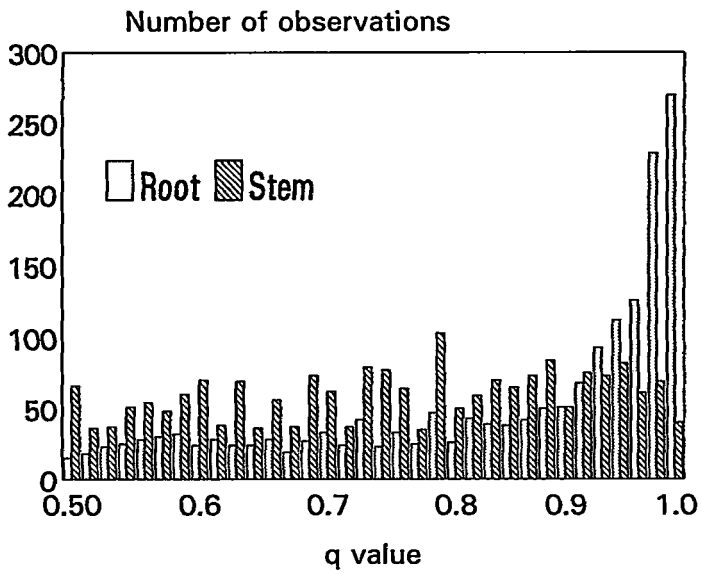


Fig. 5. Frequency distribution of q for roots and stem (based on 4607 and 5112 branching points, respectively, for all trees combined).

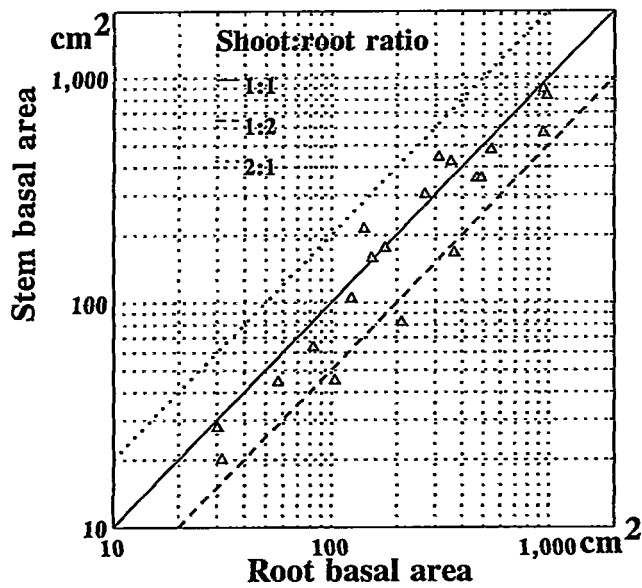


Fig. 6. Relation between the basal area of all proximal roots and stem basal area for 18 trees.

Pruning height experiment

A low pruning height did indeed lead to more but thinner adventitious roots for four of the five species tested. *G. sepium* was an exception as it made thick fleshy storage roots at low stem pruning height. Table 2 gives the main effects of tree species and pruning height. Pruning height had no effect on the ratio between cross-sectional area of the tap-root and all adventitious roots combined (A). No consistent effect was found on the index of root shallowness (last column). The average value of this index for these pruned trees was higher than that reported in Table 1 for *C. calothyrsus*, similar for *P. dasyrachis* and lower for *G. sepium*.

Discussion

Our preliminary results show that the assumptions of fractal branching models hold in that α and q are independent of root diameter. Thus, fractal models can be applied, at least as an approximation. Caution is needed, however, as the considerable variability in α and q within each root system may affect the relationships based on an average value, as the algebraic relations are non-linear.

Le Roux [1994] described root development of rubber trees and applied the SARAH model [Pagès and Aries, 1988]. The model follows root development from the primary axis and adventitious roots into secondary, tertiary and quaternary branch roots. For each class of root a different length of bare root tip and density of next order branching was found, suggesting that a fractal (scale-independent) description can only give a first approximation [Pagès et al., 1995]. Secondary thickening of roots is described as a function of time in the model of Le Roux [1994], and is not explicitly linked to branch root development. Both branch root development and diameter increase, however, are exponential functions of time and thus the model is not in contradiction with the fractal model description tested here.

