# Exploring below ground complementarity in agroforestry using sap flow and root fractal techniques

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**Abstract.** Indices of shallow rootedness and fractal methods of root system study were combined with sapflow monitoring to determine whether these 'short-cut' methods could be used to predict tree competition with crops and complementarity of below ground resource use in an agroforestry trial in semiarid Kenya. These methods were applied to *Grevillea robusta* Cunn., *Gliricidia sepium* (Jacq.) Walp., *Melia volkensii* Gürke and *Senna spectabilis* syn. *Cassia spectabilis* aged two and four years which were grown in simultaneous linear agroforestry plots with maize as the crop species. Indices of competition (shallow rootedness) differed substantially according to tree age and did not accurately predict tree:crop competition in plots containing trees aged four years. Predicted competition by trees on crops was improved by multiplying the sum of proximal diameters squared for shallow roots by diameter at breast height[2], thus taking tree size into account. Fractal methods for the quantification of total length of tree root systems worked well with the permanent structural root system of trees but seriously underestimated the length of fine roots (less than 2 mm diameter). Sap flow measurements of individual roots showed that as expected, deep tap roots provided most of the water used by the trees during the dry season. Following rainfall, substantial water uptake by shallow lateral roots occurred more or less immediately, suggesting that existing roots were functioning in the recently wetted soil and that there was no need for new fine roots to be produced to enable water uptake following rainfall.

## Introduction

Novel simultaneous agroforestry systems have generally failed to deliver the sustainably increased crop yields which were expected of them (Sanchez, 1995). Competition for resources rather than complementarity in resource sharing has been frequently reported for simultaneous agroforestry. At semiarid sites in particular, below ground competition can outweigh the perceived advantages of having trees and crops simultaneously occupying the land (Ong et al., 1996).

Numerous attempts have been made to identify tree species with root system morphologies which indicate that they are likely to compete little with shallowly rooted crops (Jonsson et al., 1988; Schroth, 1995). However, progress is slow because conventional root measurement techniques such as

coring and excavations are time-consuming and expensive. Furthermore, determination of root distributions alone is not sufficient to provide a reliable estimate of their potential competitivity with crops. For example, although Jonsson et al. (1988) reported that fine roots of *Eucalyptus camaldulensis* and *E. tereticornis* were relatively less concentrated in surface horizons than fine roots of other species, Onyewotu et al. (1994) found that the surface roots of *E. camaldulensis* devastated crop yield within 18 m of a shelterbelt in northern Nigeria. Clearly, whether tree roots will compete aggressively with crop roots for below ground resources is not simply a matter of root distribution, but also of root functioning.

Recently, Howard et al. (1997) attempted to explore below ground complementarity of *Grevillea robusta* and crops by attaching a sap flow gauge to the tree trunk in order to assess the effect on sapflow of removing the top soil which is explored by crop roots. Top soil removal enabled quantification of the water contributed by deep roots. Such an approach provides a valuable description of root functioning but requires extensive excavation and is somewhat impractical for a comparison of several tree species or for monitoring during cropping seasons.

Recently, van Noordwijk and his colleagues (van Noordwijk et al., 1994; Spek and van Noordwijk, 1994; van Noordwijk and Purnomosidhi, 1995) described simpler, less time consuming methods for studying root systems. These techniques are based on allometry, fractal branching principles from which simple equations to estimate root variables are derived, and indices of shallow rooting (root competition indices).

The overall objective of this study was to determine whether these simpler approaches to root system study could be combined with sap flow techniques to determine the extent, functioning and competitivity of tree root systems in simultaneous agroforestry.

## Materials and methods

### Study site

The study was conducted at ICRAF's uplands semiarid zone research station at Machakos in Kenya which is located about 70 km southeast of Nairobi at an elevation of 1600 m. The bimodal rainfall averages 740 mm per annum and is more or less equally distributed between the two rainy seasons. Soils are weakly to moderately leached Kandic Rhodustalfs (USDA), alternatively Lixisols (FAO). They are well drained, friable, dark reddish brown, weakly acidic, erodible and contain moderate amounts of organic matter. Trees were planted at 1 m spacing in single lines in the centres of plots which measured either 20 × 20 m (four years old) or 40 × 40 m (two years old). The trial was established in four randomised blocks with a single replicate plot of each tree species and a control plot lacking trees in each block. Most tree species

were managed as upper storey with branch pruning to limit shading and produce branch-free trunks as practiced in farmers' fields, but *Senna spectabilis* was also managed by hedging, i.e., bi-annual coppicing to about 1 m height to simulate its use in fodder/mulch production. All prunings were removed from the plots.

Plot areas surrounding the trees were cultivated by hand at the start of the rains and were sown with beans (*Phaseolus vulgaris* cv. Rosecoco) during the short rains (mid-October to January) and maize (*Zea mays* cv. Katumani composite) during the long rains (mid-March to July).

