

Tree-crop Interactions for Below-ground Resources in Drylands: Root Structure and Function

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Abstract: This paper describes recent advances in below-ground research in dryland areas, focusing mainly on studies in dryland Kenya, in which novel sap flow and allometric techniques for determining root structure and function were compared with simple, but labor-intensive methods involving soil coring and trenching. Studies using these approaches indicated that tree (*Gliricidia sepium* and *Grevillea robusta*) and crop (*Zea mays*) roots predominantly occupied the same soil volume, implying there was little spatial complementarity, and highlighted the existence of considerable variation in tree root density between seasons. The less labor-intensive approach of determining the "competitiveness index", based on measurements of main roots, was not a reliable indicator of competition unless it was adjusted for tree size. Fractal relationships provided reasonable estimates of coarse root length, but seriously underestimated the length of fine roots. Sap flow studies showed the marked capacity of tree root activity to switch from one part of the root system to others in response to changes in soil moisture availability, and highlighted the importance of root function as opposed to structure in determining the severity of below-ground competition; such effects may provide both benefits and costs to neighboring plants. Thus, there is an urgent need to develop tree management regimes which promote effective sharing of below-ground resources.

Key words: Tree-crop interactions, below-ground, drylands, roots, agroforestry.

Recent reviews of tree-crop interactions have highlighted the substantial progress made in agroforestry research in subhumid and humid tropics, primarily with regard to fertility improvements (Sanchez, 1995; Rhoades, 1997; Rao *et al.*, 1998, 1999). In sharp contrast, much less progress has been made in intensifying the management of dryland agroforestry systems, which are facing increasing human population pressure and land degradation. The introduction of

novel agroforestry systems such as hedgerow intercropping, originally developed for the subhumid tropics, into drylands has been generally disappointing, largely because the benefits provided by microclimatic and fertility improvements do not offset the substantial competitive effect of trees on crops for water and nutrients (Ong and Huxley, 1996; Tilander and Ong, 1999). Therefore, researchers have turned their attention to root distribution and function

in order to understand how to manipulate below-ground biophysical interactions (van Noordwijk *et al.*, 1996; Schroth, 1999).

Huxley (1983) suggested that exploiting the different rooting depths of trees and crops could increase resource capture in agroforestry systems without introducing intense below-ground competition; alternatively, clumped distributions of tree and crop roots within the soil volume might reduce interspecific competition (Huxley *et al.*, 1994). However, numerous studies have shown that most trees, especially fast-growing species, share the same rooting depth as crops (Jonsson *et al.*, 1988; Daniel *et al.*, 1991; van Noordwijk *et al.*, 1996), and the importance of root clumping for complementarity remains uncertain. In their recent review, Rao *et al.* (1998) concluded that there is still an inadequate understanding of below-ground interactions because of the difficulty of making root measurements and that there are few practical methods for selecting deep-rooting trees. Surprisingly, there has been no attempt to relate the phenology of the tree canopy to root activity in agroforestry research; yet if the flushing of foliage is related to root activity, it might offer a relatively simple indicator for selecting trees which are more compatible with crops.

Fortunately, considerable progress has been made in recent years regarding the concepts and the techniques for studies of below-ground interactions. Cannell *et al.* (1996) proposed a 'central' hypothesis to justify agroforestry in semi-arid regions, in which it was proposed that trees must utilize resources such as water and nutrients that are not captured by the roots of associated crops or sole cropping systems, although this should be tempered by a consideration

of the value of the respective products. In terms of new techniques, the development of simple methods for quantifying root length, based on fractal principles (Spek and van Noordwijk, 1994), and deriving 'competitiveness indices' from the proportional relationships between first-order lateral and tap roots and trunk diameter without the need for extensive excavation (van Noordwijk and Purnomosidhi, 1995), the relatively low cost heat-pulse technique for measuring root functioning (water uptake) (Khan and Ong, 1996), and the use of isotopic ratios of water utilized by plants (Ehleringer and Dawson, 1992) are the most exciting. Another technique for determining the root dynamics of trees and crops using minirhizotron methods is described by Akinnifesi *et al.* (1999a). But how useful are these methods for unraveling below-ground interactions in drylands? Can they be used to screen the large number of tree species potentially suitable for dryland agroforestry? And can these methods replace the traditional and tedious method of root excavation, with the attendant difficulties of distinguishing between the roots of the tree and crop components?

In this paper, we summarize recent advances in below-ground research in drylands, focusing on findings at ICRAF's Research Station at Machakos, Kenya, where novel sap flow and allometric techniques have been tested alongside traditional techniques such as trenching and coring to evaluate root distribution, in relation to season and soil moisture availability.

Site Description

Machakos field station is located 70 km south-east of Nairobi at an elevation of 1600

m. The bimodal rainfall averages 740 mm per annum and is approximately equally distributed between the two rainy seasons, which occur between October-December (short rains) and March-May (long rains). Soils are weakly to moderately leached Kandic Rhodustalfs (USDA) or Lixisols (FAO), and are well drained, friable, dark reddish brown, weakly acidic, erodible and contain moderate amounts of organic matter.

