



Why tree-crop interactions in agroforestry appear at odds with tree-grass interactions in tropical savannahs

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Abstract. This paper describes recent research findings on resource sharing between trees and crops in the semiarid tropics and attempts to reconcile this information with current knowledge of the interactions between savannah trees and understorey vegetation by examining agroforestry systems from the perspective of succession. In general, productivity of natural vegetation under savannah trees increases as rainfall decreases, while the opposite occurs in agroforestry. One explanation is that in the savannah, the beneficial effects of microclimatic improvements (e.g. lower temperatures and evaporation losses) are greater in more xeric environments. Mature savannah trees have a high proportion of woody above-ground structure compared to foliage, so that the amount of water 'saved' (largely by reduction in soil evaporation) is greater than water 'lost' through transpiration by trees. By contrast, in agroforestry practices such as alley cropping where tree density is high, any beneficial effects of the trees on microclimate are negated by reductions in soil moisture due to increasing interception losses and tree transpiration. While investment in woody structure can improve the water economy beneath agroforestry trees, it inevitably reduces the growth rate of the trees and thus increases the time required for improved understorey productivity. Therefore, agroforesters prefer trees with more direct and immediate benefits to farmers. The greatest opportunity for simultaneous agroforestry practices is therefore to fill niches within the landscape where resources are currently under-utilised by crops. In this way, agroforestry can mimic the large scale patch dynamics and successional progression of a natural ecosystem.

1. Introduction

Farmers in drylands have for centuries utilised a wide range of agroforestry practices, largely by preserving and managing a few scattered mature trees (Rocheleau et al., 1988; Shankarnarayan et al., 1987). Recent attempts to promote agroforestry through further tree planting in such environments have been disappointing (Singh et al., 1989; Nair, 1993; Cooper et al., 1996; Rao et al., 1998). The above reviews have highlighted the limitations of, for example, alley cropping in the semiarid tropics, where below-ground competition for water between trees and crops frequently outweighed the benefits of soil enrichment and microclimate improvements. These reviews offered few solutions, despite substantial evidence of improved soil nutrient, microclimatic conditions and increased vegetative production beneath large isolated trees in most savannah ecosystems (Huntley and Walker, 1982; Rhoades, 1997;

Belsky and Amundson, 1997). It might be expected that similar processes could be developed in agroecosystems.

The hydrological impact of fast growing exotic trees has caused concern to local peoples in many tropical countries, especially in semiarid areas, due to the 'Eucalyptus controversy'. In southern India, eucalypt plantations have been reported to not only extract all the rainfall that enters the soil, but also to utilise an additional 100 mm of water from each metre depth of soil that the roots penetrate (Calder et al., 1997). This is a matter of concern as recent studies in Karnataka, India, have shown that eucalypt roots can reach to a depth of 8 m in three years (Calder et al., 1997). In the Sahel, roots of mature, well-scattered trees can even reach the water-table at 30 m (Deans et al., 1995). Consequently, when planning trees in association with crops in drylands, it is essential to consider the implications of increased water use on the medium and longer-term water budgets. Special consideration should be paid to the source of water used by trees, the rate of water depletion below the crop rooting zone and the prospects for deep recharge as using water at faster than replacement rates demonstrates a serious ecological consequence of not mimicking the resource use patterns of locally adapted species.

2. Resource use in savannah ecosystems

According to the savannah literature, grasses utilise the topsoil water while tree roots have exclusive access to deeper water, creating a clear niche separation (Weltzin and Coughenour, 1990; Deans et al., 1995). However, Belsky and her colleagues (1993) observed that the shallow rooting baobab (*Adansonia digitata*) has the same beneficial effect on understorey soils and vegetation as the deep-rooted *Acacia tortilis*. One explanation could be that both species have a higher proportion of woody aboveground structure than foliage, so that more soil water is saved by reducing soil evaporation than is lost as transpiration, although interception loss would still exist. In contrast, the proportion of woody structure in most new simultaneous agroforestry systems is deliberately kept to a minimum by either frequent pruning or selection of leafy tree species (Van Noordwijk and Ong, this volume).

If the beneficial effects of savannah and parkland trees on soil properties are linked to trees with a high proportion of woody aboveground structures, then it would take a long time before the beneficial effects can be realised, since investment in woody structure slows tree growth. Therefore it is not surprising that the positive interactions between mature, deep-rooted and widely spaced *Faidherbia albida* trees (the 'albida' effect) would require 20–40 years in Ethiopia (Poschen, 1986). Such long time scales are well beyond the planning horizon of many farmers for the relatively small benefit in crop productivity and may well explain why farmers rarely plant these trees, even though they are well aware of tree species which improve soil and climate.

Instead of focusing agroforestry primarily on soil amelioration, it would

perhaps be more worthwhile to focus attention on selection of trees to provide direct and more immediate benefits to farmers, with minimum loss of crop productivity. It is perhaps not surprising that farmers are already beginning to experiment with such systems. For example, in the drylands of eastern Kenya, farmers have recently developed an intensive parkland system using a fast-growing indigenous species, *Melia volkensii* (Meliaceae). This tree provides high value timber in five to eight years plus fodder during the dry season, without an apparent loss in productivity in associated crops (Stewart and Bromley, 1994). Consequently, ICRAF is currently investigating the tree-crop interactions in the *Melia* system in farmers fields.