*Root architecture and competitivity indices*

To test the validity of the fractal branching principle of root structure (van Noordwijk et al., 1994), tree roots of *Grevillea robusta* Cunn., *Gliricidia sepium* (Jacq.) Walp., *Melia volkensii* Gürke and *Senna spectabilis* syn. *Cassia spectabilis* were excavated by hand using small implements. Roots were selected at random and then excavated and measured for fractal variables to determine whether fractal principles applied to the root systems under study. Figure 1 illustrates the derivation of the fractal variables but more detailed information and the equations necessary to estimate the total number of root links are provided by van Noordwijk et al. (1994). Where the fractal principles hold, there should be no significant relationship between root diameter before branching and:
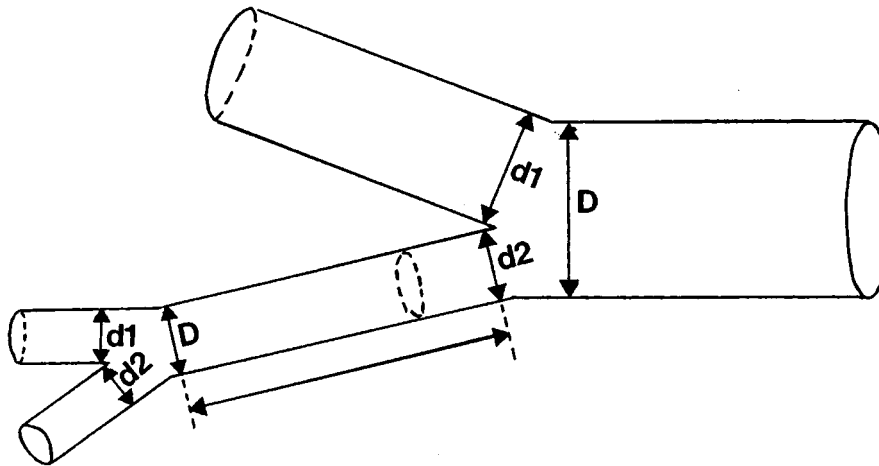a) the quotient of root diameter squared before branching to the sum of root diameters squared after branching ($\alpha$);



*Figure 1.* Representation of a piece of root showing the measurements necessary to generate fractal variables. Alpha and $Q$ (see text) are obtained from root diameters at individual branching points as follows: $\alpha = D^2/(d_1^2 + d_2^2)$; $Q = d_1^2/(d_1^2 + d_2^2)$ and link length is the length of root between successive branches as depicted by the long arrow.

b) the quotient of maximum diameter squared after branching to total diameter squared after branching ($Q$); and

c) the length of the root axis between successive branching points (link length).

Actual length was measured on 11 excavated roots of *Senna spectabilis* and compared with estimates made using fractal variables derived as above. However, whereas the validity of the technique for assessing coarse root amounts was established by van Noordwijk et al. (1994), the capacity of the method to accurately quantify fine root amounts is untested, largely because in the field, it is extremely difficult to excavate roots thinner than about 2 mm undamaged. In the current study, fractal information was collected for fine roots (< 2 mm diameter) of all studied species after washing out the root systems of two-year-old pot grown plants.

The diameters of all roots at their origins on the stem/root collars of at least two trees of *Grevillea robusta*, *Gliricidia sepium*, *Melia volkensii* and *Senna spectabilis* (hedged as well as unhedged) in each replicate block were recorded and used to calculate competitivity indices. To generate the index, stem diameter at breast height was recorded and shallow roots were defined as those that descend into soils at angles of < 45°. The index of shallow rootedness (competitivity index) was calculated following van Noordwijk and Purnomosidhi (1995), i.e.

$$CI = \frac{\sum D^2_{\text{horizontal}}}{D^2_{\text{stem}}}$$

where *CI* is competitivity index, $D^2_{\text{horizontal}}$ is proximal diameter squared of roots descending into soil at angles less than 45° and $D^2_{\text{stem}}$ is the square of stem diameter at breast height (dbh).

*Root function – sapflow*

Heat pulse sensors described by Khan and Ong (1996) were inserted into the stem, two lateral roots and two 'tap roots' (roots which originate at the root collar and penetrate soil at angles close to 90°) of four-year-old *Grevillea robusta* and *Gliricidia sepium* trees and into the stems only (because of limitations on available data logging capacity), of four-year-old *Croton megalocarpus*, *Melia volkensii* and *Senna spectabilis* trees. During each measurement period, three randomly selected individual trees were monitored in single species plots in block 3 of the randomised trial. Sensors were moved to three other randomly selected trees in the same plots after three weeks of observation to avoid causing long term wounding damage to roots and stems.

Sap velocity (cm h$^{-1}$) was converted into sap volume flow by multiplying sap flow velocity by root or stem cross-sectional area as appropriate and where roots were monitored, for each tree, total lateral and tap root volume flows were calculated by proportional scaling. That is, the average (of three)

measured sapflows (g cm$^{-2}$) in lateral roots was multiplied by total cross-sectional area of all lateral roots for each monitored tree. Similar calculations enabled assessment of sapflow through tap roots for each monitored tree.