The experimental site was planted in April 1993 with trees at 1 m spacing in single rows across plots; crops were planted on both sides of the tree rows (Odhiambo, 1999). A randomized block design was used, with one plot of each tree species in each of four blocks, plus control plots without trees. Gross plot size was 20 x 18 m, including a 2 m guard area; the stocking density of the trees was, therefore, approximately 530 ha⁻¹. At the beginning of each cropping season, 1 to 2 m deep trenches were dug around each plot to prevent roots from growing into adjacent plots. Beans (*Phaseolus vulgaris*) were planted in the short rains, and maize (*Zea mays*) in the long rains. Before establishing the experiment, a cover crop was planted to examine fertility trends across the site; these were taken into account in the layout of the experimental blocks.

During the studies reported here, rainfall was often below the long term average and very uneven in distribution. Total rainfall during the 1996 and 1997 maize seasons was 223 and 315 mm (67 and 95% of the long term average; Kiepe, 1995; Mathuva *et al.*, 1998). In the intervening 1996-97 beans season, rainfall was only 158 mm (43% of long term average), most of which fell in November, and the crop failed.

Root Distribution of Trees and Crops

Root distribution of two tree species (*Gliricidia sepium* (Jacq.) Walp. and *Grevillea robusta* Cunn.), which are widely used in agroforestry, were examined using soil coring and trenching techniques. These species differ both in their leafing phenology, as *Grevillea* retains leaf cover throughout the year, whereas, *Gliricidia* exhibits seasonal leafing, and their nutrient acquisition strategies. *Gliricidia* is an N-fixing species while *Grevillea* has proteoid roots with a high surface area:volume ratio which proliferate in small, nutrient-rich patches and release exudates into the soil to enhance the uptake of nutrients with low solubility (Skene *et al.*, 1996). Previous studies suggest that *Grevillea* is unusual among tree species commonly used in agroforestry because of its predominantly deep rooting habit and spatial complementarity with shallow rooted crops (Mwihomeke, 1993). *Gliricidia* has been described as being relatively uncompetitive in Côte d'Ivoire (Schroth, 1999) and when used as a mulch, its leaves rapidly release a high proportion of their nitrogen (Palm, 1995). However, results from the previous cropping season had indicated that *Gliricidia* was more competitive with maize than *Grevillea* (Odhiambo, 1999).

In April 1996, three years after planting, the *Gliricidia* and *Grevillea* trees were, respectively, 4.3 and 5.3 m tall and had diameter of 8.0 and 11.5 cm at breast height (dbh). The coring studies indicated that roots of both species had spread to the furthest coring points from the trunk (4.5 m distance); additional cores taken one year later at 6 m from the trunks also contained tree roots. The measurements of tree and crop root length density made using root cores taken

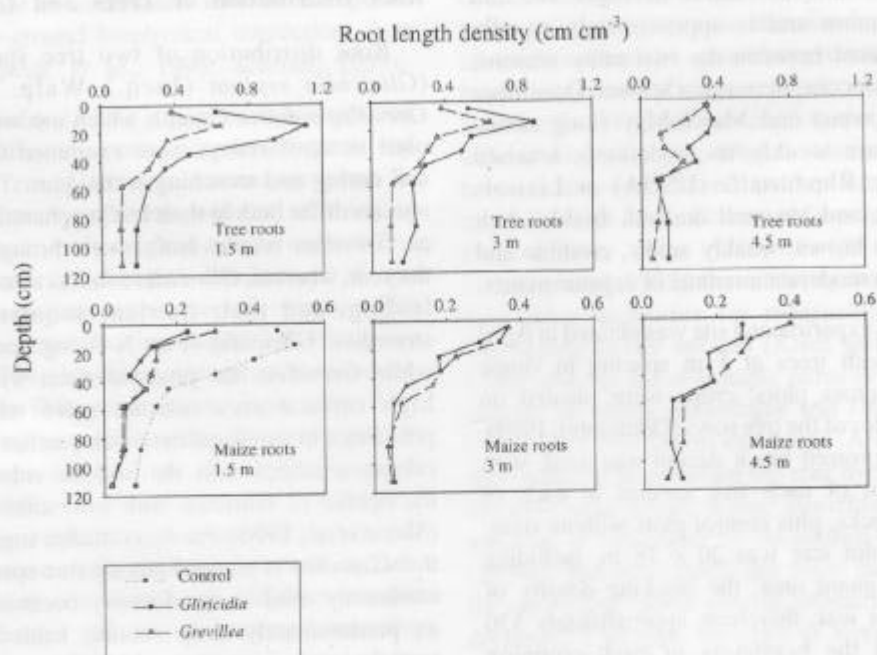


Fig. 1. Average tree and crop root length density profiles determined using soil cores taken 1.5, 3.0 and 4.5 m from trees during the 1996 long rains at Machakos, Kenya, for plots containing single rows of 3-year-old *Gliricidia sepium* or *Grevillea robusta* trees, cropped with maize. Control plots contain maize only.