3. Agroforestry in drylands

Early studies of agroforestry began with the general assumption that complementarity was the norm as trees are believed as a rule to be more deeply rooted than crops. However, researchers were soon discouraged by the substantial reduction in associated crop yield and they began to focus on below ground competition for resources. In this paper we trace the progress of agroforestry research in drylands by introducing them as a series of hypotheses. The first hypothesis states that where trees can exploit resources that are unavailable to crops, agroforestry can increase productivity per unit area of land through the efficient use of resources (Cannell et al., 1996); in other words through spatial complementarity. The second hypothesis is based on the assumption that competition for below ground resources is inevitable as tree and crop root systems are likely to have similar distribution in the soil profile (Jonsson et al., 1988; Singh et al., 1989; Schroth, 1995). It suggests that to reduce the negative effects of competition, tree spacing should be increased to minimise competition for water with crops (Singh et al., 1989). An extension of this idea is that to further minimise negative effects of trees on crops they should be matched to appropriate niches within the farm (Van Noordwijk and Ong, 1996). This hypothesis is also based on spatial complementarity but suggests it may be the exception rather than the rule. Third, it has been suggested that attention to differences in tree phenology could result in temporal complementarity, in which trees like *Faidherbia albida*, with its reverse phenology (Ong et al., 1992), make growth demands at a different time from that of the crops. Finally, it has been hypothesised that trees will harvest resources from their surroundings and accumulate them under the tree (Breman and Kessler, 1995). As the positive influences of woody plants on productivity are due to the redistribution of resources within the landscape it will always be difficult to develop agroforestry without risking the depletion resources at a distance from the tree. An intriguing possibility is the prospect of capitalising on this phenomenon of resource capture at a distance through strategic use of 'hydraulic lift'. This is the process in which water taken up by roots from moist zones of soil is transported through the root system and

released into drier soil (Dawson, 1993, Pate and Dawson, this volume). Rainfall captured through stem flow, especially by a woody canopy, can be stored deep in the soil close to the roots and be returned to the topsoil beneath the canopy by hydraulic lift for later use with associated benefit for understorey species. Current modelling studies suggest that this strategy is only important to the tree as a means of penetrating dry soil zones to reach deep reserves of water (Van Noordwijk and Ong, this volume).

This paper examines these four hypotheses using results of recent research investigations on simultaneous agroforestry practices, primarily from Machakos, Kenya. It then attempts to reconcile such information with current knowledge on the ecology of savannah vegetation. Recent insights into the effects of savannah trees on understorey vegetation and soils should provide valuable clues on how to reduce the negative effects of below-ground competition in agroforestry while retaining the positive effects of trees seen in natural ecosystems. It is this opportunity for agroforests to mimic the interactions between trees and other plants in natural ecosystems that led to the recent redefinition of agroforestry (Leakey, 1996), in which different agroforestry practices are viewed as stages in the development of an agroecological succession akin to the dynamics of natural ecosystems. Over time, the increasing integration of trees into landuse systems through agroforestry can be seen as the passage towards a mature agroforest of increasing integrity. Similarly, with increasing scale, the integration of various agroforestry practices into the landscape is like the formation of a complex mosaic of patches in an ecosystem, each of which is composed of many niches. These niches are occupied by different organisms, making the system ecologically stable and biologically diverse (Leakey, 1996). In systems like this, the physiological interactions between the tree and crop components of the agroecosystem are more likely to mimic those of natural ecosystems.

3.1. *Hypothesis 1: Agroforestry systems can increase the efficient use of resources by combining species with different patterns of resource uptake*

The concept of complementary resource use is not new in ecological studies. It was proposed by de Wit (1960) and others (Trenbath and Harper, 1973; Willey, 1985; Vandermeer, 1989), that mixtures of species may have greater capacity to exploit growth resources and hence be more productive than monocultures. The principles of resource capture have been used to examine the influence of agroforestry on ecosystem function, i.e. the capture of light, water and nutrients (Ong and Black, 1994), and to better understand the ecological basis of sustainability of tropical forests (Ewel, 1986; Ewel and Bigelow, 1995). The theme of complementary resource use has been explored extensively in intercropping studies in the tropics (Trenbath, 1974; Fukai and Trenbath, 1993; Sinoquet and Cruz, 1995; Trenbath, this volume). However, these recent re-interpretations of published results indicate that increased yield

from combinations of annual crops was *not* always associated with greater resource capture or utilisation. For example, the choice of fast-growing, competitive tree species, such as *Leucaena leucocephala* Lam., has often been found to be inappropriate for alley cropping despite their good coppicing and nitrogen-fixing capacity. Several workers have shown that in dryland conditions, leucaena is very competitive with intercrops such as millet, sorghum, groundnut and maize (Singh et al., 1989; Jama et al., 1995). Consequently, it has been recommended that research attention should focus on tree species with more compatible root distribution (i.e. better spatial complementarity – Van Noordwijk and Purnomosidhi, 1995).

The capture of growth resources by trees and crops can be grouped into the broad categories of neutral, complementary or competitive interactions (Figure 1). In the neutral or trade-off category, trees and crops exploit the same pool of resources so that increases in capture by one species result in a proportional decrease in capture by the associated species. If trees were able to tap resources unavailable to crops, then the overall capture would be increased as shown by the convex curve in Figure 1, i.e. complementary use of resources. In the third category, negative (competitive) interactions between the associated species could result in serious reduction in the ability of one or both species to capture growth resources (concave curve). It is important to bear in mind that in agroforestry, tree-crop interactions may change from one category to another depending on the age, size and population of the