Initially, the accuracy of sapflow measurements was assessed using lysimeters to independently monitor plant water use by small trees and subsequently, a potometer confirmed that sapflow measurements accurately reflected water use. The relationship between water uptake from the potometer and estimates made with sapflow sensors had $r^2 = 0.82$ (Anon., 1997), and when all sapflow was assessed in the stem and in all roots of a five-year-old *Grevillea robusta* tree, estimated total root sapflow was virtually identical to estimated sapflow through the stem.

### Soil moisture

A time domain reflectometry (TDR) system (Campbell Scientific, Shepshed, UK) with sensors located at depths of 20, 30 and 40 cm recorded soil moisture content at 20 minute intervals at distances of 1.5, 3 and 4.5 m from trees in agroforestry plots and in the centres of treeless control plots. Values were averaged and output every six hours. Soil moisture at greater depths was monitored weekly using a neutron probe; measurements were made at 20 cm intervals between 35 and 175 cm depth at distances of 1, 2.5, 4, 5.5, 7 and 8.5 m from rows of trees.

### Crop yield

Total crop yields (maize) in each plot were assessed as dry weight of grain obtained by destructive harvesting of the whole (20 m × 20 m) plot. Data were expressed as percentage of the yield in control plots lacking trees. Crop yield in control plots and in plots containing differing tree species had four replications.

## Results

### Competitivity indices and crop yield

Competitivity indices for the differing tree species showed dramatic changes as trees aged from two to four years (Table 1). Analysis of variance confirmed a significant interaction between tree species, *CI* and tree age ($P \leq 0.001$). *Grevillea robusta*, which was one of the least competitive species (Table 1), had the smallest index of competition at age two, but it had almost the largest *CI* at age four. Excepting the hedged *Senna* treatment, *CI*s of four-year-old trees were not significantly different from each other. Although hedging substantially reduced *CI* of *Senna spectabilis*, there was no significant difference in *CI* between hedged and unhedged *Senna* trees which highlights

the extent of variation in intraspecific *CI*. At two years of age, *CI*s of *Senna* and *Grevillea* were significantly smaller than those of *Gliricidia* and *Melia* ($P \leq 0.001$). *Melia volkensii*, which had the most negative effect on crop yield in this and in previous trials, had the largest (most competitive) index of competition for trees aged two years. However, competitivity indices calculated when trees were four years of age, unexpectedly suggested that *Melia* should be the *least* competitive of the unhedged species, which was not the case (Table 1).

Crop yield was recorded only in the oldest trial (aged four years, plot size 20 m × 20 m) because tree:crop competition was minimal at year 2 in the trial with 40 × 40 m plots. Analysis of variance confirmed that crop yields in plots containing *Melia* trees were significantly smaller than in plots containing other tree species ($P = 0.05$) but there were no other significant differences in crop yield between plots containing other tree species. Given that the competition index for hedged Senna was significantly smaller than those of *Grevillea* and *Gliricidia* and there were no significant differences in crop yield in plots containing these three tree species, these data do not agree with van Noordwijck and Purnomoshidi's (1995) theory that *CI* is related to competitiveness with associated crops, at least when calculated for trees at four years of age. As calculated, the index is standardised for tree size, but in use, the index neglects the importance of size differences when making actual comparisons in the field. There was a significant negative relationship between mean plot dbh and plot crop yield with $r^2 = 0.3$ and $P \leq 0.05$ and a significant positive relationship ($r^2 = 0.33$ and $P = 0.01$) between the sum of $D^2_{horizontal}$ and dbh illustrating the potential influence of overall tree size on tree:crop competition. Figure 2 illustrates the relationship between crop yield and horizontally orientated tree roots in the second season in 1996 where tree size was taken into account by using the product of dbh and sum of $D^2_{horizontal}$ as the independent variable, $r^2$ was 0.38 and $P \leq 0.01$. In contrast to the lack of relationship between *CI* and crop yield, this result shows a promising relationship between crop yield and components of the tree root system.

*Fractal determination of root length*

Figure 3 illustrates the relationships of alpha, *Q* and link length with root diameter for *G. robusta*. All of the data presented in Figure 3 were obtained in the field and hence observations for the finer root fractions are excluded. No significant relationships between the fractal variables and diameter were observed for data derived from coarse roots (thicker than 2 mm) and hence conditions required for fractal analyses were satisfied. Comparison of actual coarse root length and fractally derived coarse root length gave good overall agreement: total measured root length was 33.2 m and total fractally estimated root length was 35.3 m. Likewise, there was no significant difference between mean measured lengths of the 11 *Senna* roots 3.02 ± 0.4 m (SE) and mean

*Table 1.* Mean diameters at breast height[a] and competitivity indices[b] for root systems of four tree species aged two and four years growing in semiarid Kenya, and yield of interplanted crops at age four of trees as percent of crop yields from control plots without trees. (Figures in parenthesis are standard errors of means.)