Total basal area of stems and roots is clearly related across the tree species tested here, with a narrow range of shoot:root ratios. No architectural relationship was found, however, between shoot and root systems of the tree species in the sample, and the α and q parameters for roots cannot be predicted from the corresponding parameters for shoots, which are easier to measure.

The height of stem pruning had no consistent effect on the index of root shallowness, as the relative importance of the tap root remained constant. Possible differences in orientation of finer and thicker adventitious roots were not quantified. The hypothesis that a lower above-ground tree pruning height induces a shallower root system could not be confirmed by the present data. A lower pruning height does have an effect, however, on the number and diameter of proximal roots. The physiological basis for this effect may be

Table 2. Effect of tree pruning height on number and proximal diameter of adventitious roots; the last three columns are based on cross sectional area (diameter²) ratios; only main effects of pruning height and tree species are given, although a species × treatment interaction was indicated, with *G. septium* roots responding less than those of other trees [data re-analyzed from Hairiah et al., 1992].

	Avg. diam. of advent. roots, mm	Number of adventitious roots per diam. class (mm)			Root _{vert} : ΣRoot _{hor} : basal area ratio, A	ΣRoot:Stem basal area ratio, B	ΣRoot _{adv} :Stem basal area ratio, (1-A)/B
		< 5	5-20	20-40			
Grand mean	6.1	12.2	5.8	0.8	0.58	0.72	0.58
Pruning height (cm)							
50	5.2	15	6	0	0.59	0.86	0.48
75	6.2	11	6	1	0.55	0.63	0.71
100	6.8	10	6	1	0.60	0.67	0.60
Tree species							
<i>Paraserianthes falcataria</i>	5.9	11	6	1	0.66	1.01	0.34
<i>Girardinia septium</i>	8.5	7	5	1	0.72	0.60	0.47
<i>Peltophorum dasyrachis</i>	5.9	10	6	0	0.61	0.82	0.48
<i>Senna siamea</i>	6.7	7	4	1	0.72	0.60	0.70
<i>Calliandra calothyrsus</i>	5.1	20	8	1	0.37	0.66	0.96

found in the loss of apical control by the meristems of the main roots, as the recovery from pruning takes longer at reduced pruning height. Whether this is caused by reduced carbohydrate storage in the shorter stems or by a smaller number of buds resprouting, supplying fresh carbohydrates as well as hormonal signals, should be investigated further.

The results of this study indicate that the proximal root method and the 'index of tree root shallowness' as an indicator of competitiveness do require further testing. They may, however, provide a bridge between farmer-level observations ('trees with visible surface roots are competitive'), through the allometrics of root branching patterns to the functioning of roots in uptake of nutrients and water and thus to one of the major components of tree-soil-crop interactions. Combination of the fractal geometry and direct measurements of water flow through individual roots [Ong and Khan, 1993] may help to make this link.

Acknowledgements

Thanks are due to Mang Uyen for allowing us to dig around his homegarden trees, to Mrs Subekti Rahaya and Betha Lusiana with help in analyzing the data and to Dr Chin Ong, Dr Roger Leakey, Mr Richard Coe and two anonymous reviewers for comments on the manuscript.

