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Water Use and Water Productivity of Agroforestry Systems in the Semi-arid Tropics

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Abstract: The greatest challenge for agroforestry in dryland areas is to identify species combinations and management systems which optimize the capture of scarce available water supplies and minimize the inevitable competition between trees and crops. This review describes recent advances in research concerning water use and tree-crop interactions in the semi-arid tropics, focusing on studies in India and Africa, where farming systems involving the incorporation of trees with crops are becoming increasingly popular. We begin by establishing why and how farmers practice agroforestry in dryland areas in order to identify the rationale underlying their decisions and the tree management practices employed and to provide a starting point for developing future options; only a limited number of tree species are preferred by farmers in semi-arid areas of Kenya and elsewhere in East Africa. We explore how agroforestry may enhance rainfall utilization by improving temporal and spatial complementarity in resource capture. A key, but simple, identifiable trait is the leafing phenology of the tree species involved as this may be used to assess their suitability for effective water management in agroforestry systems. The feasibility of root pruning to reduce competition for water and optimization of the benefits of microclimatic modifications in agroforestry systems is also considered. Finally, we consider how agroforestry may be used to cope with predicted climate change, which is expected to affect subsistence farmers most severely in the semi-arid tropics.

Key words: climate change, hydraulic lift, tree-crop interactions, phenology, water use.

Why Farmers Integrate Trees and Crops in Drylands

One of the principal biophysical premises of agroforestry in dryland systems is to conserve and maximize the use of limited water supplies (Broadhead *et al.*, 2003a, b; Ong *et al.*, 2006). However, the technology must also take account of social issues regarded as important by farmers and overall management strategies (Nair *et al*., 1999; Thangata and Alavalapati, 2003; Franz *et al*., 2003). Previous research has shown that local farmers throughout the Sahel deliberately intercrop trees in a range of different systems, demonstrating innovative methods for increasing production while maintaining the viability of the resource base (Raintree, 1986; Budowski, 1993; Ayuk, 1996; Taft, 1997; Fischer and Vesseur, 2002; Oba *et al*., 2002; Johnson *et al*., 2003).

Barrow (1995) showed that, because of the importance of trees in dryland areas, local people often possess extensive knowledge of individual species and their management, which has been accumulated and refined over generations. It is therefore important to establish farmers' perception and local constraints in order to identify the rationale underlying their decisions and the tree management practices they employ, thereby providing a starting point for assessing future options.

Dryland agroforestry practices have become increasingly popular in eastern Kenya, but very few attempts have been made to assess their impact in terms of providing an effective means of increasing vegetation cover and environmental conservation at the landscape level. However, satellite imagery now provides unparalleled databases to document changes at landscape and regional levels over extended periods. A recent study by Anyango (2005) used two satellite datasets (1988 and 2000) to assess changes in vegetation cover in eastern Kenya where farmers have widely adopted various forms of agroforestry. The study area is a vast plain encompassing three districts of Kenya (Thika, Mberee and Machakos). This study showed that vegetation cover had increased by at least 20% in approximately one quarter of each district examined (Fig. 1). Vegetative cover dominated by coffee plantations (deep red color) was apparent in the upper part of Thika District, which is situated at higher altitudes than the remainder of the study area. The upper part of Mbeere District and the higher altitude areas of Yatta plateau in Machakos were dominated by scattered *Grevillea robusta* trees and annual crops (pink color).

The study area examined by Anyango (2005), i.e. the drier regions of Machakos, Mbeere and Thika Districts, reflects a recent intensive settlement trend typical of semi-arid ecological zones in Kenya, where farmers are increasingly forced to grow crops under drier climatic conditions due to the limited availability of high potential agricultural land to support increasing human and livestock populations and the associated increase in demand for food (NEAP, 1994). The study area is characterized by a mosaic of smallholdings on which various forms of land use adopted from neighboring high potential areas are common (Tyndall, 1996; Taft, 1997). Previous surveys have shown that *Grevillea robusta* and *Melia volkensii* are the dominant tree species associated with agricultural systems in this area (Thijssen *et al*., 1982; Tyndall, 1996; Kamweti, 1996; Anyango, 2005). The systems used include deliberate intercropping of woody perennials in the same land management units as agricultural crops in various configurations within and outside the cropping areas, home gardens and fallows involving some form of spatial arrangement and/or temporal sequence. Scattered, isolated, line-planted and clustered tree planting systems were all observed. Most farmers in the study area are resource-limited in terms of capital and labor and operate primarily at the subsistence level (Anyango, 2005).

The logic underpinning agroforestry systems is that trees grown in mixtures with crops should either have a beneficial influence, whereby crop performance is enhanced, or should exert minimal competitive effects on associated crops (Ong *et al*., 2006). However, other studies have

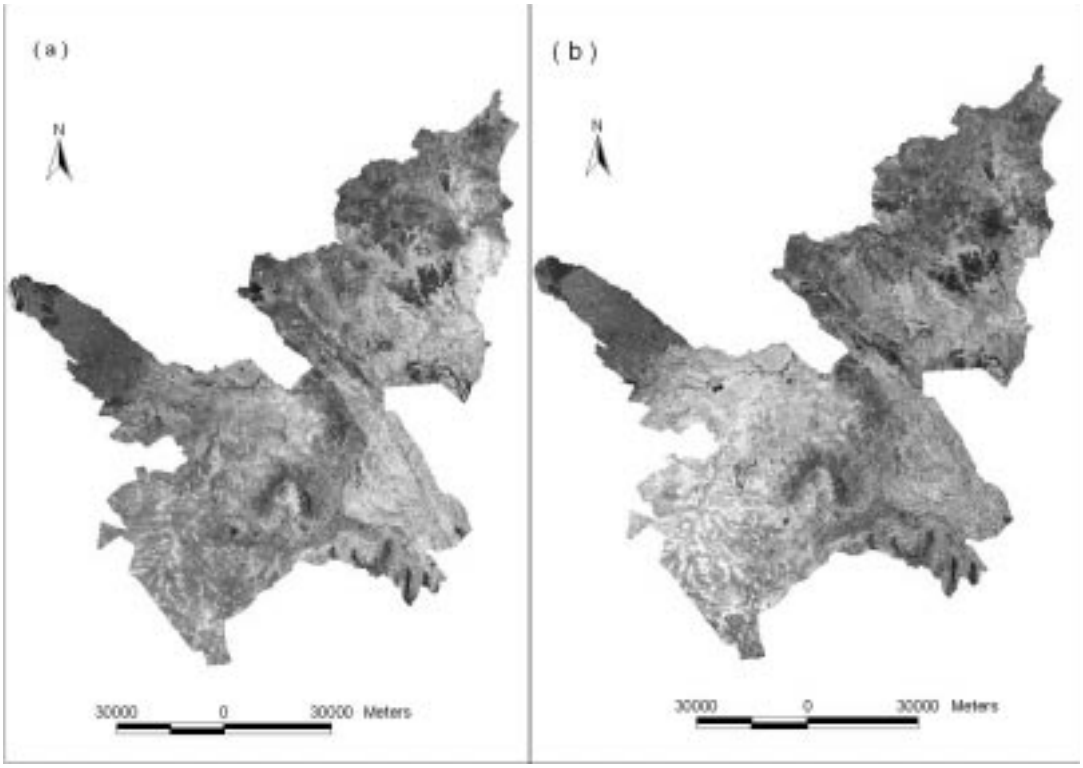


Fig. 1. Satellite map showing changes in tree cover between 1988 (a) and 2000 (b) in three adjoining Districts in Kenya (Thika, Mbeere and Machakos). Red represents dense vegetation cover, pink shows Grevillea robusta trees and annual crops, blueish/green denotes short or sparse vegetation and bright blue shows reservoirs (from Anyango, 2005).

shown that farmers change their tree planting strategies as they adapt to new challenges and experiment with tree species, which are 'new' to their environments. Farmers who were immigrants from high potential areas planted trees when they first settled on their farms primarily to obtain tree products such as fuelwood, as they often had no access to communal land. Factors such as rapid tree growth and consequent reductions in the time needed to obtain returns (benefits) were therefore important in promoting the adoption of specific tree species. Because *Grevillea robusta* is easily propagated and its seedlings are readily accessible, it was possible to plant this species systematically as hedges or overstorey trees along the margins of cropping areas. By contrast, *Melia volkensii*, although preferable to *G. robusta* in water-limited environments because of its lower competitive impact, was more difficult for farmers to adopt because seedlings were less readily available; its growth therefore occurred mainly through natural regeneration (Mulatya *et al*., 2002;

Anyango, 2005). Studies by Schaller *et al*. (2003) of mixtures of crops and fast growing trees revealed how farmers replaced traditional leguminous shade trees, managed principally for the benefit of coffee farming, with fast-growing exotic timber species such as *Eucalyptus deglupta*, which were more competitive with associated crops. This strategy was adopted because inclusion of timber trees increased the overall profitability of the system and reduced financial risks.