| Tree age (years) | Tree species | Diameter at breast height (cm) | Competitivity index | Crop yield % of control |
|---|---|---|---|---|
| 2 | *Grevillea robusta* | 2.78 (0.36) | 0.06 (0.03) | – |
| 2 | *Senna spectabilis* | 3.43 (0.27) | 0.16 (0.02) | – |
| 2 | *Melia volkensii* | 4.05 (0.24) | 1.19 (0.13) | – |
| 2 | *Gliricidia sepium* | 3.05 (0.23) | 0.48 (0.08) | – |
| 4 | *Grevillea robusta* | 8.80 (0.49) | 0.65 (0.13) | 57.5 (9.2) |
| 4 | *Senna spectabilis* | 7.42 (0.32) | 0.42 (0.07) | 42.3 (5.4) |
| 4 | *Melia volkensii* | 12.07 (0.77) | 0.41 (0.12) | 29.6 (3.1) |
| 4 | *Gliricidia sepium* | 6.30 (0.30) | 0.69 (0.12) | 50.5 (11.2) |
| 4 | *Senna spectabilis* (hedged) | 7.70 (0.14) | 0.16 (0.03) | 57.6 (3.8) |

[a] Diameters of hedged trees were measured close to the point of stem severance at c̲ 1 m height.

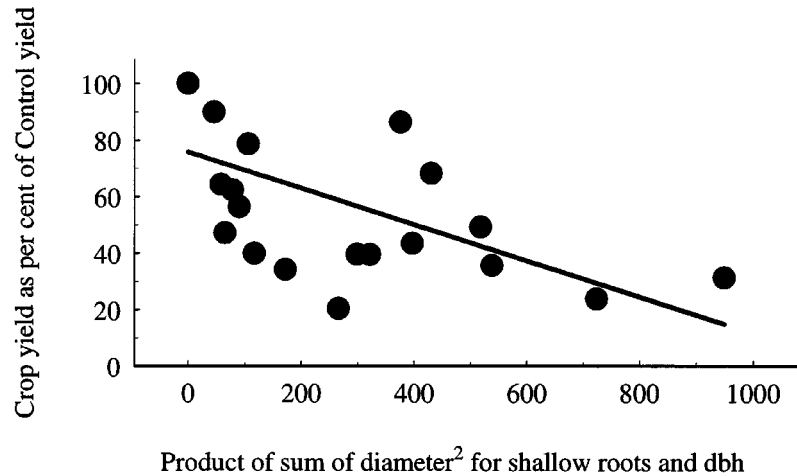[b] Sum of diameter$^2$ of all horizontal roots/stem diameter$^2$.

*Figure 2.* Relationship between the product of diameter at breast height and sum of proximal root diameter$^2$ for shallow roots and crop yield expressed as a percentage of that obtained in control plots lacking trees at Machakos in semiarid Kenya.

fractally derived length 3.21 ± 0.25 m (SE). However, differences between measured and fractally derived length for individual coarse roots were much more variable. Minimum and maximum differences were factors of 0.07 and 1.48 of measured root length respectively. Good overall agreement between both methods was not unexpected because 'fractal length' is essentially derived from the total number of root links, and average link length and thus intuitively, the method should work. Fractal variables for fine roots were derived from three to five pot grown trees for each of *Gliricidia sepium*, *Grevillea robusta* and *Senna spectabilis* and although these fractal variables were usually unrelated to root diameter, fine root length was seriously underestimated by fractal techniques. Figure 4 illustrates measured root length and root length estimated from fractal relationships for *Gliricidia sepium* roots where maximum root diameter was less than 2 mm. Comparative results for *Grevillea robusta* were even poorer; fractally derived length estimates were smaller than measured length by up to a factor of 20. When fine and coarser root data were combined for each species, a significant positive relationship between alpha and root diameter resulted. Alpha values for *Gliricidia sepium* roots in the range 0.1 to 4 mm diameter are illustrated in Figure 5, $r^2 = 0.27$ and $P < 0.001$. Such relationships invalidate the use of fractal methods for the estimation of total root system length. Further, with this particular example from a single root system, there was a significant relationship between diameter and alpha for fine roots. Diameter frequency plots (Figure 6) indicate that distinct populations of fine roots exist and that for *Gliricidia sepium*, such roots have diameters less than 0.7 mm.
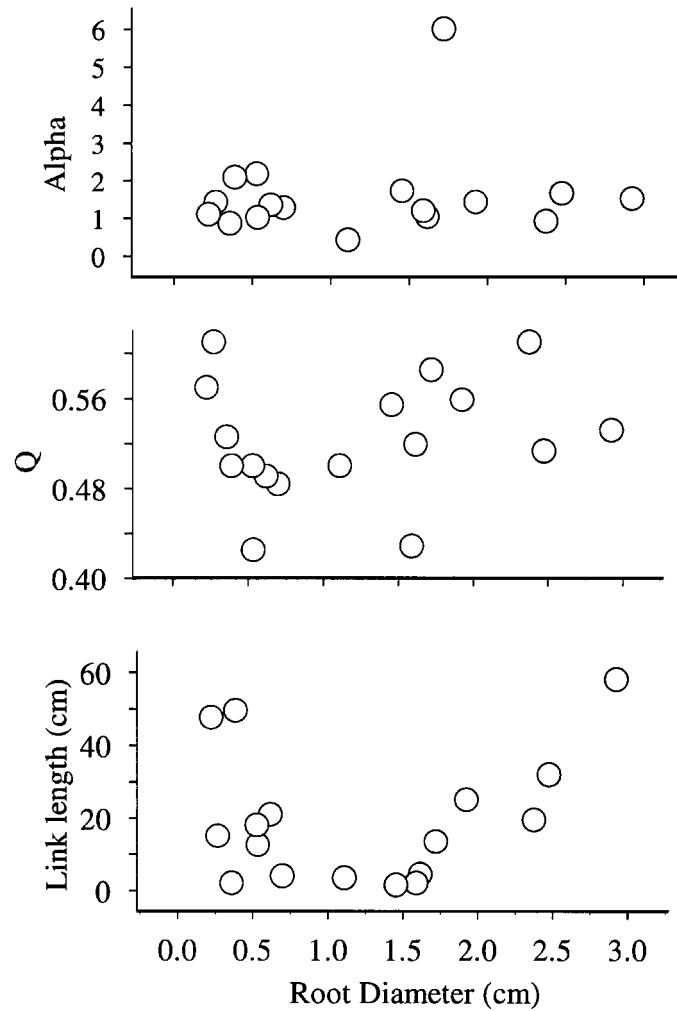
*Figure 3.* Relationship between root diameter and a) the parameter α (the quotient of total root cross-sectional area above and below branching points), b) the parameter *Q* (quotient of the square of largest root diameter after branching to sum of all root diameters squared after branching) and c) linklength (root length between successive branches) for roots of *G. robusta* trees in semiarid Kenya.