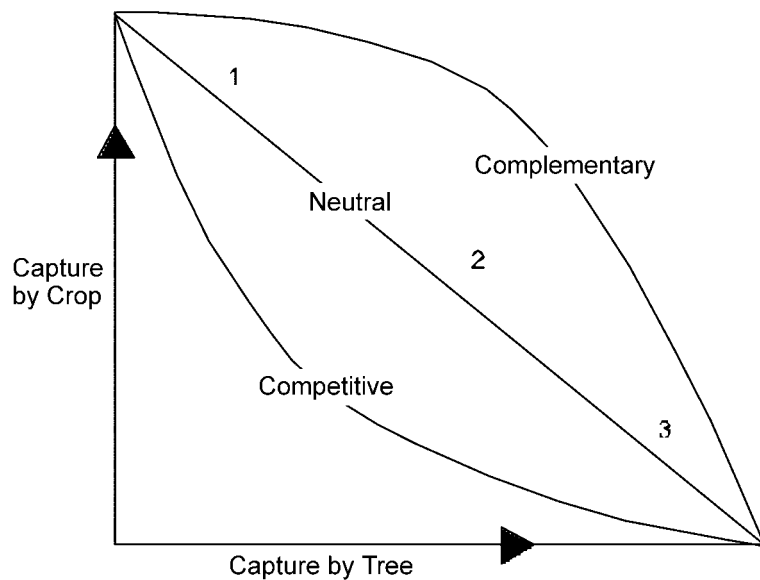


Figure 1. Resource capture by trees and crops showing competitive, complementary and neutral interactions 1. Parkland and savannah (Late stage agroecosystem), 2. Boundary planting, 3. Alley cropping (Early stage agroecosystem)

dominant species (as in a natural ecosystem), as well as the supply and accessibility of the limiting growth resources. Later, we use this diagram to illustrate the discrepancy between the findings of various agroforestry practices and that of the savannah ecosystem. We also suggest that the competitive interactions are more often associated with the early successional stages of an agroecosystem, while the complementary interactions occur during the late successional stages of mature agroforests, such as the farmed parklands of Sahelian Africa.

Such ideas on capture of water and nutrients, coupled with recent innovations in instrumentation (mini-rhizotrons, sap flow methodologies), have stimulated a resurgence in root research (Schroth, 1995; Van Noordwijk and Purnomosidhi, 1995; Khan and Ong, 1996) and attention to spatial complementarity in root distribution and the potential beneficial effects of deep rooting.

The benefit of deep rooted vegetation for maintaining ecosystem functioning is emphasised in parts of Australia, where the removal of the native perennial vegetation and its replacement by shallow-rooted annual crops and pastures has led to a profound change in the pattern of energy capture by vegetation, less efficient use of rainfall, increased vertical and lateral water movement, and hence rising water-tables and associated salinity (Hatton and Nulsen, this volume; Dunin et al., this volume). In the Sahel, removal of vegetation with deep roots has also led to increased leakiness (Cuff et al., 1993). In this situation, deep drainage on the sandy soils increased from 10–20 mm to 200–300 mm per year (Gaze et al., 1997) and a pulse of nitrogen is on its way down to the water table (Edmunds, 1991; Deans et al., 1995). In western Kenya, *Sesbania sesban* has been shown to utilise nitrogen below the rooting zone of maize (Mekonnen et al., 1997) and to make this available to crops through its leaf litter. This indicates that nutrients can be captured at depth by agroforestry trees and redistributed vertically within the soil profile. Evidence also indicates that the network of tree roots in agroforestry practices are able to reduce the leaching of nutrients from the surface soil layers, so reducing the leakiness of the nutrient cycle (Buresh and Tian, 1998). Earlier research on South African savannahs has also shown that tree roots extend into the open grassland, providing a 'safety net' for recycling water and nutrients, and accounting for 60% of the total below-ground biomass (Huntley and Morris, 1982). Walker and Noy-Meir (1982) also presented a conceptual model of the African savannah in which the grass roots are restricted to the upper layers which dry out first, while the tree roots have access to deeper layers, which are usually above the wilting point.

One of the earliest detailed studies of resource capture in agroforestry practices was that for a C_4 crop with a C_3 tree in semiarid India, described by Monteith et al. (1991) and Corlett et al. (1992a, 1992b). In this work in Hyderabad (annual rainfall of 700 mm), involving a *Leucaena leucocephala*/*Pennisetum americanum* (millet) alley cropping system, radiation interception and soil moisture were measured, but soil moisture results were unreliable

because of highly variable soil physical properties. Total intercepted radiation during the rainy season was 40% greater in the alley crop than in sole millet, primarily because the presence of leucaena increased fractional interception during the early stages of the growing season, while the millet provided a more complete ground cover across the alleys during the later stages of the season. The sole leucaena intercepted only 6% more light than the alley crop during the rainy season. The sole leucaena and alley leucaena intercepted twice as much radiation again as millet during the following long dry season after millet harvest. The evidence from this study shows that the main advantage of alley cropping was in extending the growing period into the dry season and increasing the annual light interception. However, interception by the more efficient C_4 crop was reduced to only half that of the sole millet during the rainy season and accounted for 15% of the total intercepted by the alley system. This, therefore, falls within the lower end of the complementary curve (Figure 1). In this study from India, the alley crop produced 7 t ha^{-1} biomass compared to 4.7 t ha^{-1} of sole millet and 4 t ha^{-1} by sole trees despite the high amount of light interception, because of the low photosynthetic rate or conversion coefficient of the C_3 species. The conversion coefficient or 'radiation use efficiency' (ϵ) is defined here as the ratio of biomass production to intercepted light per unit area and provides a measure of the efficiency with which the captured light is used to produce new biomass.

Subsequent resource capture studies at Hyderabad examined the partitioning of water and light in an agroforestry system comprising of two C_3 species, perennial pigeon pea (*Cajanus cajan*) and groundnut (*Arachis hypogaea*), using tube solarimeters and sap flow gauges (Marshall, 1995; Ong et al., 1996). Monocrops of each species were compared with line-planted and dispersed mixtures containing identical pigeon pea populations. Monocropped groundnut and pigeon pea intercepted about 850 MJ m^{-2} each in year two, but the dispersed system intercepted twice as much light during the same period. Although ϵ of the understorey groundnut increased by 28%, interception by groundnut contributed only 19% of the total interception in the dispersed system. Again this falls within the lower end of the complementary curve of Figure 1.