Likewise, farmers in the study area surveyed by Anyango (2005) expressed a preference for *M. volkensii* over *G. robusta* in terms of compatibility between trees and crops, although biophysical studies by Ong and Huxley (1996) and Mulatya *et al*. (2002) suggested that *M. volkensii* is more competitive with crops than *G. robusta.* Farmers perceived the use of *M. volkensii* as a coping strategy because the region is characterized by frequent crop failure resulting from low and variable rainfall; they therefore accepted a loss in terms of crop production for the eventual benefits provided by sales of the *M. volkensii* timber products, which are of higher commercial value than those from *G. robusta* (Kenya Forestry Master Plan, 1994; Mulatya, 2000). Crop yield losses resulting from competition were not considered to be a major constraint, although farmers associated competition between trees and crops with shading and employed measures to control such effects through crown pruning. Shading is known to reduce crop yield drastically, while crown pruning has been reported to improve crop yields (Namirembe, 1999; Black and Ong, 2000; Bayala *et al*., 2002).

Extension programmes are a significant factor in determining the farmer's tree(s) of choice. For example, *M. volkensii* has not been extensively promoted as an agroforestry tree by the agricultural extension system within the study area, and knowledge concerning its on-farm ecological functions is primarily based on farmers' experience. By contrast, *G. robusta* has been the subject of major extension programmes, especially in the adjacent high potential coffee and tea growing areas of Kenya (Tyndall, 1996; Kamweti, 1996).

In addition to influential ecological factors such as soil and climatic conditions, species composition and tree density on farmed land depend on sociological factors such as the attitude and interest of farmers in trees, their experience with trees, and prevailing agricultural practices. Recent studies indicate that a more realistic means of ensuring the success of agroforestry combinations is through cost-effective management of competition for limited resources within the systems that individual farmers have chosen (van Noordwijk and Purnomosidhi, 1995; Namirembe, 1999; Jackson *et al*., 2000; Ong *et al.,* 2002). Competition between trees and crops is a significant potential concern, especially where the availability of essential growth resources is limiting, as in the dryland areas; the trees often have a lower economic value than associated crops, and farmers seldom consider conservation itself to be a benefit. An understanding of the processes underlying the nature of the competition and possible management options which takes account of both farmers' interests and environmental sustainability is therefore required to optimize the productivity and

sustainability of agroforestry in dryland environments.

Can Agroforestry Systems Improve Water Productivity?

Early attempts to intensify agroforestry systems in the drylands of India and Africa were generally disappointing, largely because there was no clear understanding of the underlying biophysical processes (Ong and Huxley, 1996; Rao *et al.*, 1998). It was wrongly assumed that agroforestry systems could be intensified using the well-established principles of intercropping annual crops to mimic the beneficial ecological interactions reported for savannah ecosystems by incorporating fast-growing trees within alley cropping designs. Ong and Leakey (1999) concluded that there was little opportunity for beneficial interactions when trees and crops compete for the same below-ground resource pools (i.e. tree and crop roots occupy the same soil horizons) and use growth resources at the same time. To optimize resource capture in agroforestry systems, the trees must use resources, which cannot be used by crops (Cannell *et al.*, 1996) either in time or in space. This hypothesis led to a huge international effort in the 1990s to identify deep-rooting trees and understand how to manipulate below-ground interactions (Schroth, 1999; van Noordwijk *et al.*, 2004).

Agroforestry has the potential to improve water productivity in two ways as the presence of trees may increase the quantity of water used for tree or crop transpiration and may also improve the productivity of the water that is transpired by increasing the biomass of trees and crops produced per unit of water used. In their recent review, Ong *et al*. (2006) concluded that plot-level evidence shows that improvements in water productivity resulting from modifications of the microclimate conditions experienced by crops may be limited. Instead, evidence from the semi-arid tropics in India and Africa has shown that the greater productivity of agroforestry systems results primarily from the greater quantity of water used.

This review explores recent progress in the continuing search for improved tree management and species selection procedures to improve overall water productivity in agroforestry systems in the semi-arid tropics. We also consider how agroforestry systems may be used to cope with climate change, which is expected to have a major impact in sub-Saharan Africa where three-quarters of the countries are predicted to experience unstable water supplies and increased exposure to high temperature stress (De Wit and Stankiewicz, 2006).

Complementarity and Competition between Trees and Crops: The Balance between Microclimatic and Below-ground Interactions

In rain-fed cropping systems, water supplies to the soil originate mainly from infiltration following rainfall. However, a significant proportion of the annual rainfall may be lost by evaporation from the soil surface after low intensity rainfall or percolation to soil horizons below the crop rooting zone after heavy rainfall (Wallace, 1991, 1996). Biomass production is often constrained by limited water supplies, particularly in annual cropping systems, as

residual water in the soil profile following harvest of annual crops and off-season rainfall are unused (Ong *et al*., 1992, 1996, 2006).

Agroforestry offers substantial scope to improve system productivity by increasing the exploitation of available light, water and nutrients. To achieve this, the trees and crops must capture a greater proportion of available resources than equivalent sole stands, and/or use them more efficiently to produce dry matter (Cannell *et al*., 1996; Black and Ong, 2000; Ong *et al*., 2006). It is vital that trees are complementary rather than competitive with associated crops (Ong *et al*., 1996, 2006). Complementarity may be either spatial or temporal; the former occurs when trees and crops exploit different resource pools, for example, when deep-rooted trees exploit water and nutrients which annual crops cannot access (Cannell *et al*., 1996; Black and Ong, 2000). Temporal complementarity occurs when trees and crops impose demands on available resources at different times, for example, when trees are deciduous during part of the cropping season or continue to extract water during the dry season (Black and Ong, 2000; Broadhead *et al*., 2003a, b; Ong *et al*., 2006). Traditional cropping systems exhibiting such characteristics include the scattered mature trees of the Sahelian parklands, such as *Faidherbia albida*, which provide a discontinuous overstorey canopy (Belsky, 1994; Belsky *et al*., 1989, 1993).

The main challenge for agroforestry in dryland areas is how to identify tree species, which optimize the capture and use of limited environmental resources such as water and nutrients, but do not compete with associated crops (Muthuri *et al*., 2005; Ong *et al*., 2006). Few tree species with consistently limited competitive or complementary effects on associated crops have been identified to date (Ong *et al*., 2006). Identification of trees suitable for semi-arid agroforestry systems requires detailed mechanistic knowledge concerning species, which use limited resources efficiently, do not compete with adjacent crops and satisfy farmers' needs. Complementarity of water and nutrient use may be obtained if trees with suitable leafing phenology (e.g. leafless for at least part of the cropping season; Broadhead *et al*., 2003a, b; Muthuri *et al*., 2005) or rooting architecture (e.g. root systems which access deep water reserves (Ong *et al*., 1996, 2006) are used. However, as the root systems of many trees promoted for use in agroforestry systems have a similar vertical root distribution to food crops (Jonsson *et al*., 1988; Akinnifesi *et al*., 1999; Rowe *et al*., 1999), they often compete with associated crops. Management options such as shoot or root pruning prior to the cropping season may be used to modify the temporal patterns of resource use by trees and suppress competition (Schroth, 1999).

There is good experimental evidence that a suitable choice of agroforestry systems may enhance system productivity by increasing the use of available resources (Ong *et al*., 1992, 1996, 2006), although this is not invariably the case as the high water requirements of rapidly growing exotic trees may be problematic for farmers in dryland areas. Calder *et al*. (1997) reported that eucalyptus plantations in India transpired all of the rainfall infiltrating the

soil and abstracted a further 100 mm of water for each 1 m penetrated by the roots, posing a serious risk to sustainability as the roots may reach depths of 8 m within three years of planting. Govindarajan *et al*. (1996) found that alley cropping involving *Leucaena leucocephala* greatly reduced crop yield because competition for water outweighed the benefits of improvements in soil fertility resulting from applications of green leaf manure, nitrogen fixation and increased root turnover; both tree species are recognized as being highly competitive with crops. Other studies have shown that repeated root pruning in alley cropping systems encourages proliferation of fine tree roots in the surface soil, decreasing the spatial niche separation between trees and crops and hence complementarity in the use of below-ground resources (van Noordwijk and Purnomosidhi, 1995; Ong and Leakey, 1999). It is therefore essential to consider the implications of increased water use in agroforestry systems for medium and long-term water budgets and system productivity. Particular attention must be given to the source of water used by trees, rate of depletion and prospects for deep recharge during periods of high rainfall (Smith *et al*., 1997). As noted previously, it is essential to choose trees with appropriate leafing phenology or rooting architecture to enforce spatial and/or temporal complementarity and avoid major crop yield losses.