*Sapflow studies*

Figure 7 illustrates velocity of sapflow through the stem and lateral roots of a *Grevillea robusta* tree. Before day 316, little rain fell and although the soil surface was wetted, rain penetrated less than 20 cm as shown by the lack of response of the TDR sensors situated at that depth (Figure 8). Concurrently, sapflow velocities in lateral roots approximated half the velocity of stem
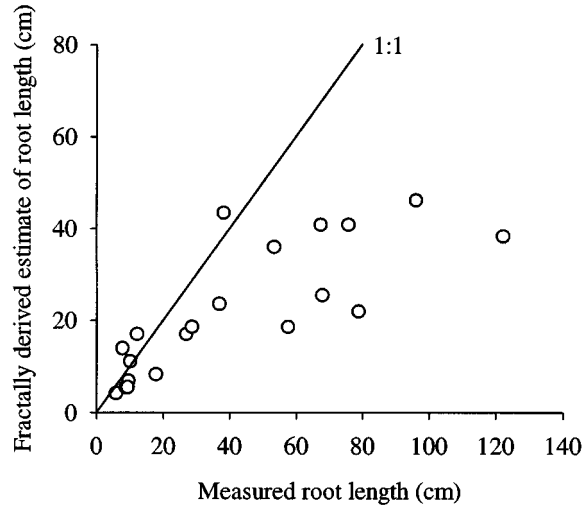
*Figure 4.* Relationship between root length estimated from fractal variables and measured root length for pot grown *Gliricidia sepium* roots less than 2 mm diameter.
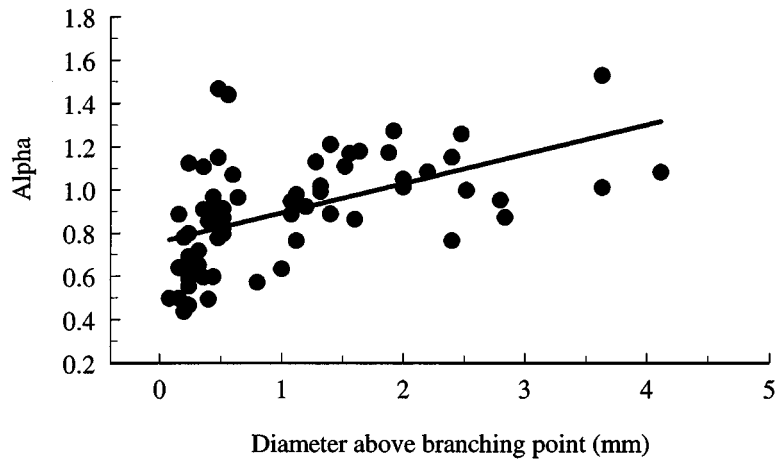


*Figure 5.* Relationship between diameter above branching points on *Gliricidia sepium* roots in the range 0.1 to 4.4 mm diameter and the fractal variable $\alpha$.