during the 1996 maize season (Fig. 1) showed that the values for the trees tended to be greatest between 10 and 20 cm below the soil surface, whereas, those for maize were usually greatest in the 0 to 10 cm horizon. Analysis of variance using \log_{10} transformed data indicated that there were fewer maize roots overall in plots containing trees than in control plots, and that maize roots were least numerous close to trees. Overall, *Gliricidia* had a greater root length density than *Grevillea*, though trees of the former species were shorter and had a smaller dbh, and tree root length density declined with

increasing distance from the trees. The distribution of tree roots with depth also changed with increasing distance from the trees. Root length density was greatest in the 10 to 30 cm horizons at a distance of 1.5 m from the trees and peaked in the 10 to 20 cm horizon at a distance of 3 m; however, no pattern was apparent 4.5 m from the trees, where there were fewest roots.

These observations contrast with previous reports for a range of agroforestry species which indicate that tree root numbers are usually greatest close to the soil surface

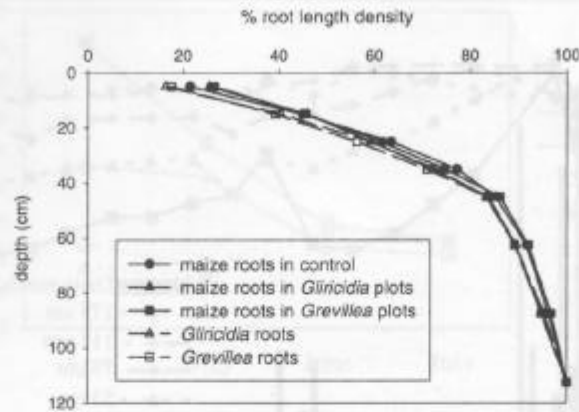


Fig. 2. Cumulative root length density as a function of soil depth for maize roots in control and agroforestry plots and *Grevillea robusta* and *Gliricidia sepium* roots in the agroforestry plots during the 1996 long rains. Values were calculated from mean values determined over the whole cropping season and at distances of 1.5, 3.0 and 4.5 m from the tree rows.

(Jonsson *et al.*, 1988; Dhyani *et al.*, 1990; Ruhigwa *et al.*, 1992; Akinnifesi *et al.*, 1999b). Smith *et al.* (1999) and Livesley *et al.* (in preparation) also found that root length density was greatest close to the soil surface in *Grevillea*. Root architecture may be affected by a variety of factors, including tree spacing, crown pruning, and interplanting with competitive species (Schroth, 1995); soil moisture supplies and manual cultivation of the site prior to sowing the crop may also have been an influence.

The soil cores showed that the cumulative distribution of roots was very similar for both tree and crop species within the upper 125 cm of the profile (Fig. 2), although tree roots would also have explored the soil to greater depths. Very large proportions of the root systems occurred in zones where soil moisture was not stable and would have

been subject to alternating drying and wetting cycles (Fig. 3). Jackson *et al.* (1996) have previously reported that 70 and 69% of the root biomass in tropical deciduous and evergreen forests was located within the top 30 cm of soil; in the present study, the equivalent values for root length were 60 and 55% for *Gliricidia* and *Grevillea*, respectively.

There were marked differences between rainy seasons in the overall numbers of fine tree roots and their temporal and spatial distribution. Overall, roots were more numerous in *Gliricidia* than in *Grevillea* during both the 1996 and 1997 long rains; however, the root length densities for both tree species were substantially lower in 1997 than in 1996, and declined from a maximum close to the soil surface in 1997, rather than peaking below the surface, as in 1996.

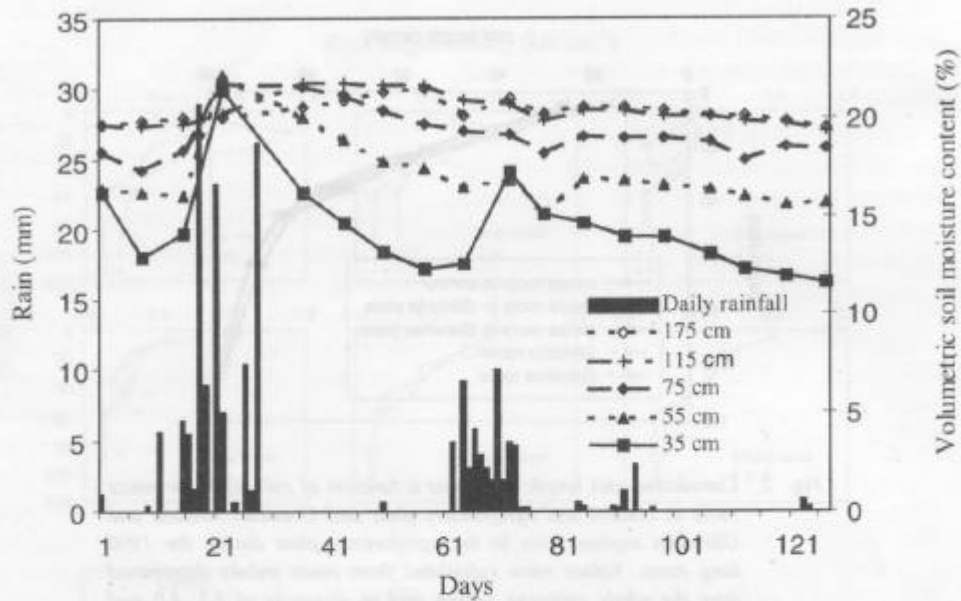


Fig. 3. Volumetric soil moisture content (%) at different depths and daily rainfall during the 1996 long rains for the sole maize plots; day 1 corresponds to 12 March 1996.