The importance of microclimatic conditions in determining crop performance is well documented (Ong *et al*., 1996; Black and Ong, 2000; Azam-Ali and Squire, 2002), and microclimatic and physiological factors have been incorporated into simulation models to predict growth over a wide range of species and environments (Spitters, 1990; Overman and Scholtz, 2002). The growth of trees in natural forests or plantations and their impact on the wider environment have also been widely researched (Cannell, 1989; Friend *et al*., 1997). However, the influence of trees on microclimatic conditions and the physiological responses of understorey crops are less well understood (Brenner, 1996; Ong *et al*., 1996). Previous studies have focussed mainly on alley cropping systems (e.g. Corlett *et al*., 1992; McIntyre *et al*., 1996) or large trees grown as shelter belts (e.g. McNaughton, 1988; Brenner *et al*., 1995), but few have examined the impact of dispersed overstorey trees (Vandenbeldt and Williams, 1992; Jonsson *et al*., 1999; Lott *et al*., 2000a, b; Muthuri *et al*., 2005).

There is good evidence from savannah systems of the beneficial influence of scattered trees on understorey vegetation. Belsky *et al*. (1989, 1993) reported that scattered *Acacia tortilis* and *Adansonia digitata* trees improved microclimatic conditions for understorey vegetation in eastern Kenya by moderating the thermal environment and reducing incident radiation and atmospheric saturation vapor pressure deficit, thereby increasing growth. Kinyamario *et al*. (1995) reported that the water status, gas exchange and water use efficiency of understorey grasses were all improved by tree shade in Nairobi National Park. However, more recent attempts to reproduce these positive interactions in agroforestry systems under similar climatic conditions have proved disappointing (van Noordwijk and Ong, 1999; Lott *et al*., 2000a,

b; Muthuri *et al*., 2005), suggesting that the potentially beneficial effect of microclimatic amelioration for understorey crops may be negated by reduced soil water supplies resulting from increased interception losses and water consumption associated with the presence of trees.

Trees may modify understorey microclimate in ways which either improve or reduce crop yield. Thus, Kater *et al.* (1992) and Kessler (1992) reported that sorghum and millet yields were reduced under scattered trees of *Vitellaria paradoxa* and *Parkia biglobossa* in the Sahel due to intense shading, whereas Vandenbelt and Williams (1992) and Jonsson *et al.* (1999) reported that the beneficial influence of reductions in temperature and improvements in soil fertility exceeded the adverse effect of tree shade. Huxley *et al.* (1989) reported that the presence of shade during the afternoon greatly improved maize yields in a *Cassia*/maize agroforestry system during seasons of low rainfall in semi-arid Kenya, while Huxley *et al.* (1994) found that the growth and yield of maize were increased by up to 80% on the sheltered down-wind side of tree lines compared to sole maize. These studies are by no means the only ones reporting benefits of shade for crop yield (Nicholas, 1988; Brenner *et al*., 1995; Smith, 1995), although the nature and impact of the microclimatic modifications remain unclear. Effects on the thermal and radiation environments experienced by understorey crops are likely to be key factors, as considered in detail below.

Temperature modification

A key question is whether temperature moderation by overstorey trees improves the performance of understorey vegetation in the semi-arid tropics. Direct benefits may be expected when soil or air temperatures in the open exceeds the optimum of *c*. 35°C for several hours during the day (Khalifa and Ong, 1990). In the Sahel and other dryland areas where supra-optimal temperatures are common, the benefits of temperature amelioration for understorey crops are well documented (Vandenbelt and Williams, 1992; Jonsson *et al.*, 1999). However, the lower temperatures at Machakos and elsewhere in the East African highlands are more favorable for plant growth, with the result that meristem temperatures persistently exceed the optimum only during periods of drought. Detailed studies were carried out to determine the influence of dispersed overstorey trees on the microclimate experienced by understorey crops at ICRAF's Machakos Field Station in Kenya. The objective was to test the hypothesis that, although the microclimatic changes induced are potentially beneficial for understorey crops, they may be negated by competition for water and nutrients. The impact of overstorey *Grevillea robusta* (A. Cunn.) trees on understorey maize was examined over a 4.5 year period on a site with no previous cropping history. Trees were planted in a dispersed arrangement as sole stands (Td) or in combination with maize (*Zea mays* L.) (CTd); sole maize was also grown (Cg 0%). The intensity of shade, cumulative intercepted radiation, meristem temperature and the phenology and productivity of maize were monitored for both sole crops and the agroforestry system. Maize was also grown under spectrally neutral shade netting which reduced incident radiation by 25 or 50% (Cg 25% and Cg 50%) to establish the

relative importance of shade and competition for water and nutrients in determining crop performance. Full details are given by Lott *et al*. (2000a, b) and Ong *et al*. (2000, 2006).

The results showed that, even in less extreme areas in the semi-arid tropics, such as Machakos, shade may have a substantial and potentially beneficial moderating influence on meristem temperature in understorey crops (Fig. 2a). The mean diurnal temperature range was 20°C for unshaded sole maize (Cg 0%) during the 1995/6 short cropping season, but was much smaller in all shade treatments. The effect of the tree canopy was comparable to the Cg 25% shade net treatment and maximum meristem temperature was 6°C lower than in unshaded sole maize. These results concur with Ovalle and Avendano (1987), who found that maximum soil temperature in an *Acacia* woodland was 3-10°C lower than under unshaded plants. However, the moderating influence of the tree canopy at Machakos declined during the observation period due to the continued increase in tree height (Lott *et al*., 2000a) and progressive removal of the lower branches, which increased the distance between the ground and the base of the tree canopy to over 2 m, providing greater through-flow of air in the understorey environment.

Fig. 2b shows the relative proportions of sub-optimal, optimal and supra-optimal temperatures experienced by maize in all treatments during the same cropping season. The thermal environment was most favorable in the Cg 50% treatment as the fraction of time when temperature was supra-optimal was much smaller than in the other treatments, particularly unshaded Cg 0% maize. Temperature is an important rate-modifier for growth and developmental processes, which often increase almost linearly between a base temperature (T_b) where the process begins and an optimum (T_o) where it reaches its maximum rate, before declining again between T_o and a maximum (T_m) where the process ceases (Black and Ong, 2000). Shading may therefore be advantageous in environments where sole crops regularly experience supra-optimal temperatures (Jonsson *et al*., 1999).

The long-term effect of temperature amelioration may be assessed by determining the relationship between key developmental events and accumulated thermal time (Fig. 2c). The slope of the relations for each treatment represents the rate of thermal time accumulation, while the vertical and horizontal lines indicate the mean date of flowering (DAS) and associated thermal duration (^{o}Cd) for each treatment. The substantial variation in the quantity of thermal time required to reach flowering suggests that development was affected by factors other than temperature as flowering occurred much later in terms of both chronological and thermal time in the agroforestry treatment (CTd) than in unshaded sole maize (Cg 0%), i.e. an additional 24 days and 400°Cd were required. Moreover, the thermal time required to reach flowering in CTd maize increased as the trees grew larger (Lott, 1998), suggesting that factors other than thermal time became increasingly important. The difference between shade net treatments was no greater than five days or 80°Cd. Thus, in contrast to savannah systems where shading of understorey vegetation was most

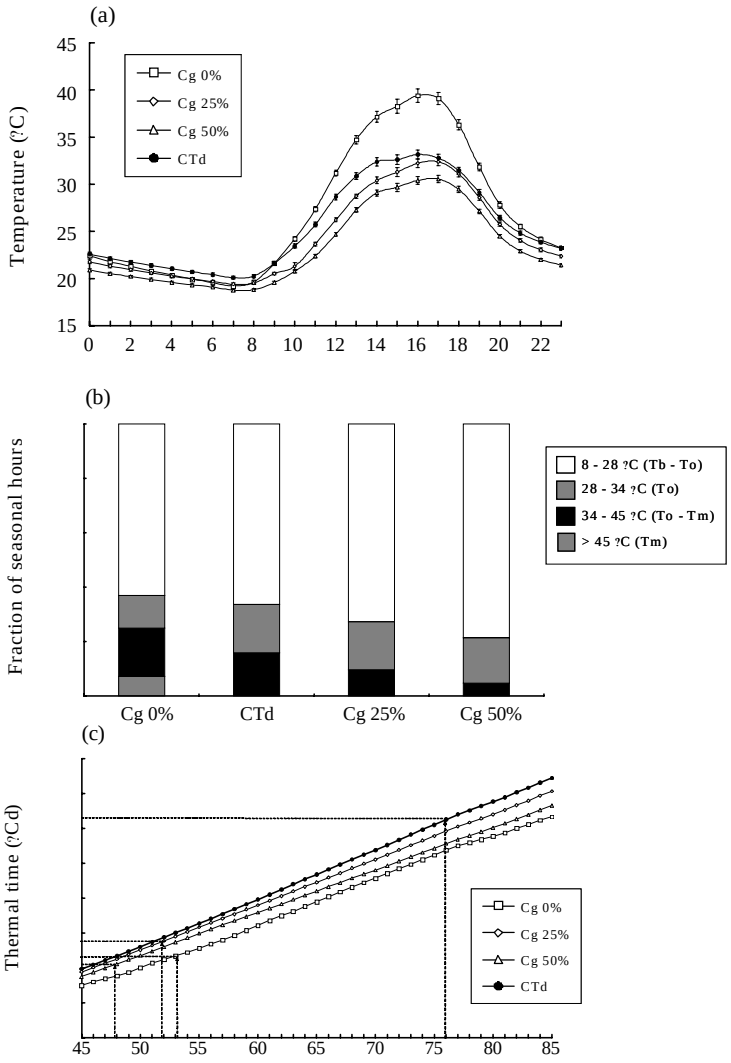


Fig. 2. (a) Diurnal time courses for mean stem meristem temperature in maize grown as an unshaded sole crop (Cg 0%), under shade nets which reduced incident radiation by 25 or 50% (Cg 25% and Cg 50% respectively), or in a dispersed agroforestry system with Grevillea robusta (CTd); (b) fraction of growing season when meristem temperature in maize was sub-optimal (8-28°C), optimal (28-34°C), supra-optimal (34-45°C) or above the maximum for developmental processes in maize (45°C); (c) relationship between accumulated thermal time (^{0}Cd) and the number of days after planting maize. All data are for the 1995/6 short cropping season at Machakos, Kenya. Double standard errors of the mean are shown where these are larger than the datapoints in (a) (modified from Lott, 1998).