sapflow (Figure 7), and at night, lateral root sapflow was negligible. On day 316 a much greater volume of rain fell. Sap velocity in the stem immediately doubled indicating that prior to the rain, transpiration was limited by water availability rather than atmospheric demand. At the same time, sap velocity in lateral roots increased from about 50% of that in the stem to about 80% of that in the stem and at night, sap velocity in lateral roots greatly exceeded that in the stem.
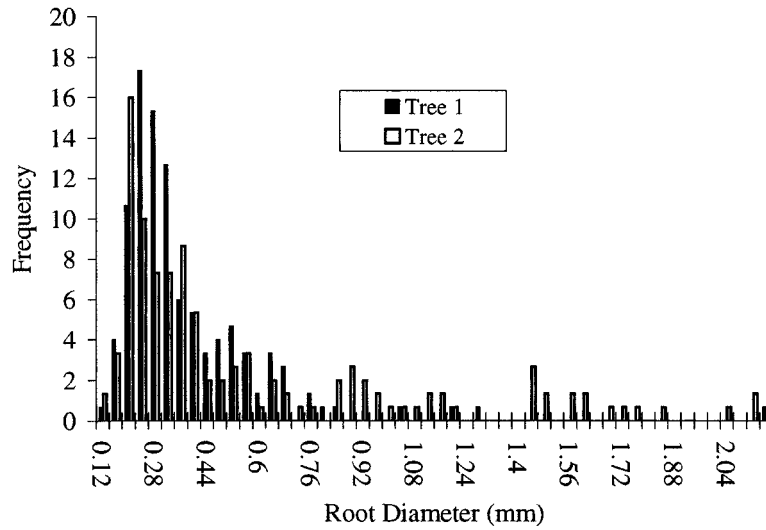
*Figure 6.* Diameter frequency distributions for *Gliricidia sepium* roots 0.1 to 2.3 mm diameter which were cut from two pot grown trees.
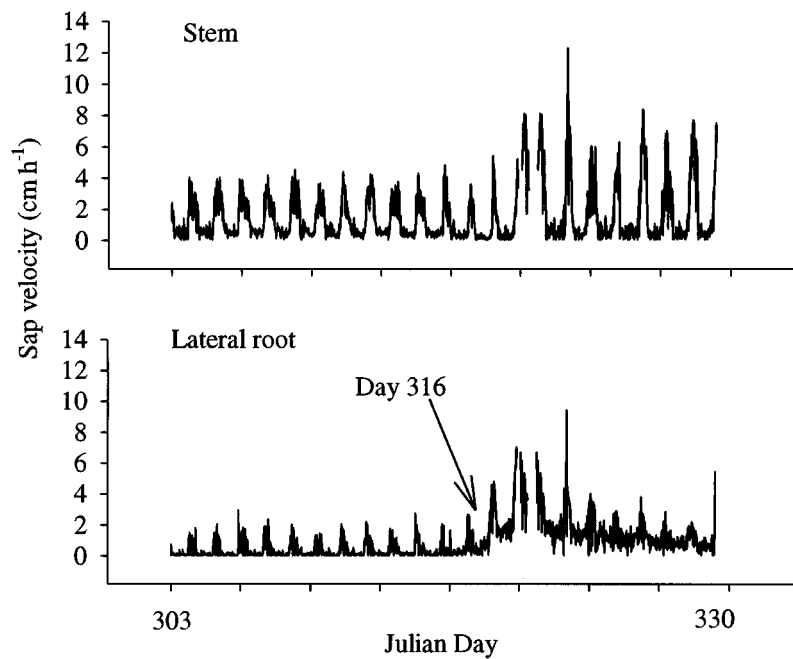


*Figure 7.* Xylem sap velocity in the stem and a lateral root of a *Grevillea robusta* tree when the surface soil was dry (up to Julian Day 316) and after substantial rainfall at Machakos in semiarid Kenya.
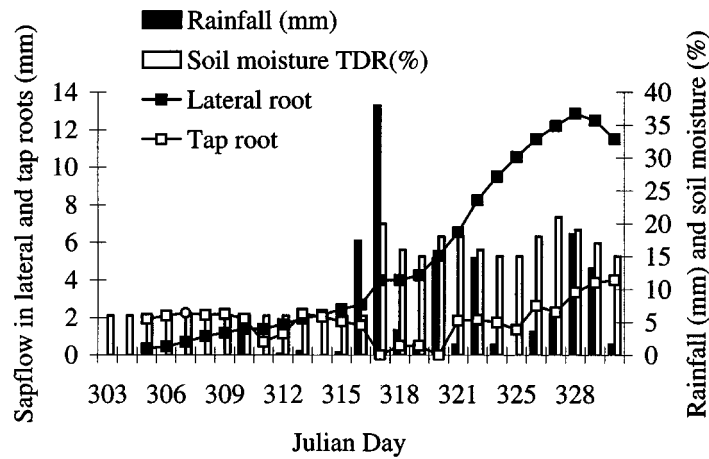
*Figure 8.* Rainfall, soil volumetric moisture content 20 cm below ground and sap flow in lateral and tap roots of a *Grevillea robusta* tree between Julian Days 303 and 330 at Machakos in semiarid Kenya.

