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Tree and crop productivity in *Grevillea*, *Alnus* and *Paulownia*-based agroforestry systems in semi-arid Kenya

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Abstract

This study tested the hypothesis that deciduous (*Paulownia fortunei*) (Hemsl.) and semi-deciduous (*Alnus acuminata* (HBK)) trees are less competitive with crops than evergreen species (*Grevillea robusta* (A. Cunn.)) due to their differing leafing phenology. Tree growth, seasonal patterns of leaf flushing and fall and effects on associated maize crops were examined. *P. fortunei* and *A. acuminata* established well at two experimental sites (Naro Moru and Thika), and basal stem diameter, diameter at breast height (DBH) and tree height were comparable to *G. robusta*. *P. fortunei* was leafless for approximately three months during the annual cycle, partly during the cropping season, providing potential benefits for associated crops. *A. acuminata* shed some leaves during the dry season in August and September, while *G. robusta* was evergreen. The presence of trees affected maize growth and yield 2.5 years after planting to an extent which depended on tree species and location. A positive interaction between *A. acuminata* and maize was apparent at Thika, but growth was suppressed in the first two crop rows at Naro Moru. *G. robusta* reduced maize yield by 36% close to the tree rows at Thika, whereas yield reductions were negligible adjacent to *P. fortunei*. These findings suggest there was some complementarity of resource use between *A. acuminata* and maize at Thika, and neutral or competitive interactions between trees and crops in all other treatments.

Keywords: Grevillea robusta; Alnus acuminata; Paulownia fortunei; Leafing phenology; Competition

1. Introduction

The semi-arid and arid regions of Kenya are a focus for migration from adjacent high potential areas due to

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continuing population growth. Settlement of such areas has increased demand for timber (Okello et al., 2001) and other commodities already in short supply due to the rapid degradation of Kenyan forests to meet householders' needs and provide land for cultivation. The need to maintain and increase tree cover is a priority, although the choice of species presents a major challenge. Although indigenous species provide

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essential products such as charcoal (Okello et al., 2001), their growth rate and population density are generally low, and it is also difficult to obtain suitable propagation materials. Thus, as human and domesticated livestock populations increase and the size of land-holdings decreases, the possibility of incorporating trees into farmlands becomes increasingly attractive. However, the challenge in agroforestry systems in dryland areas is how to retain the positive effects of tree species while limiting the negative effects of below-ground competition with crops (Lott et al., 2000a). A key criterion when choosing appropriate tree species is leafing phenology. The frequency with which trees replace their leaves, and the timing within the annual cycle when they do so may 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, provide invaluable assistance when estimating annual carbon fluxes and managing water resources within ecosystems (Eamus, 1999). Moreover, characterisation of component interactions in agroforestry systems is crucial in determining the extent of competition and complementarity between trees and crops.

Trees are commonly planted among crops such as maize, beans and bananas. For example, ca. 750 000 ha in the Central Highlands of Kenya are used for agroforestry systems involving mixtures of Grevillea robusta and maize (Muchiri et al., 2002). Boundary plantings increase tree cover, fuelwood supplies and infiltration of rain, provide protection against wind, and reduce runoff (Otengi et al., 2000). Numerous studies have examined complementarity and competition between trees and crops (Namirembe, 1999; Lott et al., 2000b). Yield increases are common under open, well-managed canopies of mature trees due to a combination of improvements in soil structure and fertility (Rao et al., 1998) and increases in soil water content resulting from reduced evaporation. However, increased tree cover may generate competition for water between trees and crops in areas where water supplies are already insufficient to meet livestock and human needs (Ong et al., 2000; Otengi et al., 2000). Competition for soil moisture may reduce stem diameter, plant height and yield in maize in agroforestry systems relative to sole crops (Namirembe, 1999).

Although the impact of *G. robusta* on crop growth has been widely examined, there are no equivalent

studies for *Paulownia fortunei* and limited information regarding *A. acuminata*. Previous studies of *G. robusta* in Kenya have focused primarily on areas such as Embu and Machakos, which experience differing environmental conditions and where the impact of trees on crop yield depends on site conditions and tree age. There is also an urgent need to identify additional tree species with limited competitive effects on crops. The present study sought to address this question by determining the growth of *G. robusta*, *A. acuminata* and *P. fortunei* and establishing their influence on understorey maize crops at two experimental sites.

2. Materials and methods

2.1. Site characteristics

The experimental sites were at Naro Moru, to the west of Mount Kenya, and Jomo Kenyatta University of Agriculture and Technology (JKUAT). The former is in Nyeri District, 160 km north of Nairobi (latitude, 0°05'S; longitude, 37°00'E; altitude, 2060 m), while the latter is in Thika District, 35 km from Nairobi (latitude, $1^{\circ}06'S$; longitude, $37^{\circ}01'E$; altitude, 1520 m). Both sites are located in Agro-climatic Zone 4 (Jaetzold and Schmidt, 1983). Mean annual rainfall at Naro Moru is 800 mm and mean potential evaporation ranges from 3.3 mm d^{-1} during the rainy seasons to 4.5 mm d^{-1} during the dry season (March and July-September; Jaetzold and Schmidt, 1983). Mean annual maximum and minimum temperatures are 22.7 and 10.4 °C. Mean annual rainfall at Thika is 856 mm and is bimodal, with primary and secondary peaks in April and November; mean annual maximum and minimum temperatures are 26.1 and 13.6 °C (Muchena et al., 1978). Mean annual potential evaporation is 5.05 mm d^{-1} . The natural vegetation comprises grass and scattered acacia shrubs at both sites.