beneficial during periods of low rainfall (Belsky *et al*., 1993), the present study suggests that crop water stress resulting from below-ground competition with trees outweighed the beneficial influence of temperature moderation. The results from the shade net treatments are consistent with previous studies in Kenya (Belsky *et al*., 1993; Belsky, 1994). Van Noordwijk and Ong (1999) suggested that the contrast between savannah and agroforestry systems may occur because water use per unit of shade provided by trees is greater in agroforestry systems.

Shading and radiation interception by crops

Fig. 3a shows mean diurnal time courses for short-wave radiation incident on maize in all treatments for an 11-day period centerd around anthesis during the 1994/5 short cropping season. Radiation incident on maize decreased with increased shade intensity in the shade net treatments; values for CTd maize were intermediate between the Cg 25% and Cg 50% treatments. Although values for CTd maize were calculated on the assumption that shading was uniform in the area bounded by four neighboring trees, the discontinuous nature of the tree canopy caused substantial local variation depending on proximity to the trees and solar angle. Incident radiation for understorey maize was greatest near the center of the area between neighboring trees and least beneath their canopies. This pattern corresponds closely with the growth of individual maize plants in this treatment (Lott *et al*., 2000b), suggesting that resource availability to crops increased with distance from the trees.

Cumulative interception of short wave solar radiation was calculated from hourly measurements for each treatment (Fig. 3b). Incident radiation frequently exceeded 20 MJ m^{-2} d^{-1} and cumulative incident radiation during the 123 day cropping season was 2432 MJ m^{-2}. The sole tree and crop canopies intercepted 718 and 630 MJ m^{-2} respectively, while the combined tree and crop canopies in the CTd treatment intercepted 952 MJ m^{-2} (Table 1), 33 and 50% more than in the Td and Cg 0% treatments.

Fractional interception of incident radiation (*f*) increased rapidly in Cg 0% maize during the first 70 days after sowing (DAS) to reach a maximum of 0.42 at flowering, close to the time of maximum leaf area index (LAI; Lott *et al*., 2000b); similar values were maintained for 30 d prior to the onset of rapid senescence. *f* values for the Td tree canopy increased steadily from 0.15 to 0.40 during the season as LAI increased (Lott *et al*., 2000a). *f* values were invariably greater for the combined tree and crop canopies in the CTd treatment than in the sole tree and crop systems, reaching a maximum of 0.54 and following a similar timecourse to unshaded sole maize. The seasonal mean *f* value for unshaded sole maize (Cg 0%) was only 0.26 (Table 1), suggesting that canopy size was limited by shortage of water, even during this season of relatively high rainfall, nutrients or population density, as seasonal means for tropical cereals grown under favorable conditions are typically *c*. 0.5 (Squire, 1990). The corresponding value for sole grevillea was comparable to that for sole maize (Table 1), whereas the seasonal mean of 0.39 for the combined tree and crop canopies in the CTd treatment

was 50% greater than in sole maize, suggesting the existence of spatial complementarity. Somewhat surprisingly in view of the C_4 and C_3 photosynthetic pathways of maize and grevillea respectively, the seasonal mean conversion coefficient for intercepted radiation (*e*) was lower for sole maize than in the Td and CTd treatments. As a consequence of the combined effects of the lower *f* and *e* values in the Cg 0% treatment, above-ground biomass production was only half of that in the CTd system (3.28 vs. 6.65 t ha^{-1}). Biomass production in the Td treatment was intermediate between the Cg 0% and CTd treatments, reflecting the higher conversion coefficient in the latter treatment (Table 1).

Fig. 3c illustrates the influence of shade on net photosynthetic (*A*) and transpiration rates (*E*) for maize in all treatments at 46 DAS during the relatively dry 1995 long cropping season (302 mm). Incident PAR flux on the maize canopy declined with increasing shade in the shade net treatments; similar values were obtained for the CTd and Cg 25% treatments. *A* and *E* declined proportionately to incident radiation in the shade net treatments, but were much lower in the CTd treatment than in the Cg 25% treatment (p), even though incident PAR fluxes were similar, suggesting that gas exchange was limited by factors other than solar radiation. The impact of the trees on gas exchange by understorey maize increased as the season progressed and their canopy increased in size (Lott, 1998). Inter-seasonal variation in response was also apparent as *A* and *E* values for CTd maize were much greater than those in the Cg 25% and Cg 50% shade net treatments during the relatively dry 1995 long rains (Fig. 3c), but were comparable during the wetter 1994/5 short rains (302 vs. 628 mm; Lott, 1998). Although the presence of trees reduced mean PAR flux to understorey maize by *c*. 30% in the CTd treatment, the decrease in yield at maturity was much greater than in the Cg 25% treatment during four consecutive seasons with highly variable rainfall (Lott *et al*., 2000b), suggesting that competition for water was an important factor limiting crop production in all seasons.

Our observation that microclimatic amelioration resulting from shading provides potential benefits for crop growth is consistent with previous studies of African savannah ecosystems. However, the evidence for agroforestry systems is inconsistent. For example, Jonsson *et al*. (1999) suggested that the positive effect of microclimatic modifications and improvements in soil fertility may exceed the negative influence of shade in the Sahel, whereas Kater *et al.* (1992) and Kessler (1992) reported that sorghum and millet yields in the Sahel were linearly related to the quantity of incident radiation beneath the tree canopy; the latter observation may be attributed to the fact that both crops examined are C_4 species with high light saturating PAR fluxes for photosynthesis and so are susceptible even to moderate shading (Ong *et al*., 1996; Black and Ong 2000). Other studies of dryland agroforestry systems suggest that shading is less important than competition for below-ground resources (e.g. Singh *et al*., 1989; Corlett *et al*., 1992; Jose *et al*., 2000; Muthuri *et al*., 2005). The available evidence therefore suggests that the potentially

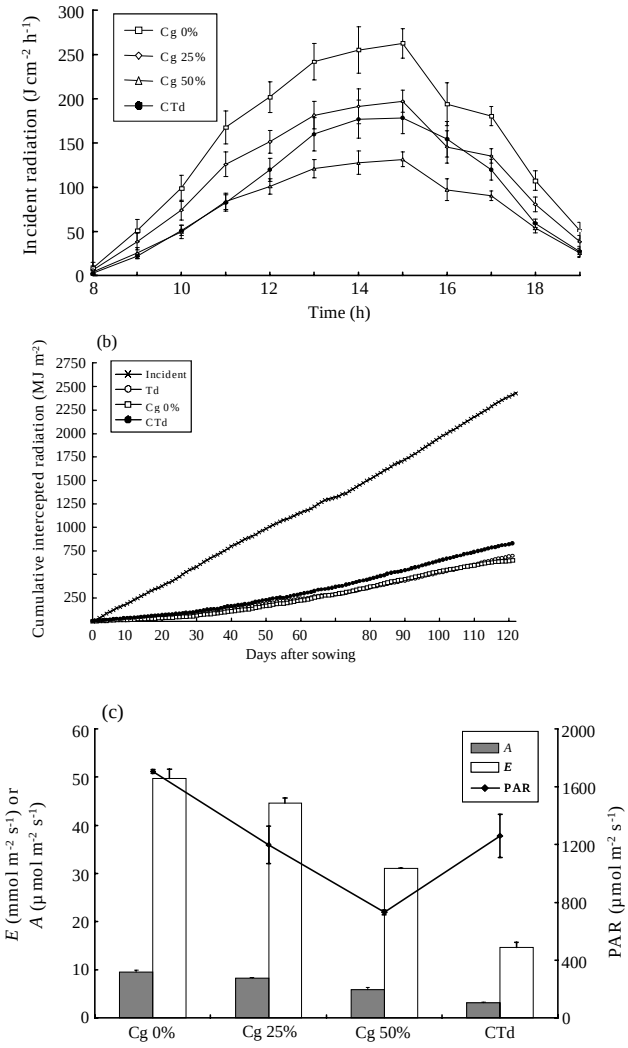


Fig. 3. (a) Diurnal time courses for incident radiation on maize grown as an unshaded sole crop (Cg 0%), under shade nets reducing incident radiation by 25% (Cg 25%) or 50% (Cg 50%), or in a dispersed agroforestry system with G. robusta (CTd) during the 1994/5 short cropping season at Machakos, Kenya; (b) seasonal time courses for cumulative seasonal incident radiation and intercepted radiation by unshaded sole maize (Cg 0%), sole G. robusta (Td) and the agroforestry treatment (CTd) during the 1994/5 short cropping season; (c) mean incident photosynthetically active radiation (PAR), net assimilation (A) and transpiration rate (E) for the Cg 0%, Cg 25%, Cg 50% and CTd treatments at 46 days after planting during the 1995 long cropping season. Double standard errors of the mean are shown in (a) and (c) (modified from Lott, 1998).