With *Grevillea*, the sum of the sap volume flow from all roots gave good agreement with the volume of sap flowing through the stem in each 24 hour period (Figure 9). Even although sapflow through the stem exceeded that from roots during daylight hours, at night, root sapflow exceeded sapflow in stems. Consequently, each day, sapflow through roots, more or less balanced that through the stem, and water transpired from storage in plant organs during daylight was replenished at night.
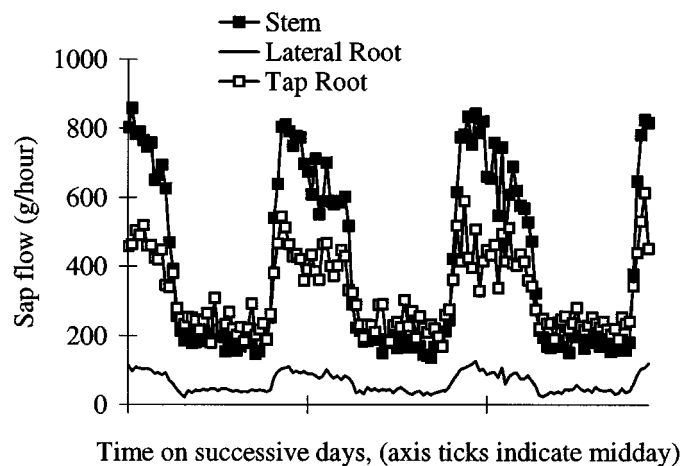


*Figure 9.* Sap volume flow in the stem, and in lateral and tap roots of a *Grevillea robusta* tree on four successive days immediately prior to the rains at Machakos in semiarid Kenya.

**Discussion**

Data obtained in this study demonstrate that competitivity indices change as trees age. Such differences in competitivity indices within species probably arise because not all of the structural elements of the root system have been laid down by age two. Previous studies, with temperate zone trees, indicate that structural roots continue to be produced for several years after planting. Working with coniferous species, Fayle (1975) concluded that most vertically orientated roots were developed in the five years following planting. Deans (1981) determined that most lateral roots were adventitious in origin and developed after transplantation into the field and similarly, Coutts and Lewis (1983) found that the permanent structural root system of Sitka spruce took about eight years to develop. From these studies, it seems doubtful that all of the main elements of the root system would have been present even at age four.

Competitivity indices based on gross root system morphology did not reliably predict competition between trees and crops. However, multiplying the sum of $D^2_{horizontal}$ by dbh which adjusted for tree size, did result in a promising relationship between root system variables and crop yield. The poor relationship between competition index and crop yield may have arisen because in each plot, root data were collected from only two or three individual trees (of 20) growing closely together in a single row. These data were subsequently combined to form a mean competitivity index for comparison with crop yield from the entire plot. Standard errors for the mean indices presented in Table 1 indicate that there was substantial intraspecific variation of the index. However, because crop yield data were obtained only at plot level in this study, it was impossible to test the robustness of the index for individual trees. Accordingly, it is possible that the index may perform better when used on individual (isolated) trees and where the compared trees are of similar size. However, the prospects for using the index are not promising and further studies are required not only to determine whether the index reliably predicts competition for individual trees, but also to determine the age at which the index stabilises, i.e. the age at which new root production ceases as trees age. This latter information will be especially important when tree rotations exceed five years because index information based on trees only one or two years old could be very misleading and there may be an optimal age/size at which to undertake index calculation.

That prediction of competition was better when estimates were based on shallow roots and dbh, suggests that there is merit in further similar root competition studies. However, in reality, transpiration (which increases as trees grow larger), formed the strongest relationship with crop yield. Figure 10 illustrates the relationship between transpiration and crop yield for five tree species. Transpiration data are means for all monitored trees in single plots where sapflow was measured. Crop yield data in these plots are expressed as percent of the yield of the treeless control plot in the same block (3) of the
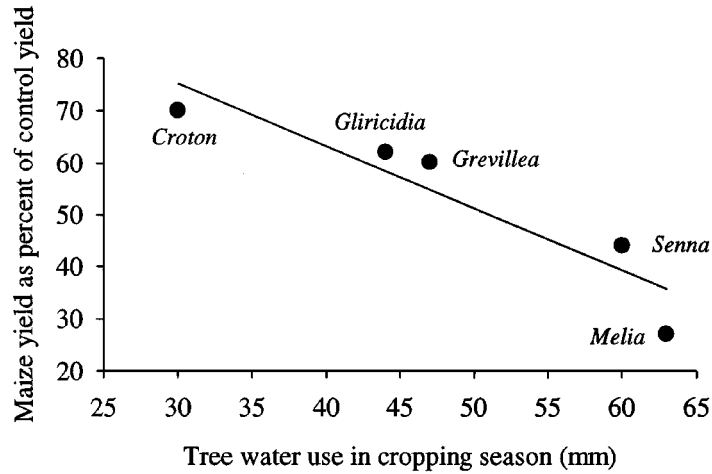
*Figure 10.* Relationship between mean tree water use during the crop growing season for five different tree species and crop yield expressed as percentage of yield obtained in control plots lacking trees at Machakos in semiarid Kenya.