Both Hyderabad studies showed that the less efficient C_3 overstorey (tree) component dominated the total light interception, while the increased ϵ of the understorey component was insufficient to compensate for the reduced light interception. These results are typical of many alley cropping studies where the tree populations were so dense that reduction in crop yield was inevitable, because the trees captured most of the resources at the expense of the crops. Although crop yields were seriously reduced, these are examples of complementary interactions, but are often misinterpreted as competitive, because without the sole tree controls it was not possible to determine whether the alley cropping did capture more resources.

Similar investigations in semiarid Kenya confirmed that, on deep alfisols, alley cropping leucaena/maize has the potential to increase light interception

and to double water use as compared to sole maize stands (Howard et al., 1995), but that this is unlikely on shallow soils (McIntyre et al., 1996). These findings show that, by extending the period of growth, tropical agroforestry practices can substantially increase light interception and water use as compared to the shorter growth period of most annual cropping systems. This will only be the case if the water resource is not fully utilised by the annual crop. However, the conversion efficiency of the intercepted light in agroforestry practices will generally be lower than that reported for crops and savannah grasslands, since the photosynthetic system of trees is invariably C_3 and, thus, less efficient than that of C_4 crop plants. However, values of ϵ obtained from trees and forests are highly variable and greatly underestimated, since they are usually based on above-ground production. This focus on above-ground production is because quantification of tree root biomass is notoriously difficult, due to continuous decay (turnover) and consumption by soil biota.

As shown above for light, agroforestry offers substantial scope for spatial and temporal complementarity of water use, resulting from improved exploitation of soil water and off-season rainfall. However, the opportunity for significant complementarity is likely to be limited unless the species involved differ appreciably in their patterns or duration of rooting. One very successful form of agroforestry in drylands, which is characterised by complementarity, is the scattered mature trees of the Sahelian parklands, which have a discontinuous tree canopy (5–10 trees ha^{-1}). The more limited potential complementarity between high density trees and crops has been highlighted by recent work for a range of tree species at Machakos, Kenya. This showed that when rainfall was low (250 mm) maize yield was linearly and negatively related to the amount of water used by the trees (Figure 2). However, this relationship broke down when rainfall exceeded 650 mm, illustrating that the trees can then use water from the same soil profile as the maize without major negative effects on crop yield.

In water-limited environments, the quantity of biomass produced (W) depends on the quantity of water captured and the efficiency (e_w) with which this is used to produce biomass (expressed as units of biomass per unit water transpired). W is often linearly related to the quantity of water transpired, indicating that e_w is conservative (de Wit, 1958; Azam-Ali, 1983; Cooper et al., 1987). This relationship depends on the close linkage between CO_2 and water vapour fluxes due to the role of stomata in regulating the exchange of both gases. However, atmospheric saturation deficit (D) may exert a strong modifying influence on e_w , as is considered further below.

The e_w values for tropical C_4 cereals are often a little more than double those for C_3 species under equivalent conditions. For example, experiments in India under similar mean saturation deficits (2.0–2.5 kPa) provided season-long values of 3.9 and 4.6 $g\ kg^{-1}$ for millet, compared to 1.5–2.0 $g\ kg^{-1}$ for groundnut (Ong et al., 1987; Matthews et al., 1988; Azam-Ali et al., 1989). However, e_w is not always higher in C_4 species. Similar values of e_w have been

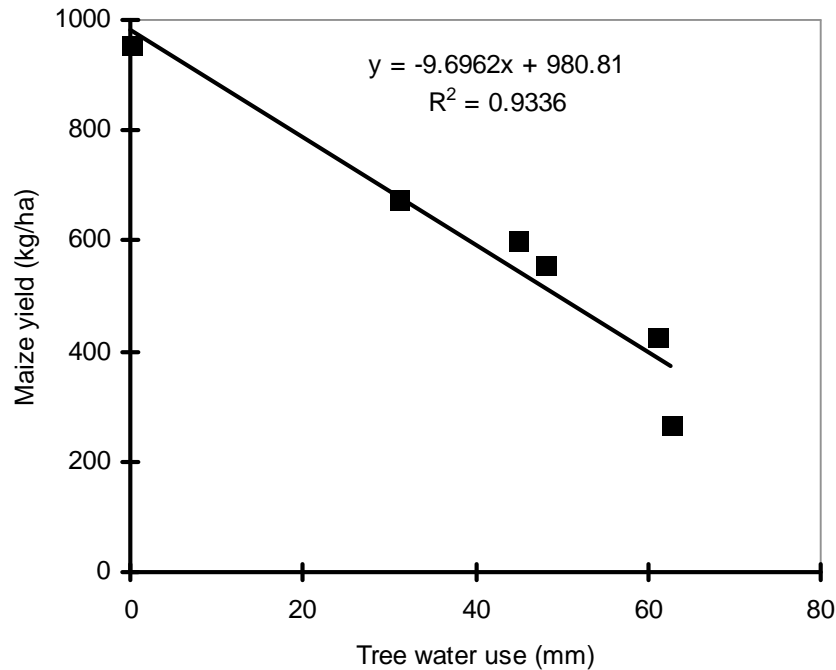


Figure 2. Regression of tree water use and maize yield in the 1996 long rains, Matchakos, Kenya.

reported for drought tolerant C_3 species, such as cowpea and cotton, as well as for relatively drought-sensitive cultivars of the C_4 species, sorghum and maize (Rees, 1986).