Table 1. Total seasonal intercepted shortwave radiation, seasonal mean fractional interception (f), above-ground biomass at final harvest, seasonal mean radiation conversion coefficient (e) during the 1994/5 short cropping season (from Lott, 1998)

Treatment	Intercepted radiation (MJ m^{-2})	Seasonal *f*	Biomass (t ha^{-1})	e (g MJ^{-1})
Cg 0%	630	0.26	3.28	0.52
Td	718	0.29	5.07	0.71
CTd	952	0.39	6.65	0.70

beneficial influence of tree shade on microclimatic conditions experienced by understorey crops may be outweighed by competition for water and nutrients between trees and crops, particularly during seasons of below average rainfall. Detailed and reliable information concerning below-ground competition is essential for the design of agroforestry systems which make best advantage of the trade-offs between microclimatic benefits and competitive interactions in semi-arid environments.

Comparing the Phenology and Water Use of Native and Exotic Trees

Continued settlement and population growth in semi-arid and arid regions of the world have dramatically increased demand for timber products (Ayuk *et al*., 1999; Okello *et al*., 2001) and other commodities already in short supply due to the rapid degradation of forests to satisfy householders' needs and the clearance of land for cultivation (KWS, 1999). The need to maintain and increase tree cover is a priority in Kenya and elsewhere in East Africa, although the choice of tree species presents a major challenge due to the limited availability of suitable species. Although indigenous species can provide some essential products such as charcoal (Okello *et al*., 2001), their growth rate and population density are generally low and it is often difficult to obtain propagation materials. It is therefore essential to identify appropriate species and design effective management regimes, which optimize the capture and use of environmental resources while fulfilling farmers' objectives (Ong *et al*., 1996; Lott *et al*., 2000a, b; Ong *et al*., 2006).

Compatibility and the potential for complementarity of resource use are key factors when selecting tree species for agroforestry systems. The dilemma of how to increase resource capture and system productivity without compromising crop production following the introduction of trees may be resolved by choosing species with an appropriate leafing phenology. The frequency with which trees replace their leaves and the timing within the annual cycle when they do so vary depending on species and the nature and severity of internal and environmental stress factors and other stimuli. Studies of the seasonality of tree activity may therefore improve our understanding of the nature of the interactions between trees and crops (ICRAF, 1997) and the extent of competition and complementarity (Muthuri *et al.*, 2005), so providing invaluable assistance when estimating annual carbon fluxes and managing water resources within ecosystems (Eamus, 1999).

The patterns of leaf flushing may be complex and have evolved in response to factors unrelated to resource capture (Huxley, 1996). Studies at Machakos, Kenya, using four tree species with a range of leafing phonologies, examined the hypothesis that temporal complementarity may be used to reduce competition for water with crops during the cropping period and enhance utilization of annual rainfall (Broadhead *et al*., 2003a). The species examined were *Melia volkensii*, which sheds its leaves twice annually, *Senna spectabilis* and *Gliricidia sepium*, which shed their leaves during the long dry season, and the evergreen *Croton megalocarpus* (Broadhead *et al*., 2003a, b). Further studies at Thika and Naro Moru in Kenya of the deciduous species, *Paulownia fortunei*, the semi-deciduous *Alnus acuminata* and the evergreen *Grevillea robusta* support these conclusions (Muthuri, 2004a; Muthuri *et al*., 2005). *P. fortunei* remained leafless for approximately three months during the annual cycle, partly during the cropping season, providing potential benefits for associated crops (Fig. 4). *A. acuminata* shed only some of its leaves during the dry season, although it is fully deciduous elsewhere (Okorio *et al*., 1994), while *G. robusta* was evergreen. The leaf fall pattern for *P. fortunei* resembled that reported previously for the exotic species, *S. spectabilis* and *G. sepium* (Broadhead *et al*., 2003b). However, leaf fall in *P. fortunei* occurred earlier, at the end of the long rains and also differed from the indigenous species examined by Broadhead *et al*. (2003a, b), which showed reduced leaf cover during both the dry seasons. These findings support the view that the main contrast in leaf cover dynamics is between indigenous and exotic species (Broadhead *et al*., 2003b).

It has been reported that, in seasonally dry tropical forests, competition for limited soil water during the dry season may be reduced by species-related differences in leafing phonology, coupled with differences in rooting patterns and activity (Meinzer *et al*., 2001). Meinzer *et al*. (1999) observed that the seasonal time courses for the partitioning of soil moisture were associated with leafing phenology as species showing the smallest seasonal variation in leaf area tapped increasingly deep sources of soil water as the dry season progressed. These experiments suggest that leafing phenology has an important role in determining the patterns and rates of soil water abstraction. It is therefore not surprising that Eamus (1999) emphasized the importance of studying the response of trees with differing leafing phenologies to drought as such information would help to provide an improved understanding of how to manage water use in agroforestry systems. Vegetation type also influences WUE, as Zhang *et al*. (1997) reported that pine trees had higher annual values than deciduous trees due to their differing leaf morphology.

Management of Below-ground Interactions for Water: Root Pruning and Sap Flow

Previous studies have shown that trees and crops often share the same soil horizons, even when the species involved are regarded as being compatible (Johnson *et al*., 1988; Ong *et al*., 1991; Smith *et al*., 1997; Schroth, 1999; Odhiambo *et al*., 1999). Thus, tree rooting densities may be greatest in the surface soil horizons (Dhyani *et al*., 1990;