In 1996, tree root length density was greatest at the onset of the cropping season and declined progressively; by contrast, the roots of both tree species were much less numerous at the start of the 1997 cropping season and showed weaker trends over time (Fig. 4). Although the causes of these differences are uncertain, the generally poor rainfall and consequent drought during the intervening cropping season may have affected fine root development.

Observations of trench walls (1 m wide x 1.6 m depth, cut parallel to the tree rows) were made 1.5, 3.0 and 4.5 m from tree rows at the end of all the cropping seasons. Counts of exposed tree and crop root ends were made within 20 x 20 cm grid squares (Fig. 5). The mean root counts for all species

(*Gliricidia*, *Grevillea*, maize and bean) and all distances and depths were substantially lower than the variances, indicating that, at this scale of observation, the roots were clumped (Sokal and Rohlf, 1995). The data obtained were examined to determine whether the presence of tree roots was correlated with the presence of crop roots at each depth; no significant correlations, either positive or negative, were found, indicating that tree and crop root distributions were independent at this scale of observation.

Crop Production

Maize production was reduced in the agroforestry treatments, particularly close to the trees. Not only was germination adversely affected by proximity to trees (Fig. 6), but

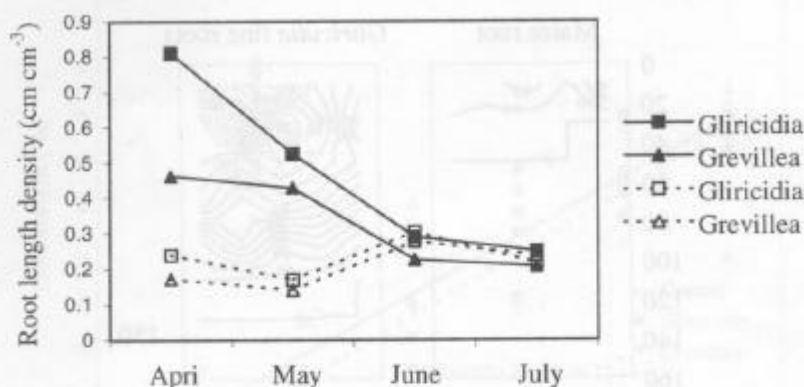


Fig. 4. Root length density (cm cm^{-3}) for *Gliricidia sepium* and *Grevillea robusta* during the 1996 and 1997 long rains; means were calculated for cores taken at distances of 1.5, 3.0 and 4.5 m from trees and to a depth of 75 cm in 1996 and 60 cm in 1997.

similar negative logarithmic relationships were found between cob yield and tree root length density (Fig. 7) for both tree species. This is surprising since the two species examined have contrasting nutrient acquisition characteristics, although soil nutrient supplies were not limiting at this site.

Phenology

Leafing phenology was also observed over a 22 month period for two indigenous (*Croton megalocarpus* and *Melia volkensii*) and two exotic species (*Senna spectabilis* and *Gliricidia sepium*) which were also planted in the same experiment (Broadhead, 2000). Although *Grevillea* retained leaf cover throughout the year, *Senna* and *Gliricidia* exhibited one main period of low leaf cover during each year, which coincided approximately with the dry season preceding the short rains. By contrast, the indigenous species showed reduced leaf cover during

both dry seasons, although the decline in leaf cover was substantially greater in *Melia* than in *Croton*. The timing of leaf loss and leaf flushing differed between species; thus *Melia* and *Senna* began flushing during the dry season in the absence of recent rainfall and returned to maximum leaf cover early in the cropping seasons, whereas *Gliricidia*, in which a minority of trees began flushing during the dry season, did not return to maximum leaf cover until late in the cropping season (Fig. 8). Although detailed root observations were not made during the short rains, the changes in root length density with time in *Gliricidia* and *Grevillea* do not appear to reflect their contrasting leafing phenologies.