In theory then, the potential to improve the e_w of 'late-stages' in agroforestry succession is limited compared to 'early-stage' practices, such as intercropping, because the understorey crops are usually C_4 species and the overstorey trees are invariably C_3 species. Improvement in e_w is most likely if the understorey crop is a C_3 species. Such species are usually light saturated in the open and partial shade may have little effect on assimilation with the result that e_w is improved by concurrent reduction in transpiration. This may explain why cotton yield in the Sahel is not reduced by the heavy shading of karité (*Vitellaria paradoxa*) and néré (*Parkia biglobosa*) in parklands, while yields of millet and sorghum were reduced by 60% under the same trees (Kater et al., 1992). The same reason may explain the observation in the South and Central American savannahs that C_3 grasses are found only under trees and never grow in open grassland dominated by C_4 grasses (Medina, 1982). Surprisingly, there is no clear distinction between the C_3 and C_4 species under the trees in African savannahs, which are dominated by C_4 grasses. For example, in Zimbabwe, *Panicum maximum*, a C_4 grass, occurs as pure stands under *Combretum molle*, *Terminalia sericea* and *Albizia* spp. trees but

seldom occur in the open. The successful establishment of *P. maximum* under the savannah trees appears to be determined by its ability to germinate through the tree leaf litter, which prevents the survival of other C_4 grasses, abundant in the open (Kennard and Walker, 1973). In East Africa, the dominance of *P. maximum* under tree canopies was attributed to its higher water use efficiency and the higher grazing selection pressure in the open (Kinyamario et al., 1995). These examples of the parkland and savannah systems suggest that they represent the upper end of the complementary curve in Figure 1.

3.2. *Hypothesis 2: Competition for below-ground resources is inevitable and it is best managed by manipulating the interface between species in a mixture*

Early studies of spatial complementarity in agroforestry began by examining the rooting architecture of trees and crops grown as pure stands. For example, Jonsson et al. (1988) described the vertical distribution of five tree species at Morogoro, Tanzania, and concluded that their root distribution were similar to maize except for *Eucalyptus camaldulensis*, which had uniform distribution to 1 m. Thus, they concluded that there is little prospect of spatial complementarity if these trees and crops were grown in combination. Gregory (1996) summarised six other such studies of root distribution of trees, which essentially supported the conclusion of Jonsson et al. (1988). The study of roots of agroforestry systems where crops and trees are grown concurrently is much more difficult and tends to be confined to species which are easily distinguishable on the basis of visual features. Therefore species such as *Cassia* or *Senna* spp. which have a black outer coating on their roots are very convenient and frequently used (Hauser, 1993; Rao et al., 1993). These studies also showed that in semiarid environments, there was still considerable overlap between the roots of trees and crops especially in the top 0.5–1.0 m of the soil, implying that most trees will be competing with crops for both water and nutrients in the top 0.5 m of most soils.

What is the extent of spatial complementarity in water use when there is such a considerable overlap of the two rooting systems? Early results at Machakos, Kenya showed that there was no advantage in water uptake between a *Senna spectabilis*/maize or cowpea alley cropping and sole crop stands when rainfall ranged from 200–250 mm during the rainy season. This was because there was little water recharge below the crop root zone (McIntyre et al., 1997). However, recent measurements of soil moisture profiles of the same alley cropping systems indicate that when recharge occurred following 547 mm of rainfall, tree roots are still able to exploit more moisture below the rooting zone of the crops (Figure 3) even when there was a complete overlap of the root systems of trees and crops. Before the onset of the long rains, soil moisture content under the alleys was already 26 mm drier than in the pure crop treatment and the differences between the treatments increased to 31 mm after the long rains when only 235 mm of rain fell. During the dry

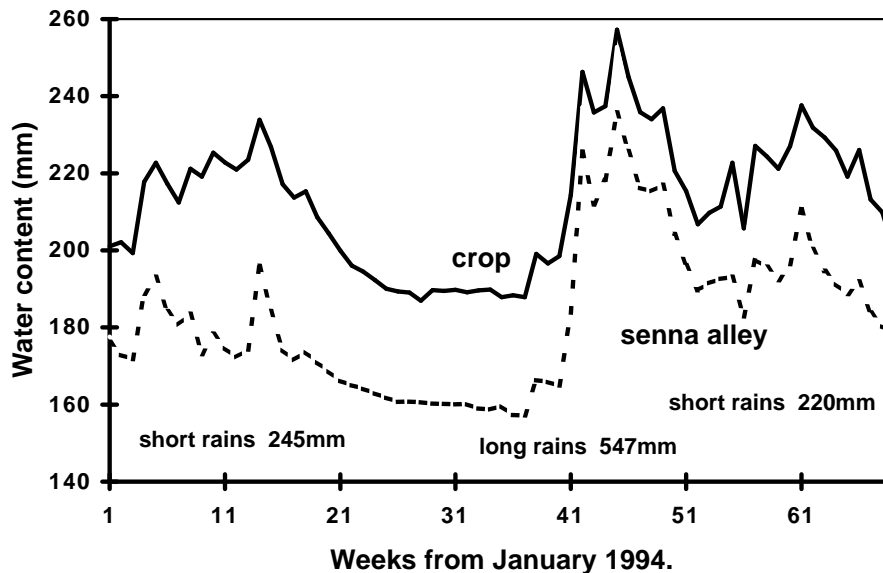


Figure 3. Weekly soil water content to 165 cm under annual crops (maize-cowpea rotation) and alley cropping with *Senna spectabilis* during three cropping seasons from January 1994 to November 1995 at Machakos, Kenya.

season, only a small amount of water was left under the alleys as soil moisture content had reached 14%, which is close to the permanent wilting point (12%) at 1.6 m depth. In this case, crop yield was reduced by 40%, indicating this is an example of the competitive interaction shown in Figure 1. In sharp contrast, soil moisture content remained at 18% below 1.0 m depth (not shown) under the pure crop treatment even after two successive low rainfall seasons. The profile was almost completely recharged in the short rains of 1995, when 547 mm of rain fell. Again, the moisture depletion rate under the alley was significantly greater than in the sole crop treatment. It is the extent of this competition for water by trees that has led to the conclusion by modellers that agroforestry is inappropriate in tropical areas with rainfall less than 800 mm (Cannell et al., 1998). It is relevant to note that the traditional and highly successful agroforestry parklands of semiarid areas are characterised by discontinuous tree canopies with only 15% cover (Breman and Kessler, 1995), while the model is based on continuous tree cover.