References

- Coster Ch (1932) Wortelstudiën in de tropen (Root studies in the tropics). I. De jeugdontwikkeling van het wortelstelsel van een zeventigtal boomen en groenbemesters (Early development of the root system of seventy trees and green manure species). Korte Meded vh Boschb Proefst no. 29
- Coutts MP (1983) Root architecture and tree stability. *Plant and Soil* 71: 171–188
- De Foresta H and Michon G (1994) Agroforests in Sumatra, where ecology meets economy. *Agroforestry Today* 6(4): 12–13
- De Reffye P, Houllier F, Blaise F, Barthelemy D, Dauzat J. and Auclair D (1995) A model simulating above- and below-ground tree architecture with agroforestry applications. *Agroforestry Systems* (this issue)
- Fitter AH and Stickland TR (1992) Fractal characterization of root architecture. *Functional Ecology* 6: 632–635
- Hairiah K, Van Noordwijk M, Santoso B and Syekhfani MS (1992) Biomass production and root distribution of eight trees and their potential for hedgerow intercropping on an ultisol in Lampung. *AGRIVITA* 15: 54–68
- Kooistra MJ and Van Noordwijk M (1995) Soil architecture and distribution of organic carbon. In: Carter MR (ed) *Structure and Organic Carbon Storage in Agricultural Soils*. *Advances in Soil Science* (in press)
- Kuiper LC, Bakker AJJ and Van Dijk GJE (1990) Stem and crown parameters related to structural root systems of Douglas fir. *Wageningen Agric Univ Papers* 90-6: 57–67
- Le Roux Y (1994) Mise en place de l'architecture racinaire d'*Hevea brasiliensis*, étude comparée du semis et de la microbouture. Thesis doctorat, Université d'Aix Marseille III, Aix Marseille, France

- Mandelbrot BB (1983) *The Fractal Geometry of Nature*. Freeman, New York, NY, USA
- Ong CK and Khan AAH (1993) The direct measurement of water uptake by individual tree roots. *Agroforestry Today* 5(4): 2–4
- Pagès, L, Le Roux Y and Thaler P (1995) Modélisation de l'architecture racinaire. *Plantations, Recherche, Développement* 1995(1): 19–34
- Pagès L. and Aries F (1988) SARAH: Modèle de simulation de la croissance, du développement et de l'architecture des systèmes racinaires. *Agronomie* 8: 889–896
- Prusinkiewicz P and Lindenmayer A (1990) *The Algorithmic Beauty of Plants*. Springer-Verlag, Berlin, Germany, 302 pp
- Shinozaki K, Yoda K, Hozumi K and Kira T (1964) A quantitative analysis of plant form – the pipe model theory. *Japanese Journal of Ecology* 14: 97–105
- Soumaré A, Groot JJR, Koné D and Radersma S (1994) Structure spatiale du système racinaire de deux arbres du Sahel: *Acacia seyal* and *Sclerocarya birrea*. Rapport PSS no. 5, Wageningen, The Netherlands, 45 pp
- Spek LY and Van Noordwijk M (1994) Proximal root diameters as predictors of total root system size for fractal branching models. II. Numerical model. *Plant and Soil* 164: 119–128
- Van Noordwijk M, Widiyanto, Heinen M and Hairiah K (1991a) Old tree root channels in acid soils in the humid tropics: important for crop root penetration, water infiltration and nitrogen management. *Plant and Soil* 134: 37–44
- Van Noordwijk M, Hairiah K, Syekhfani M and Flach EN (1991b) *Peltophorum pterocarpa*: a tree with a root distribution suitable for alley cropping. In: Persson H and McMichael BL (eds) *Plant Roots and Their Environment*, pp 526–532. Elsevier, Amsterdam, The Netherlands
- Van Noordwijk M, Widiyanto, Sitompul SM, Hairiah K and Guritno B (1992) Nitrogen management under high rainfall conditions for shallow rooted crops: principles and hypotheses. *AGRIVITA* 15: 10–18
- Van Noordwijk M, Spek LY and De Willigen P (1994) Proximal root diameters as predictors of total root system size for fractal branching models. I. Theory. *Plant and Soil* 164: 107–118
- Van Noordwijk M (in press) A simple model to quantify mulch and shade effects. In: Huxley PA and Ong CK (eds) *Tree-Crop Interactions – a Physiological Approach*, Chapter 3. CAB International, Wallingford, UK
- Van Noordwijk M and Brouwer G (1995) Roots as sinks and sources of carbon and nutrients in agricultural systems. *Advances in Agroecology* (in press)
- Van Noordwijk M, Lawson G, Groot JJR and Hairiah K (in press) Root distribution in relation to nutrients and competition. In: Huxley PA and Ong CK (eds) *Tree-Crop Interactions – a Physiological Approach*, Chapter 10. CAB International, Wallingford, UK