Root length, root architecture and competition indices

Working from fractal principles, it should be possible to estimate the total length of tree roots from simple non-destructive

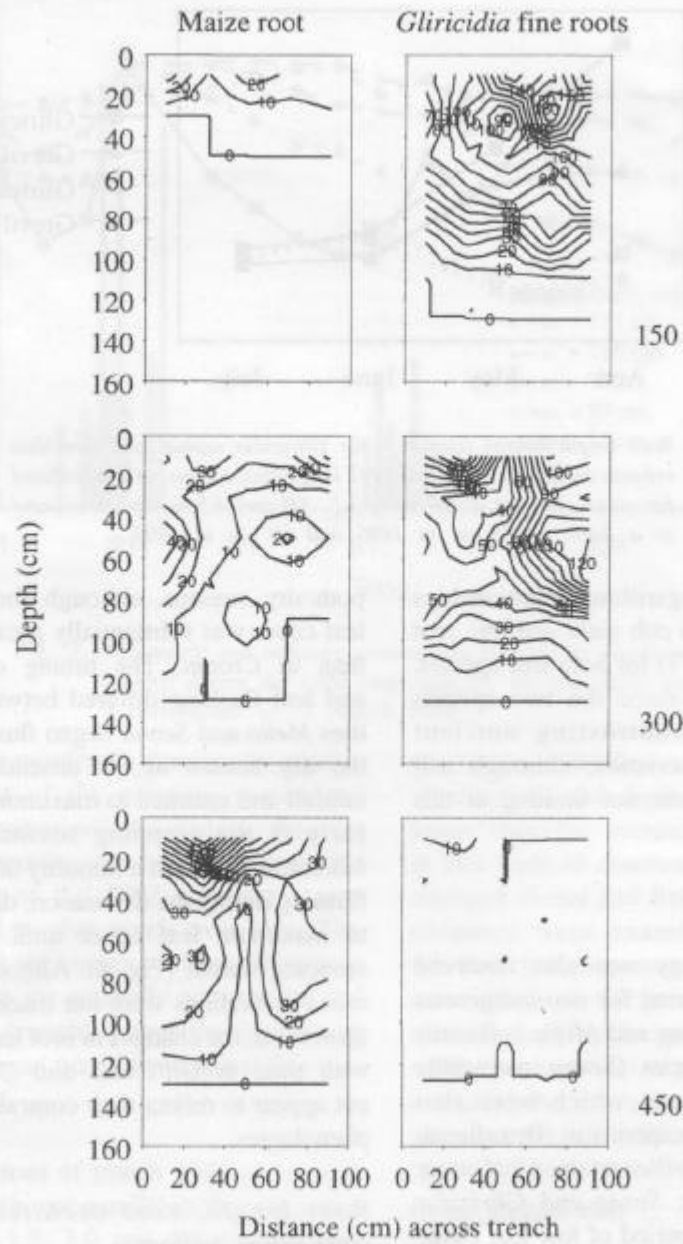


Fig. 5. Distribution of *Gliricidia sepium* and maize roots in trenches at the end of the 1996 cropping season at distances of 1.5, 3.0 and 4.5 m from the tree row. Trenches were cut parallel to tree rows.

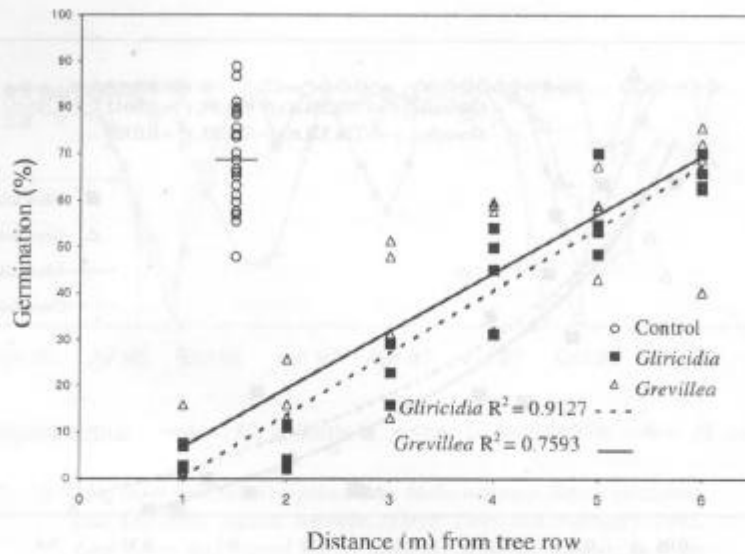


Fig. 6. Relationship between maize germination measured two weeks after sowing and distance from the tree rows in 1996.

measures of root diameter and link lengths. Previous studies (van Noordwijk *et al.*, 1994) have demonstrated that these principles hold for coarse roots, but are less useful for fine roots. The validity of the method was tested for several tree species at the Machakos experimental site by examining both the coarse and fine fractions of the root systems of *Grevillea robusta*, *Gliricidia sepium* and *Senna spectabilis* syn. *Cassia spectabilis* (Ong *et al.*, 1999). Because of the difficulty involved in the field excavation of fine roots, results from field measurements of coarse roots (>2 mm diameter) were combined with observations of the fine (<2 mm diameter) roots of pot-grown plants.

Coarse root parameters were found to adhere to fractal principles, but the fine root parameters did not and the method seriously underestimated fine root length, which is the most important component of the root

system for the uptake of water and nutrients. Consequently, although the fractal approach is appropriate for determining coarse root length in the field, it is not appropriate for determining either fine or total root length (Ong *et al.*, 1999).