Where soil wetting is mainly confined to the crop root zone, competition by trees for soil moisture can be so severe that the risk of crop failure is greatly increased. For example, McIntyre et al. (1996) reported that total evapotranspiration in *Senna spectabilis*/maize or cowpea alley cropping systems in Machakos, Kenya, was either the same as or less than that of pure crops. Measurements in this and other experiments at Machakos revealed that there were still soil evaporation losses (42–48%) in both agroforestry and sole crop treatments because most of the rains occurred early in the cropping

season, before: (i) there was adequate tree canopy cover, and (ii) crop roots were extensive enough to exploit the soil water.

Further explanations for the lack of spatial complementarity in alley cropping were advanced by Van Noordwijk and Purnomosidhi (1995), who observed that repeated shoot pruning of trees in alley cropping had the danger of enhancing below-ground competition by increasing the proportion of superficial roots. Van Noordwijk and Purnomosidhi imposed three pruning heights (50, 75, 100 cm) on five tree species (*Paraserianthes falcataria*, *Gliricidia sepium*, *Peltophorum dasyrachis*, *Senna siamea*, and *Calliandra calothyrsus*) in the sub-humid site at Lampung, Sumatra, Indonesia and they found that while pruning had no effect on shoot:root ratios or the relative importance of the tap root, lower pruning regimes promoted more horizontal root growth, providing less spatial complementarity.

Direct measurement of tree transpiration with porometry is tedious and complex. The recent availability of robust sap flow gauges offers a unique opportunity for partitioning water use between trees and crops. Heat balance and heat pulse systems have been used routinely for several years at ICRISAT and ICRAF in a range of agroforestry practices (e.g. Howard et al., 1995, 1997; Lott et al., 1996). The sap flow approach confers the major benefit of allowing daily transpiration by the components of agroforestry systems to be followed continuously and reliably. The heat balance and heat pulse techniques have been modified to measure water movement through the main roots of trees in an approach which is proving invaluable in establishing the quantity of water extracted from the crop rooting zone, and hence the below-ground competitive impact of the trees on crops. The time courses for sap flow through the lateral roots of grevillea in semiarid Kenya (Figure 4) show considerable diurnal variation and indicate that sap flow decreased with increasing distance from the trunk. The trees nevertheless extracted significant quantities of water from the crop rooting zone at distances of up to 190 cm from the trunk. Experiments in which the lateral roots were progressively severed, indicated that these three-year old trees were capable of extracting up to 80% of their water requirements from beneath the crop rooting zone, in agreement with results obtained for the same species from experiments in which sap flow through the trunk was measured while the soil around the trees was excavated to a depth of 60 cm (Howard et al., 1997). In this case the effects on crop yield were minimal, illustrating spatial complementarity.

Recent measurements of the long term (three year) effects of shoot pruning on two species, *S. spectabilis* and *G. sepium*, at Machakos, Kenya confirmed the findings in Lampung, Indonesia in showing that rooting depths of both pruned trees and crops were almost identical and restricted to the top 1 m, whereas the rooting depth of unpruned trees was much deeper and extended to 160 cm. Thus, the rooting profile of the unpruned trees had a greater spatial complementarity with crops than that of pruned trees. However, there was little difference in terms of their competitiveness with associated crops because of the higher leaf area and hence transpiration of the unpruned trees. The

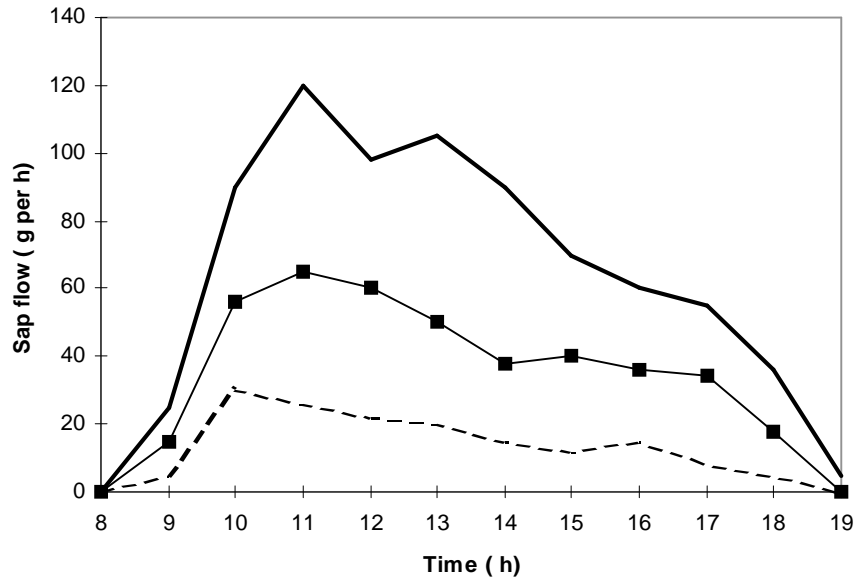


Figure 4. Diurnal trends in sapflow of lateral roots at distances of 50 cm (solid line), 115 cm (filled squares) and 150 cm (dashed line) from trunk of *Grevillea robusta* trees. Source: Modified from Lott et al. (1996).

evidence so far suggests that below-ground competition is inevitable in alley cropping where water is limiting (i.e. evaporation exceeds rainfall). This suggests that successful design of alley cropping in each environment hinges on managing the degree of interface between trees and crops to optimise the value of tree products while minimising the impact on crop yield (Lefroy and Stirzaker, this volume).