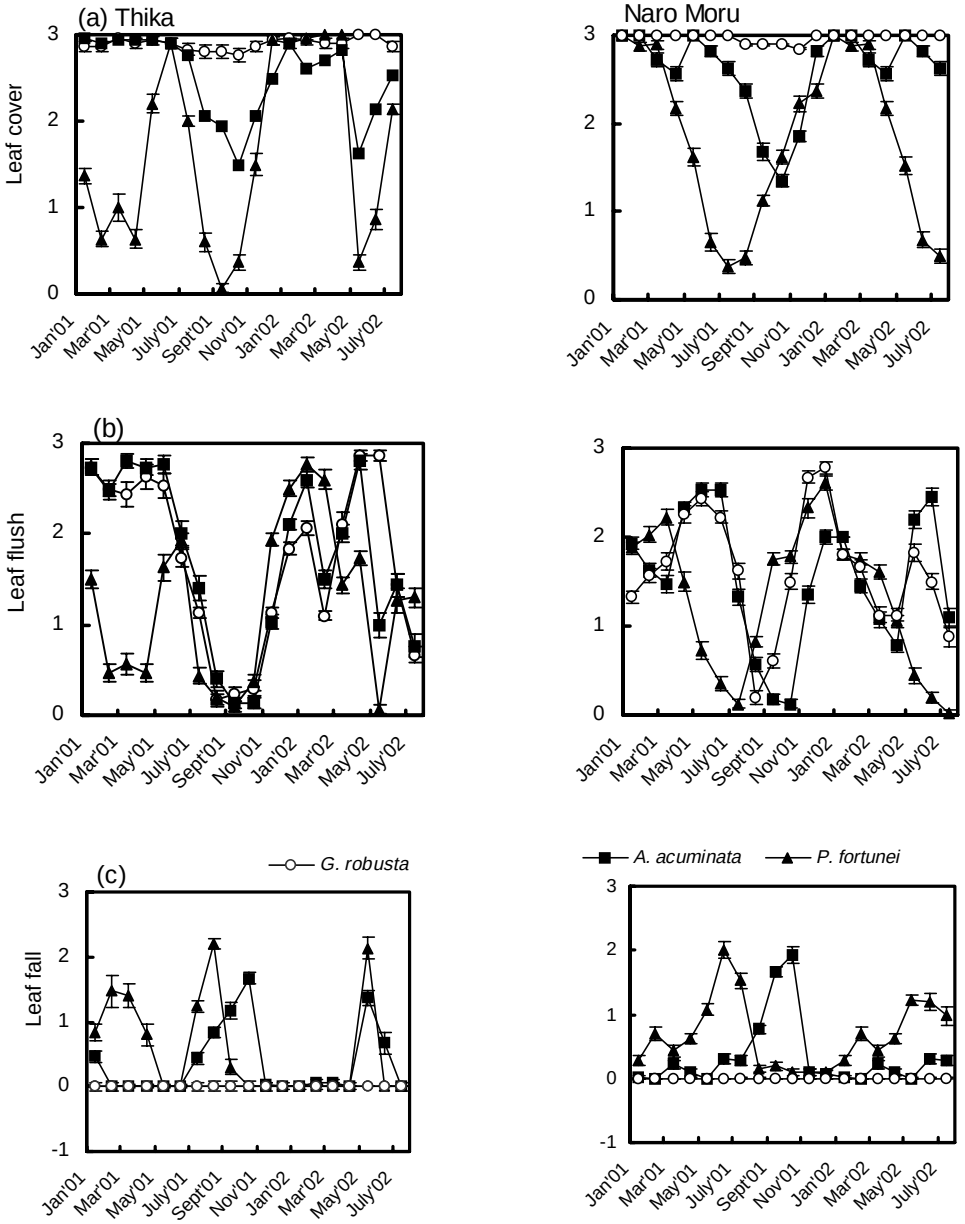


Fig. 4. Time courses of (a) leaf cover, (b) leaf flushing and (c) leaf fall for G. robusta, A. acuminata and P. fortunei at Thika and Naro Moru, Kenya, between January 2001 and July 2002. Vertical bars show double standard errors of the mean (from Muthuri et al., 2005).

Toky and Bisht, 1992; Singh, 1994) and the root systems of both annual and perennial species may preferentially deplete the surface horizons before shifting their activities to deeper horizons as the topsoil dries (Comerford *et al*., 1984; Lehmann *et al*., 1998). Most models of water uptake by trees and agroforestry systems associate the rate of soil water abstraction with root length per unit soil volume (Barataud *et al*., 1995; Mobbs *et al*., 1998; Mayus *et al*., 1999; van Noordwijk and Lusiana, 2000).

Although attempts to reduce water uptake by trees through silvicultural management practices such as shoot pruning have proved at least partially successful for some species, their application has been limited (Jones *et al*., 1998; Namirembe, 1999; Elfadl and Luukkanen, 2002; Ong *et al*., 2002). Several studies have shown that exclusion of tree roots from the crop rooting zone may increase crop yield in the humid tropics by preventing the extension of tree roots into the cropping zone, thereby avoiding competition (Singh *et al*., 1989; Corlett *et al*., 1992; Okorio *et al*., 1994; Hocking and Islam, 1998). Under such conditions, trees may use their deeper roots to exploit residual water reserves and continue growth when absorption from the crop rooting zone decreases or ceases. Previous studies have shown that ploughing the 0-20 cm soil horizon destroys fine roots, confining tree roots to the deeper horizons and decreasing competition between trees and crops (Schroth, 1999; Newaj *et al*., 2001). There is a pressing need for further studies to establish the role of root manipulation as a management tool for controlling spatial zonation and the extent of water uptake by the roots of trees currently used in dryland agroforestry systems.

Sap flow is influenced by a range of soil and atmospheric factors including soil moisture content, root distribution, hydraulic conductance of the xylem, leaf area (determined by leaf number and size), stomatal conductance (determined by stomatal density and aperture; Jarvis and McNaughton, 1986) and atmospheric demand (determined by climatic factors such as incident radiation, vapor pressure deficit and air temperature; Granier *et al*., 2000; Black and Ong, 2000; Ong *et al*., 2006). Studies of sap flow in the roots and trunks of *G. robusta* before and after severing approximately half of the lateral roots have shown that, although stem sap flow velocity was initially significantly reduced, values recovered to a level similar to unpruned trees within five days of root excision (Ong *et al*., 2002). This observation is consistent with Zimmerman (1983) and Woodall and Ward (2002), who reported that the vascular bundles in the stems of herbaceous plants are interconnected and that each branch in the crowns of trees receives water from many roots, providing a safety net in the event of injury to part of root system. Thus, any section of the root system may supply any part of the shoot. Ong *et al*. (2002) and Woodall and Ward (2002) suggested that the severed lateral roots were not the principal providers of moisture to the tree canopy and proposed that sap velocity through stems was maintained by increased flow through the remaining intact roots.

By contrast, more recent experiments have shown that root pruning to a depth of 0.6 m at a distance of 0.5 m from tree rows may be used to limit water uptake by reducing the surface area of tree roots in the surface soil horizons; for example, studies of *G. robusta* and *A. acuminata* in Kenya showed

that sap flow was greatly reduced in root-pruned trees for at least nine months after root pruning (Fig. 4; Anyango, 2005). Root pruning greatly reduced sap flow in both species, particularly during the period when transpiration was greatest, and especially in the more rapidly transpiring grevillea (Fig. 4); mean diurnal transpiration rates over a seven day period, nine months after root pruning, were reduced by *c*. 25 and 35% respectively in *G. robusta* and *A. acuminata* (Table 2). It is conceivable that the pruned trees examined in this study may not have extended their roots sufficiently to tap deep soil water reserves when moisture in the surface soil horizons became inaccessible following root pruning due to their relatively young age or the susceptibility of the site to waterlogging (Muthuri, 2004a). Woodall and Ward (2002) reported that sap flow in another tree species, *Schinus areira*, decreased after root pruning, and that leaf area one year after root excision was less than 10% of that prior to root pruning. It appears that root pruning alters the functional balance of trees as they exhibited both morphological and physiological responses and alterations in the growth and development of the shoots and foliage (Singh and Thompson, 1995; Anyango, 2005). These observations suggest that factors such as tree age and biomass, proportion of the root system affected, initial root architecture and soil type and water availability contribute significantly in determining water uptake by trees following root pruning, especially during the period before they can implement long-term morphological and physiological adjustments to cope with the stress imposed.

Anyango (2005) found that most of the roots produced following root pruning exceeded 4 mm in diameter and were concentrated in the 0-30 cm soil horizon, where conditions are more favorable for root re-growth than in deeper horizons due to its higher soil moisture content and better aeration (Gautam *et al*., 2003). Thus, root pruning of trees may, in the longer term, increase rooting density in the surface soil horizon, so increasing rather than reducing competition with crops in subsequent cropping seasons. It is therefore advisable that, once farmers adopt the practice, they should root-prune their trees prior to every cropping season as the roots may re-grow quickly in some species, rendering the practice ineffective if carried out less frequently.

Table 2. Mean diurnal transpiration rates for root pruned and unpruned trees of Grevillea robusta and Alnus acuminata derived from measurements made over 7 consecutive days, nine months after imposing the root-pruning treatment. SED denotes the standard error of the difference between means (from Anyango, 2005).

Species	Treatment	Volume of water transpired (ml h^{-1})
Grevillea	Unpruned	0.41
	Pruned	0.31
Alnu	Unpruned	0.47
	Pruned	0.31
SED		0.074

Impact at Landscape Level; Application of the WaNuLCAS Model

Computer simulation models have important roles in research, including their use as tools to predict the future behavior of vegetation under changing climatic conditions or land management practices. They may also be used for planning, as

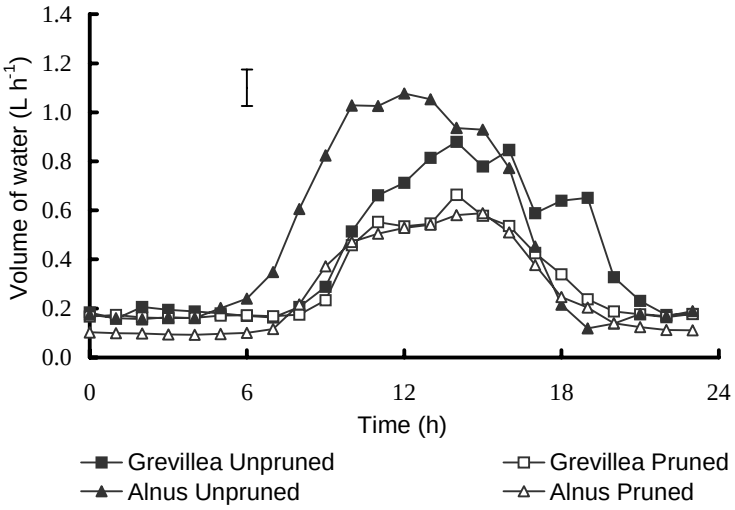


Fig. 5. Mean diurnal time courses for transpiration rate for root pruned and unpruned trees of Grevillea robusta and Alnus acuminata. Measurements were made nine months after root pruning. Vertical bar shows the standard error of the difference between treatment means (SED) (from Anyango, 2005).

well as scenario and impact analysis (Muthuri, 2004b), and are useful for interpreting experimental observations, generating hypotheses and exploring the significance of theoretical developments. The application of modelling approaches is especially attractive in view of the substantial period required for trees to achieve their full impact in agroforestry systems and the substantial cost of running long-term field experiments; modelling approaches may therefore provide substantial time and financial savings over field experiments. However, to be useful, Mobbs *et al*. (1998) proposed that agroforestry models must represent the simultaneous capture and use of at least two of the three essential resources, light, water and nutrients, while Monteith (1997) cautioned that agroforestry models should be tested rigorously in the field, for example, by examining the impact of species and management practices on yield responses.