Competition index

The competition index has been suggested as a simple measure of tree root competitiveness, which is based on the ratio of the cross sectional area of horizontally orientated roots to stem diameter, i.e.,

$$CI = \frac{\sum D_{horizontal}^2}{dbh^2}$$

where,

CI represents the competition index, $D_{horizontal}^2$ is the proximal diameter of roots descending into the soil at angles less

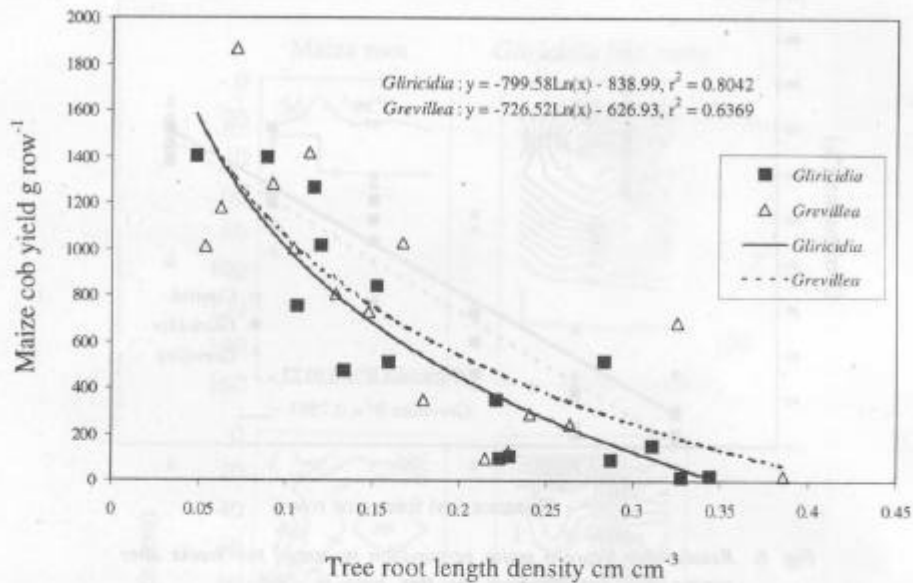


Fig. 7. Relationship between maize cob yield during the 1997 cropping season and mean root length density for *Grevillea* and *Gliricidia* during the cropping season, averaged over all sampling times to a depth of 60 cm. Maize yields (per 8 m row) at distances of 1 and 2 m, 3 m, 4 and 5 m, and 6 m from the tree row, respectively, were plotted against root length density determined 1.5, 3.0, 4.5 and 6.0 m from the tree rows.

than 45°, and dbh is the stem diameter at breast height (van Noordwijk and Purnomosidhi, 1995).

Previous studies in Indonesia (van Noordwijk and Purnomosidhi, 1995) have shown a 15-fold variation in CI among 19 tree species aged between 5 and 7 years, in which *Leucaena leucocephala* exhibited the highest CI and *Mangifera indica* the lowest. In the present study, CI was determined for 2 to 4-year-old trees of several species at the Machakos site and related to crop yield (Table 1; Ong *et al.*,

1999). When the trees were 2-year-old, the CI values for *Senna* and *Grevillea* were significantly smaller than those for *Melia* and *Gliricidia*; the CI values for 4-year-old trees had changed dramatically, and there were no significant differences between species. However, the crop yield data for year 4 indicated that *Melia* was the most competitive species, even though this was not reflected by its CI value.

A difficulty with the CI approach is that it does not allow for differences in tree size when comparing species under

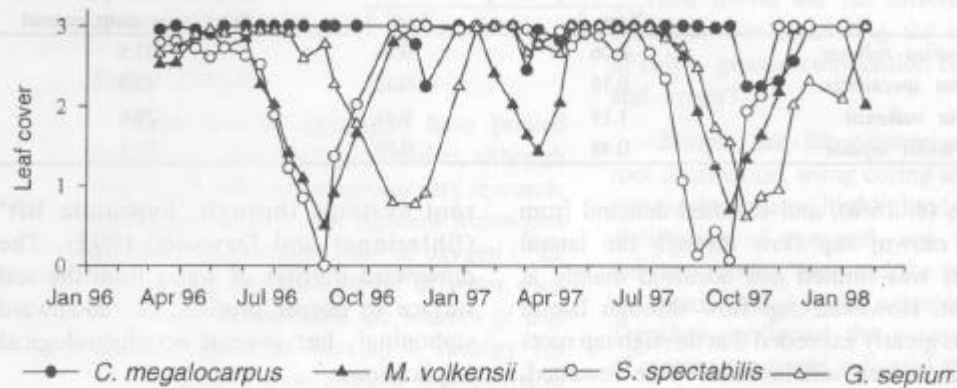


Fig. 8. Leaf cover for *Croton megalocarpus*, *Melia volkensii*, *Senna spectabilis* and *Gliricidia sepium* between March 1996 and February 1998. Leaf cover was scored on an arbitrary scale as follows: 0 = no leaves, 1 = low leaf cover, 2 = intermediate leaf cover, 3 = full cover.

field conditions. By year 4, *Melia* had a mean dbh of 12.1 cm, whereas *Gliricidia* was the smallest species with a mean dbh of 6.3 cm. However, as reported by Ong *et al.* (1999), there was a significant negative relationship between crop yield and ($\text{dbh} \times D_{\text{horizontal}}^2$), suggesting that this may offer a promising approach for incorporating the root system attributes of trees into tree-crop evaluations.