Recently, the opposite of hydraulic lift described by Dawson (1993) has been reported from Machakos and elsewhere, in which water is taken from the topsoil and transported into the subsoil (Burgess et al., 1998; Smith et al., 1998). This mechanism would enhance the competitiveness of deep-rooted trees and shrubs. Perhaps the selection of fast-growing, deep-rooting trees in agroforestry designs has inadvertently favoured such competitive species?

3.3. Hypothesis 3: Tree phenology can be selectively used to create temporal complementarity

In the semiarid tropics, water competition between trees and crops can occur both within the rainy season and through the build-up of a soil water deficit caused by tree transpiration during the dry season. Inter-seasonal water deficit can be particularly severe when there is a succession of droughts and when recharge is small and infrequent (McIntyre et al., 1996; Govindarajan et al., 1996). Thus, temporal complementarity is only possible if residual water is

available after the crop harvest or if rainfall occurs when there is no scope for cropping. For example, in Hyderabad, India, 20% (152 mm) of the annual rainfall occurs outside the normal cropping season and even the traditional intercrop of sorghum/pigeonpea utilises only 41% of the annual rainfall. The remainder of the rain is lost as runoff (26%) or deep percolation (33%). In such environments, agroforestry practices increase rainfall utilisation by extending the growing season. Thus, the total rainfall utilisation of perennial pigeonpea/ groundnut systems was 84%, about twice the value reported for the most productive intercrop systems in Hyderabad (Ong et al., 1992). This is one of the largest complementary interactions reported (Ranganathan and de Wit, 1996) and falls on the middle of the complementary curve in Figure 1.

The most remarkable example of temporal complementarity in water use is the unusual phenology of the Sahelian tree, *Faidherbia albida*, which is in leaf in the dry season and sheds its leaves in the rainy season. It retains this phenology even when planted in the Deccan plateau of India, where the water-table is too deep for access by tree roots. One of the few deliberate experiments in which *F. albida* was compared with a tree with conventional leaf phenology is that reported by Ong et al. (1992) at Hyderabad. Comparison of sap flow rates of *F. albida* and a local Indian tree, *Albizia lebbek*, show that transpiration by *F. albida* begins when the understory crops have developed a full canopy later in the rainy season. In contrast, *A. lebbeck* produces a full canopy well before the onset of the rains and sheds its leaves when the *F. albida* starts to develop its canopy. This is clearly an example of the neutral category (Figure 1).

3.4. Hypothesis 4: Trees cause a redistribution of resources within the landscape

Unlike the evidence presented for early-successional agroforestry practices like alley cropping, improved soil water and nutrient status have been reported under single mature tree canopies (late stage agroecosystems) in savannah areas in Africa, Central and South America and North America (Belsky and Amundson, 1997; Rhoades, 1997). There is strong evidence that nutrient redistribution by deep and extensive root systems as well as capture of resources by tree canopies are responsible for the improved soil nutrition beneath *Prosopis juliflora* (Triedmann and Klemmedson, 1973). In Kenyan savannahs, Belsky and her colleagues observed improved microclimate, greater soil biotic activity and N-mineralisation, greater infiltration rate and greater beneficial effects in more xeric (from 750 mm to 450 mm rainfall) environments (Belsky, 1994). They also demonstrated that plants grown in the open sites were more nutrient-limited than those under the tree canopy, and that artificial shade applied to plants in the open generated smaller increases than that of vegetation observed under trees. However, Belsky was unable to firmly conclude whether nutrient enrichment or microclimate changes were more important

in increasing understorey productivity. It is significant to note that the positive effects of trees on understorey vegetation are limited to certain sites and species combinations, including both nitrogen-fixing and non-nitrogen fixing trees. It is also difficult to determine precisely whether the tree-grass interactions in tropical savannahs are typical of the competitive category (Figure 1). The problem is that evidence from the literature is primarily based on plot level analyses. Belsky et al. (1989) postulated that the canopy zones of savannah trees, which are mostly shallow-rooted, were enriched by nutrients brought from surrounding grasslands by both tree roots and seed-eating weaver birds, and not from deep underground. It has also been suggested that water taken up by plant roots from moist zones of soil is transported through the root system and released into drier soil (Dawson, 1993). These two examples of resource redistribution would thus be an example of the neutral category in Figure 1 because they compensate for competition for other resources.

Evidence from a series of shade cloth trials on maize and beans at Machakos indicated a small beneficial effect of shading on crop temperature and crop production when rainfall is sub-optimal for crop production (Lott, unpublished PhD thesis). There was no evidence of improved soil moisture under the shade of tree canopies. In contrast, Rhoades (1995) reported increased soil water (4–53% greater than in the open) in the crop root zone beneath *Faidherbia albida* canopies in Malawi (see also Joffre, this volume). In theory, trees can increase soil water content underneath their canopies, if the water saved by shading effects on soil evaporation and rainfall redistribution (e.g. funnelling of intercepted rainfall as stem flow), exceeds that removed by the root systems beneath tree canopies. At high tree densities, the proportion of rainfall lost as interception by tree canopies and used for tree transpiration would exceed that saved by shading and stem flow, resulting in drier soil below the tree canopy. This may be one of the most important factors for the observed difference savannah and alley cropping findings.