randomised trial. Crop yield was significantly and negatively related to transpiration with $P \leq 0.05$ and $r^2 = 0.86$. Although there are clearly a number of 'short cut' options for examining potential competition by trees on crops, it is unfortunate that transpiration data are not available for most potential agroforestry trees. However, shallow roots, index of shallow rootedness (van Noordwijk and Purnomosidhi, 1995), stem diameter, diameter increment, and combinations of these variables, may provide a useful competition index, provided that tree size is always taken into account when making comparisons in the field. In this study, fractal methods accurately predicted average length of the coarse roots of trees confirming earlier work by van Noordwijk and Purnomoshidi (1995). However, fractal methods seriously underestimated fine root length. The significant relationship between alpha and root diameter which contravened the fractal rules when trying to determine total root system length, i.e. fine + coarse roots, probably arose because for thick roots, alpha normally has a value of about one (mean of 1.03 for data presented in Figure 5), but for fine roots, alpha values are typically $< 1$ (mean 0.8 for data presented in Figure 5). The trend of increasing values of alpha as root diameter increases generates a positive correlation. The small values of alpha for fine roots indicate that $D^2$ above branching points was smaller than $\Sigma d^2$ after branching and probably reflects the primary structure of many fine roots which had not sloughed off their cortices. Consequently, using fractal methods to quantify coarse roots and another 'short cut' method to quantify fine roots, may offer a solution to the problem of total root system quantification. The use of multiple methods for total root system quantification were also suggested by van Noordwijk et al. (1996), who described a technique which enabled fine roots to be quantified from the ratio of fine to coarser roots.

However, Figure 11 demonstrates that even for fine roots, there are significant relationships between root diameter and subtended root length, $r^2$ was about 0.65 and $P \leq 0.001$. Therefore applying fractal methods to coarse roots until root diameter declines to that of fine roots and then separately estimating fine roots does seem worthy of consideration.

Before the rains, tap roots supplied most of the water to satisfy the demand from the tree crown (Figure 6). At that time, only small amounts of sap flowed through lateral roots, particularly at night. However, sap flow through lateral roots greatly exceeded that through tap roots after surface soils were rewetted and at night, lateral roots supplied substantial water for aerial rehydration. That the lateral roots increased their sapflow rates immediately surface soils rewetted was unexpected. It is frequently assumed that full resumption of root system functioning is delayed pending the flush of new fine root growth which follows a few days after soil rewetting (Kavanagh and Kellman, 1992). These observations for existing lateral roots refute the often stated need for new fine roots to be produced to enable exploitation of soil resources.

The second 1996 cropping season was seriously affected by drought and the crop plants died in early December. Concurrently, the trees showed little sign of water stress and the more or less immediate response to rainfall by shallow lateral roots clearly demonstrates that even although the trees possessed deep roots, the potential for root competition between shallow lateral roots and crop roots is large. That the trees survived in the dry conditions which killed the crop plants demonstrates that the trees were accessing water which was located below the rooting zone of the crop. To that extent, there is evidence of complementarity, and even although no rain fell between December and the beginning of March 1997, there was little evidence of a serious trend of accumulating pre-dawn moisture deficits for three of the tree
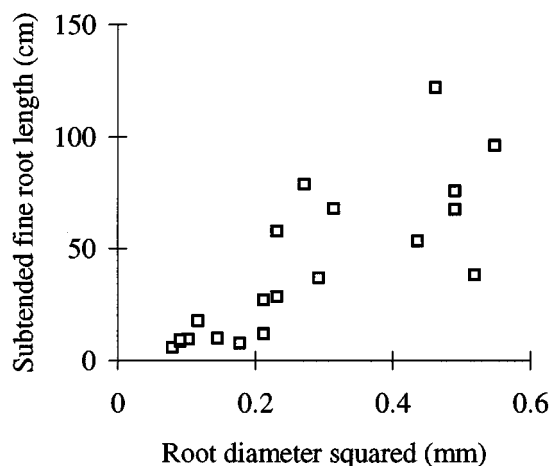


*Figure 11.* Relationship between root diameter and subtended fine root length for *Gliricidia sepium* trees grown in a glasshouse near Edinburgh, Scotland.

species (Dennis Kerengo, pers. comm.). Although the crop plants died from drought in early December 1996, concurrent pre-dawn water potentials for trees (–0.8 MPa,) were more or less stable. However, by March 1997, *S. spectabilis* which had the greatest leaf area, tended to wilt around midday and had pre-dawn water potential of about –1.4 MPa. Concurrently, pre-dawn water potential was about –1.0 MPa for the other less leafy tree species (Dennis Kerengo, pers. comm.).

## Conclusions

- Index of shallow rootedness changed as trees aged from two to four years.
- Tree:crop competition was not reliably predicted by index of shallow rootedness but a modified index generated by multiplying $\Sigma D^2_{horizontal}$ by dbh to take tree size into account gave better predictions of competition in alley farming systems.
- Fractal methods accurately predict root length for the permanent structural roots of trees but underestimate the length of fine roots.
- When surface soils are dry, tap roots supply most of the water used by trees but existing shallow lateral roots can respond more or less immediately to rainfall.
- There is no need for new fine roots to be produced to enable uptake of water from rainfall falling on dry soil.

## Acknowledgements

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