The WaNuLCAS (**Wa**ter, **Nu**trient and **L**ight **C**apture in **A**groforestry **S**ystems) model has been used to investigate the impact of the leafing phenology of trees on tree and crop growth and water use by selected agroforestry species in semi-arid Central Kenya (Muthuri *et al*., 2004) and elsewhere. Water shortage is particularly acute in the Naro Moru area to the west of Mount Kenya, where immigration has led to rapid changes in land use and increased demand for water. Having originated from high potential areas where water is not limiting, immigrant farmers lack knowledge of water conservation techniques. Small- scale mixed farming is the predominant form of land use, with 70% of the plots being between 0.25 and 1.6 ha; in such dry environments, these plots are too small to support families

at a sustainable level. Moreover, maize production in the area is water-limited (Liniger *et al*., 1998), resulting in frequent crop failure. A further potential concern is the introduction of agroforestry, as this may increase water use in an area which is already water-limited. WaNuLCAS was chosen for this study as it can be applied to both simultaneous and sequential agroforestry systems and has been suggested to be helpful for researchers wishing to explore the continuum of options extending from improved fallows, through relay-planting of trees to rotational and simultaneous hedgerow intercropping (van Noordwijk *et al*., 2004). The model has an open framework which allows users to add relationships as appropriate, thus making it sufficiently broad to include a range of parameters, yet sufficiently narrow to cater for specific needs (van Noordwijk *et al*., 2004).

Three agroforestry tree species, *G. robusta*, *A. acuminata* and *P. fortunei*, respectively providing evergreen, semi-deciduous and deciduous leafing phenologies, were intercropped with maize within WaNuLCAS. It was hypothesized that the deciduous and semi-deciduous habits of *P. fortunei* and *A. acuminata* would reduce demand for water relative to the evergreen *G. robusta*, particularly under conditions of limited water supplies (Muthuri, 2004a). Simulated above-ground biomass accumulation over five years by *G. robusta* (1.9 kg m^{-2}) compares favorably with the experimental value of 1.7 kg m^{-2} obtained over a 4.5 year period for a dispersed-planted agroforestry system containing grevillea at Machakos, Kenya (Lott *et al*., 2000a). The WaNuLCAS simulations showed that altering leafing phenology from evergreen through semi-deciduous to deciduous decreased water uptake and interception losses by the trees and increased crop water uptake, drainage and soil evaporation for agroforestry systems containing all three tree species (Fig. 6; Muthuri *et al*., 2004). Drainage and soil evaporation were respectively 14 and 17% greater in the deciduous *P. fortunei* system than in the evergreen *G. robusta* system. Simulated water uptake by *G. robusta* was more than double the corresponding value for *P. fortunei*, while water uptake by crops in the *G. robusta* and *P. fortunei* systems was reduced by 6 and 0.2 % respectively compared to sole maize. Simulated water uptake by maize was greater than that for the tree component. Previous studies of grevillea at Machakos, Kenya using heat balance gauges (Lott *et al*., 2003) showed that water use ranged from 2.6 mm d^{-1} during the dry season to 4.0 mm d^{-1} during the wet season. Over a five-year period, these values would translate into a greater cumulative water use than the simulated values reported by Muthuri *et al*. (2004), for instance, 640 mm under the evergreen leafing phenology. WaNuLCAS therefore generally underestimated water use by the tree species examined, particularly grevillea and alnus, demonstrating that this aspect of model simulations needs to be refined to improve accuracy. However, climatic and soil conditions differ between the two experimental locations.

The simulations imply that water use by *P. fortunei* is lower than that for *G. robusta* and suggest that leafing phenology is a key attribute affecting water use by trees (Muthuri *et al*., 2004). They also suggest that trees with deciduous or semi-

deciduous leafing phenologies provide a good compromize between evergreen tree and sole maize systems because their water requirements are intermediate between these two extremes (Ong *et al*., 2006). This view is supported by observations that leafing phenology may influence the partitioning of water, as species exhibiting the smallest seasonal variation in leaf area have been shown to tap increasingly deep soil water reserves as the dry season progresses (Meinzer *et al*., 1999).

Conclusions: Main Lessons Learned to Date

Our review of recent progress in the understanding of water use in agroforestry systems provides two important lessons for the intensification of agroforestry in the semi-arid tropics. Firstly, leafing phenology is a powerful selection criterion for reducing competition for water with associated crops. In semi-arid Kenya, the most notable example is *Melia volkensii*, which sheds its leaves twice during the bimodal annual rainfall regime experienced in East Africa, although it is uncertain whether this leafing phenology can be extrapolated to other regions as it is unknown whether this behavior is controlled by internal or external mechanisms. Attempts to introduce other exotic deciduous species, which shed their leaves during the dry season to East Africa, such as *Gliricidia sepium*, *Paulownia fortunei* and *Senna spectabilis*, have been partially successful. Another important tree species exhibiting similar leafing phenology to *M. volkensii* in the bimodal rainfall regions of East Africa is *Cordia africana*, another popular agroforestry species in the region. However, even a single substantial episode of leaf fall during the main dry season may substantially reduce water use and competition, as in the case of *P. fortunei* (Muthuri, 2004a).

Secondly, root pruning of trees provides a powerful management tool for manipulating below-ground competition, although a potentially serious drawback is that lateral roots may re-grow quickly, making it necessary to prune prior to each cropping season. A further potential disadvantage of pruning lateral roots is the interruption of bi-directional flow of water from deeper horizons to lateral roots located in the surface soil horizons and *vice-versa*, also respectively referred to as hydraulic lift and reverse hydraulic lift. According to a recent review by Smith *et al.* (2004), bi-directional flow may benefit shallow- rooted crops growing in drying soils if adjacent trees can provide water from depth by accessing groundwater. By contrast, if water added to the topsoil by rainfall or irrigation is absorbed and transferred to depth by tree roots, this would facilitate rehydration of the soil profile, but might exaggerate competition. The greatest uncertainty regarding hydraulic lift is the precise amount of water involved.

The ameliorative influence of tree canopies on microclimatic conditions experienced by understorey crops is likely to increase in importance with the anticipated increase in global warming, which is expected to have a greater affect in the semi-arid tropics than in other climatic zones. According to recent predictions (IPCC, 2007), some parts of Africa may expect an increase in annual mean temperature of 2.5^{o}C by 2030, with the result that much of sub-Saharan Africa will experience even higher frequencies of supra-optimal temperatures than reported here for Machakos. Clearly,