4. Trees and deep water use

A study of water recharge was made at Machakos, Kenya, over four consecutive drought seasons (220, 250, 120, 230 mm) in two different layers of the 1.75 m deep soil profile over a 12-month period (Figure 5). It examined patterns of soil moisture content under: (a) a sole annual crop plot and (b), a plot of crop with a single row of four year-old *Grevillea robusta* trees. As expected from root profile observations (ICRAF, 1996) the annual crops utilised water mainly from the top 75 cm of the soil profile and substantial amounts of water remained below this depth, even during the short rains 1996/7 when only 180 mm fell compared to average rainfall of 350 mm. Recharge below 75 cm did occur in the long rains of 1997, but during this period there was less evidence of increasing soil moisture below the crop

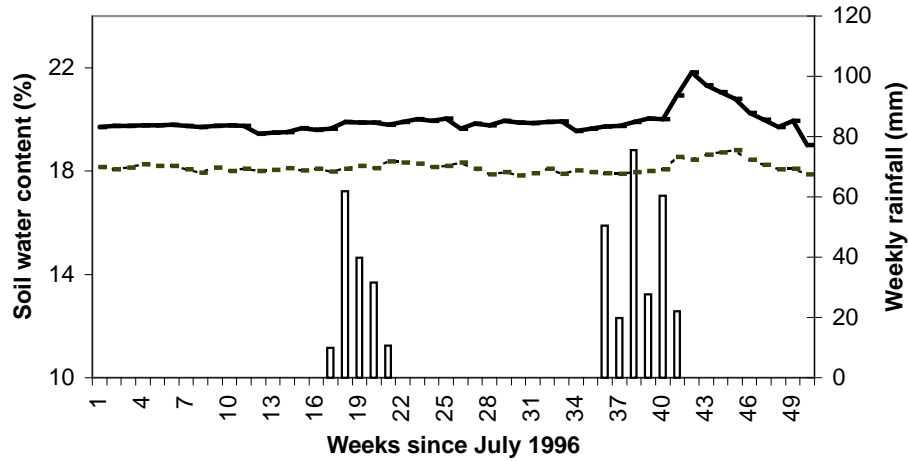


Figure 5. Soil moisture content below the crop rooting zone (75–175 cm) under an annual cropping system of maize and beans (solid line) and under *Grevillea robusta* plus crops (dashed line), Matchakos, Kenya.

rooting depth in the *G. robusta* plot. Over the twelve-month period, *G. robusta* abstracted only an extra 14.5 mm of subsoil water more than the annual crop treatment.

Our evidence suggests that although *G. robusta* is able to utilise water from below the crop-rooting zone, the annual rate of subsoil depletion is slow, unlike the high rate reported for eucalypt plantations (Calder et al., 1997). Nevertheless, the soil profile was not recharged until the fifth season. In contrast, a similar analysis for a fast growing native species, *Melia volkensii*, in the same trial provided a much higher rate (42 mm per annum) of subsoil water depletion. Clearly, this rate of water depletion is unsustainable, unless the *M. volkensii* tree population is greatly reduced. Water extraction will clearly increase as trees grow larger, which could have serious implications for water relations on sites with shallow soils and low water holding capacity, unless canopy management, such as pruning, is applied to reduce tree water use.

Where groundwater is accessible to tree roots, there is clear evidence for spatial complementarity. In the Majjia valley of Niger, measurements of stable isotopes of oxygen in plant sap, groundwater and water in the soil profile of windbreaks showed that neem trees, *Azadirachta indica*, obtained a large portion of their water from the surface layers of the soil only after rain. During the dry season, the tree roots extracted groundwater at 6 m depth (Smith et al., 1997). In contrast, at Sadore, where groundwater was at a depth of 35 m, they found that both the trees and millet obtained water from the same 2–3 m of the soil throughout the year (rainfall of 450 mm).

5. Conclusions

Our understanding of the ecological processes in alley cropping and other simultaneous agroforestry practices in the drylands has advanced considerably during the last few years. In reconciling this information with the vast ecological literature on tropical savannahs we suggest it is useful to consider agroforestry practices in terms of early and later stages of succession. From this perspective, alley cropping with fast growing, regularly pruned trees is analogous to early succession characterised by a high degree of competition while parkland agroforestry with widely spaced trees is analogous to later stage succession with opportunities for temporal and spatial complementarity. Furthermore, it would probably take a long time for the beneficial effects of microclimate and soil improvements of mature savannah trees to be realised. It would probably be more realistic to select trees which could provide direct cash benefits to farmers through their products, and to accept that in the longer term they will provide indirect environmental benefits arising from a more complex agroecosystem (Leakey, 1998). Economic gains from marketable products could compensate for any loss in crop yield (Kessler, 1992). It is, however, important to point out that current understanding of resource capture by agroforestry practices is based on well-managed small plots, often in research stations, in which about 30–45% of the rainfall is used for transpiration. Such levels of rainfall utilisation are rarely achieved in farmers' fields, or at the landscape level, in sub-Saharan Africa because of low inputs, and there are still ample opportunities for increasing water use by incorporating trees into landuse practices. For example, Rockstrom (1997) reported that only 6 to 16% of the total rainfall in a watershed in Niger is utilised by pearl millet for transpiration and the remainder is lost by soil evaporation (40%) or by deep drainage (33 to 40%). In contrast, plot level studies at Machakos by McIntyre et al. (1997) reported a rainfall utilisation of 40–45% by maize and cowpea for transpiration and the rest was lost as soil evaporation, thus limiting the opportunity for agroforestry.

The greatest opportunity for simultaneous agroforestry practices in the drylands of the tropics would seem to be the exploitation of the complementary interactions between crops and mature trees grown for their marketable products. Such trees can be fitted into the landscape by (i) exploiting the under-utilised niches within and around the farms, such as footpaths and home compounds, (ii) by integrating crops with boundary plantings, scattered trees and vegetable gardens and (iii) by integrating crops with fodder banks protected by hedges. In this way, agroforestry would allow the regeneration of parklands and lead to the successional development and patch dynamics of an agroecosystem that is akin to natural ecological succession (Leakey, 1996).

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