Root Function

Sapflow

The presence of deep roots alone does not guarantee complementarity of water use, and knowledge of root distribution is of limited value in the absence of corresponding information concerning water and nutrient uptake. Howard *et al.* (1997) and Lott *et al.* (1996) used sap

flow gauges (heat balance method) to quantify water uptake by tree roots from below the crop rooting zone in agroforestry systems and concluded that deep rooting trees like *Grevillea robusta* can obtain a large portion of their water requirements from deep roots, suggesting a high degree of below-ground complementarity.

Miniature heat pulse sensors (Khan and Ong, 1996) have recently been developed which can be inserted into individual roots to examine their responses to changes in soil moisture availability (Ong *et al.*, 1999). These were used in studies encompassing the end of the dry season and the onset of the rainy season, when soil moisture distribution changes rapidly and the crop rooting zone becomes moist. Before the rains, tap roots of *Grevillea* supplied most of the water, probably drawn from depths below 1.5 m where soil moisture was still

Table 1. Variation in competitiveness index and crop yield with time and tree species

Tree species	Competitiveness index		Crop yield in year 4 as % of sole crop control
	Year 2	Year 4	
<i>Grevillea robusta</i>	0.06	0.65	57.5
<i>Senna spectabilis</i>	0.16	0.42	42.3
<i>Melia volkensii</i>	1.19	0.41	29.6
<i>Gliricidia sepium</i>	0.48	0.69	50.5

high (c. 16%), and satisfied demand from the crown; sap flow through the lateral roots was limited and occurred mainly at night. However, sap flow through lateral roots greatly exceeded that through tap roots after surface soil horizons were rewetted, and the lateral roots supplied substantial quantities of water to rehydrate the shoot during the night. The increase in the sap flow through the lateral roots immediately after the surface soil layers were rewetted was unexpected as it is frequently assumed that full resumption of root system functioning is delayed pending the flush of new fine root growth which occurs several 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.

Even more intriguing is the ability of heat pulse probes to detect changes in the direction of flow within roots. For example, Burgess *et al.* (1998) and Smith *et al.* (1999) found that lateral roots of *Grevillea* were able to supply water from the wet surface soil to the tap roots. This movement of sap from lateral roots to tap roots occurred when the root systems experienced steep gradients of soil water potential. It has previously been demonstrated that water can be redistributed from deeper in the soil profile to dry surface horizons by the

root systems through 'hydraulic lift' (Ehleringer and Dawson, 1992). The downward transfer of water from the soil surface to deeper profiles, or 'downward siphoning', has several ecophysiological implications.

For instance, hydraulic redistribution of water by root systems may maintain fine root function in dry soil so that they can rapidly acquire water on the day of the 'break of the season' rainfall or when off-season rainfall occurs. Such opportunistic uptake is likely to increase the plant's success as a competitor for water. The transfer of water from wet topsoil to deeper dry layers would prevent shallow-rooted competitors from utilizing the water, thus enhancing the competitiveness of trees. Downward siphoning would also allow trees to 'store' water for use later in the season when the shallow layers are dry. Furthermore, the growth and viability of deep roots located in extremely dry subsoil may be supported by water transferred from the wet topsoil. Such a mechanism may explain how certain tree species become established in extremely dry environments, as it would facilitate root growth through dry subsoil, allowing them to reach deep water tables. Thus, water redistribution within the root system may provide both benefits and costs for neighboring plants; further investigations

are required to examine their importance in agroforestry systems with and without access to groundwater.

Stable isotopes

Stable isotope techniques have proved valuable in many ecological studies, although their use is still rare in agroforestry research. Smith *et al.* (1998) used sap flow techniques and the stable isotope ratio of oxygen ($^{18}\text{O}/^{16}\text{O}$) to quantify the amount of water used by windbreak trees and the sources of that water in order to develop a strategy for minimizing below-ground competition between trees and crops. They compared water use by neem (*Azadirachta indica*) windbreaks in two contrasting sites in Niger, one in the Majjia valley with a shallow water table (6 to 8 m) and one at Sadore with a deep water table (35 m) which the trees could not access. At both sites, the trees and millet utilized water (similar ratios of oxygen) from the top 1 m of the soil profile when it was wet following rainfall. However, during dry periods, the trees and millet used spatially distinct sources of water at Majjia Valley, where the water table was accessible to the trees, while at Sadore, where the water table was inaccessible, the trees competed for water within the crop rooting zone. Thus spatial complementarity between the trees and crops was enhanced when the trees had access to groundwater. When trees have access to groundwater, they are likely to extract a large proportion of their water requirements from the surface layers only during periods when surface water is plentiful, which may help explain why millet production was enhanced (20 to 25%) in fields in the Majjia Valley sheltered by neem windbreaks, while windbreaks at Sadore had little effect on millet production.

Concluding comments

How useful are the different methods described for unraveling the complexities of below-ground competition between trees and crops?