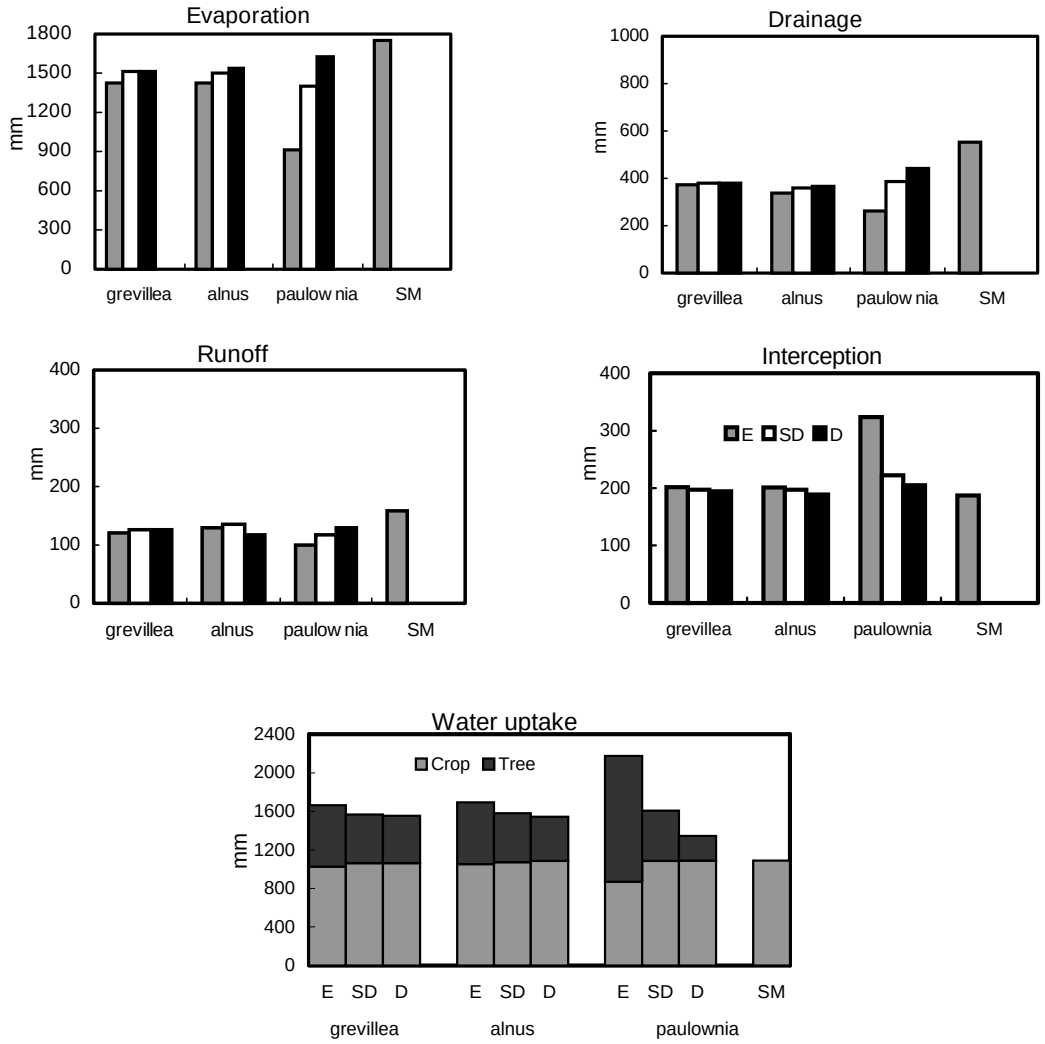
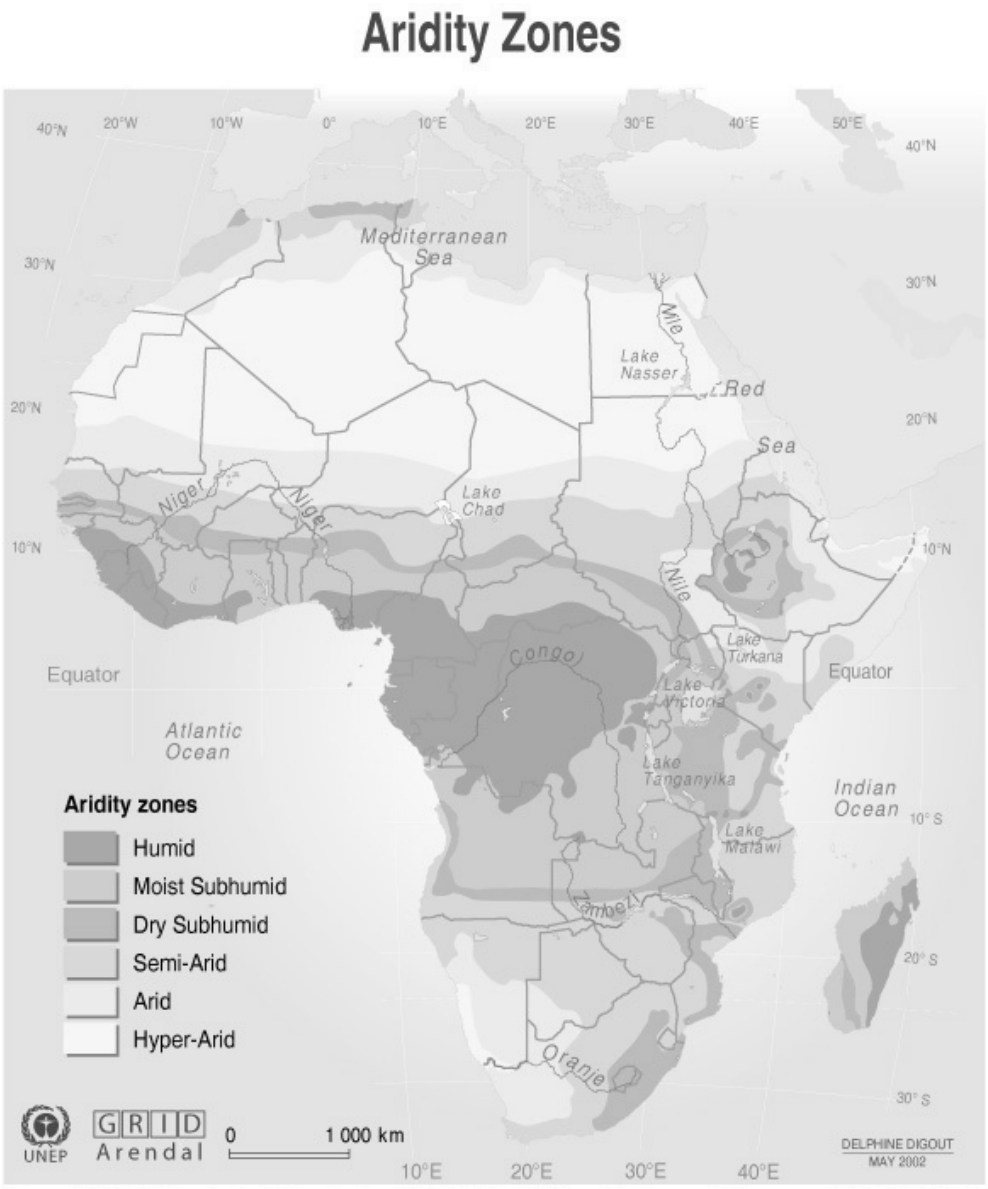


Fig. 6. Simulated values for water balance components for sole maize (SM) and agroforestry systems containing grevillea, alnus or paulownia in a five year simulation involving evergreen (E), semi-deciduous (SD) and deciduous (D) leafing phenology scenarios (from Muthuri et al., 2004).

research activities must be redirected to facilitate the development of agroforestry strategies and improved crop varieties which allow farmers to cope with increasing heat stress. Ewell (1999) suggested that natural systems are more able to cope with biotic and abiotic stress more readily than less diverse agricultural systems. The concept of using agroforestry systems to protect against extremes of climate conditions and soil moisture supplies may provide a financially accessible way of protecting crop



Source: World Meteorological Organization (WMO), United Nations Environment Programme (UNEP), *Climate Change 2001: Impacts, Adaptation, and Vulnerability*, Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC).

Fig. 7. Areas at most risk from climate change in Africa are in the arid and semi-arid zones. (from: World Meteorological Organization, United Nations Environmental Programme, Climate Change 2001: Impacts, Adaptation, and Vulnerability, Contribution of Working Group 2 to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC).

yields for smallholder farmers who cannot afford irrigation.

Research Needs

According to the latest predictions of the UN's Intergovernmental Panel on Climate Change (IPCC, 2007), the impact of climate change on Africa will be more severe than on any other continent; thus, drylands adjacent to deserts are likely to become drier, while wetlands will become wetter. The IPCC report suggests that supplies of food in Africa will be severely compromized by climate change, with crop yields being in danger of collapsing completely in some countries. Annual crops such as maize and sorghum are most threatened as warmer temperatures will reduce the duration of the growing season. The African countries most at risk are shown in Fig. 7. In many parts of sub-Saharan Africa, the effects of climate change are already apparent and there is no time to await further evidence before taking action. The best documented case is the Kilimanjaro ecosystem, which has experienced a drastic 70% decline in rainfall during the past 100 years and a dramatic increase in mean daily maximum temperature of 2^{o}C per decade between 1976 and 2002. The most famous agroforestry system in the Kilimanjaro region is the Chagga homegardens, which have undergone serious degradation as shade trees have been removed for firewood and perennial streams are drying up (Hemp, 2005). Even more alarming are recent reports that increases in temperature may significantly affect the ability of trees to store carbon dioxide, thereby increasing its concentration in atmosphere (Feeley *et al.*, 2007).

Although considerable information is available concerning the ability of crop plants in the semi-arid tropics to withstand high temperatures (Challinor *et al.*, 2007), little is known about the impact of temperature on trees. Sustained periods of high temperature are likely to shorten the duration of important crops such as millet, sorghum and groundnut. Episodes of high temperature during critical stages of crop development may affect yield independently of any substantial changes in mean daily or seasonal temperatures. Using various crop models, Challinor *et al*. (2007) predicted that the reduction in the mean yield of groundnut crops would be as large as 70%, indicating the importance of genotypic adaptation in determining responses to alterations in both mean temperature and temperature extremes associated with climate change. In view of these findings, there is an urgent need to establish the responses of key physiological and developmental processes, such as respiration and phenology, to rising mean temperatures and temperature extremes for important agroforestry tree species such as *G. robusta* and *M. volkensii*. Future studies should also examine a range of tree and crop species and varieties with the objective of identifying agroforestry systems capable of tolerating the anticipated more extreme thermal environments induced by climate change.

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