Simple, but labor-intensive studies of root distribution, using coring and trenching approaches, have highlighted the similar distribution of tree and crop roots within the crop rooting zone and the apparent lack of significant spatial complementarity. Trenches confirmed the extensive overlap of rooting zones and indicated that, although root clumping occurred, that of tree roots was neither positively nor negatively associated with that of crop roots, although this observation needs to be re-evaluated at a finer scale. The coincidence of tree and crop roots in the upper soil layers in agroforestry systems corresponds to the situation in savannah systems with tree-grass interactions (Scholes and Walker, 1993), although in the latter system, grass roots dominate. In both systems, only trees can access deep water, whereas trees and crops/grasses are in competition for shallow water. In the root coring studies, a strong inverse correlation between maize yield and tree root length density was observed for *Gliricidia* and *Grevillea*, despite their differing nutrient acquisition strategies, indicating that the root length density of tree roots within the crop rooting zone may be important in determining the intensity of competition between trees and crops.

Less labor-intensive approaches, such as competition index, were poor indicators of competition, partly because the index ignores the influence of tree size, although this may be overcome by making adjustments to the calculations. However, the method still poses

difficulties as the measurements would not detect the substantial variation in fine root length density observed between seasons, and measurements of dbh and lateral root diameters at the base of the trunk would not account for changes in crown size resulting, for example, from pruning, which may dramatically affect transpirational requirements. Studies of fractal relationships suggest that these underestimate the length of fine roots, which are the crucial component for nutrient uptake. As for CI measurements, neither the impact of the crown management techniques commonly used in agroforestry nor the substantial variation in fine root length observed between the 1996 and 1997 seasons (50%) would have been detected by fractal measurements. Thus, we conclude that these methods need further modifications before they can replace the traditional and tedious methods of direct observation of roots by trenching and coring or be used for screening the large number of tree species potentially suitable for dryland agroforestry.

The observed differences in leafing phenology were not reflected by the behavior of fine tree roots during the long rains; further studies are needed to determine if there are effects during the short rains when differences in leaf cover between *Grevillea* and *Gliricidia* are substantial. However, regardless of whether there are differences in root development, evidence from soil water studies (Odhiambo, 1999) indicates that *Gliricidia* used more water than *Grevillea* in both the long and the short rains. If there is water available to support leaf flushing during the dry seasons (as occurred for *Melia*, *Senna* and *Gliricidia*, which continued flushing at a low rate), this would suggest that an equivalent

flushing of fine roots may also occur as there should be water available in the profile to allow rehydration of the surface layers by hydraulic lift. Clearly, more work is needed to relate flushing of foliage to root activity.

Root and crown functions are the driving forces determining the severity of tree-crop competition. The sap flow studies indicate the capacity of tree root activity to switch from one part of the root system to another in response to changes in soil moisture. This observation suggests that overall root system architecture is not the crucial arbiter of competition, although the link between root length density and maize yield suggests that the density of tree roots in the surface layers at the time when they are functioning is important. The isotope studies reported by Smith *et al.* (1998) highlight the importance of understanding the range of exploration of tree roots and site hydrology, and show how the competitiveness of an individual tree species can vary between sites with different hydrological characteristics.

Not only should the structure and function of root systems be considered when selecting tree species for agroforestry in dryland areas, but so also should the physiological differences between tree species in their demand for water (Smith *et al.*, 1998; Ehleringer and Dawson, 1992). Once planted, competition may be controlled by reducing transpiration by crown pruning, and probably also by controlling the zones of water extraction by lateral root pruning (Korwar and Radder, 1994; Schroth, 1995; Hocking, 1998; Hocking and Islam, 1998). The efficacy of these methods and their acceptability to farmers is currently being explored in Kenya and Uganda. Crown pruning not only reduces

transpiration but also leads to root dieback (van Noordwijk *et al.*, 1996; Jones *et al.*, 1998; Schroth 1999), but, unfortunately, may also lead to the development of a more superficial root system (Hairiah *et al.*, 1992), an undesirable outcome. Downward displacement of functional tree roots following root pruning should not significantly affect their 'safety net' role in the interception of mineral nutrients leaching from the crop root zone (van Noordwijk *et al.*, 1996). Although lateral root pruning appears to be a promising approach for shifting tree water extraction below the cropping zone, the long term hydrological implications of encouraging the use of groundwater must not be ignored when attempting to meet demand for trees and their products (Leakey and Wilson, 1999).

Despite recent attention to root research, progress in selecting suitable tree species for intercropping in drylands has been surprisingly slow, and it appears probable that the twin goals of fast growing trees, preferred by farmers and researchers, and low competitiveness are mutually exclusive when nutrients and water are confined to the topsoil (van Noordwijk *et al.*, 1996). If competition is to be minimized, tree planting must be combined with appropriate management practices. This does not mean that agroforestry systems are undesirable, but reinforces the message that their evaluation must include consideration of the value of both the tree and intercrop components and the tradeoffs between the need to obtain products from both components and meet long term goals such as sustainability and ecological resilience within semi-arid production systems.

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