The Naro Moru site was previously virgin land with one cropping season under vegetables before being adopted for the present study, while the Thika site was formerly used for grazing. The soils at Naro Moru and Thika are, respectively, a verto-luvic Phaeozem and Pellic Vertisol (Muchena et al., 1978), derived from volcanic material. Soil depth ranged from 50 to 110 cm at Naro Moru and 60–100 cm at Thika. Soil analysis at Thika (0–90 cm) showed an average pH of 5.3, organic carbon content of 1.24%, nitrogen content of 0.18%, and a %P content below 0.04%, indicating acute deficiency. The corresponding values for Naro Moru (0–100 cm) were 6.95%, 1.36%, 0.16% and 0.08%. Soil composition in the 0–30 horizon was 19.5% sand, 54.3% clay and 26.2% silt at Thika, compared to 35.5%, 42.7% and 21.5% at Naro Moru. Measurements of rainfall and air temperature at both sites were supplemented by records from Munyaka and JKUAT meteorological stations, located within 1 and 0.5 km, respectively, of the experimental sites.

2.2. Experimental design

The trials were established in June 2000 as Randomised Complete Block Designs (RCBD) containing three replicates at Thika and four at Naro Moru. Four treatments were examined, i.e. agroforestry systems containing G. robusta, A. acuminata or P. fortunei and maize plus a sole maize control. A single tree row was planted along the centre of each $20 \text{ m} \times 20 \text{ m}$ plot at a spacing of 1 m within rows, giving a total of 19 trees per plot. The treatment area was $18 \text{ m} \times 18 \text{ m}$, leaving a 1 m guard area around each plot. The tree rows at Thika were oriented east-west to minimise shading of adjacent crops. Those at Naro Moru were planted along the contours to reduce erosion and act as windbreaks; row orientation was close to east-west. Maize was grown at a spacing of 0.3 m within rows and 1 m between rows, providing 10 rows on each side of the tree row. Sole maize plots contained 20 rows planted at the same spacing. Measurements were made between May 2001 and September 2002. The first maize crop was grown during the 2001–2002 short rains (October-February), 17 months after planting the trees, and the second during the long rains commencing in April 2002. Cv. Pioneer was chosen because of its popularity at both locations.

2.3. Tree species

G. robusta (proteaceae) is native to Australia and a popular agroforestry species in Kenya. It grows at altitudes of 850–2500 m with an annual rainfall of 900–1500 mm. Its uses include provision of poles, firewood, mulch, climatic improvement, erosion control, demarcation of farm boundaries, shade and

various economic benefits. Its suitability for agroforestry may be restricted in areas of limited water supply, where it may substantially reduce crop yields (Lott et al., 2000b). *G. robusta* was chosen because of its popularity with farmers in Ecoclimatic Zone 4.

A. acuminata (Betulaceae) originated from mountainous areas of Central and South America and thrives on well-drained, fertile soils in cool tropical highlands. It can reach heights exceeding 25 m and achieve diameters at breast height (DBH) of 50 cm within 30 years (Okorio, 2000). As A. acuminata is host to the nitrogen-fixing actinomycete, Frankia, it enhances soil fertility and provides beneficial interactions with associated crops (Caru et al., 2000). Other uses include provision of organic matter, fibre, fodder, forage, logs and fuel. A. acuminata was chosen because of its suitability for upland areas, ability to fix nitrogen and because its semi-deciduous leafing phenology was expected to reduce water use.

P. fortunei (Scrophulariaceae) is native to China, Vietnam and Laos (Wu, 1996) and grows in relatively low annual rainfall areas (ca. 770 mm). Trees reach a height of 8 m in five years and are used to produce timber for construction, manufacture of furniture and musical instruments (Wu, 1996), remediation of animal waste and mine sites, microclimatic improvement and afforestation. They also provide high quality fodder. *P. fortunei* was chosen because of its deciduous habit and considerable potential as an agroforestry species due to its deep rooting habit and sparse crown.

2.4. Tree growth analysis

Height from ground level to the tip of the youngest leaf was measured fortnightly for the central 10 trees in each plot using a tape measure. Basal stem diameter was measured 1 cm above the soil using Vernier callipers and a line painted on the stem as a reference point. A similar approach was used to measure diameter at breast height (DBH, 1.3 m above the soil). DBH measurements began when most trees reached a height of at least 1.5 m. As the nodes in *P. fortunei* were significantly thicker than the internodes, DBH was measured immediately below the node if this coincided with a height of 1.3 m.

The following parameters were recorded fortnightly to define the contrasting leafing phenologies of the tree species examined (cf. Broadhead et al., 2003).

- (i) Flushing: proportion of the canopy bearing new foliage, which was easily distinguishable on the basis of leaf size and colour. A scale of 0, 1, 2 or 3 was used to represent absent, low, intermediate or high flushing intensities.
- (ii) Leaf fall: the proportion of the canopy composed of senescent leaves, including newly shed leaves identifiable by their colour, was assessed as described above.
- (iii) Leaf cover: canopy cover was categorised by the proportion of branches bearing leaves as described above.

2.5. Crop growth analysis

The agroforestry plots were sub-divided into three portions on both sides of the tree rows. The smaller central portion between trees 9 and 11 was reserved for measurements of soil moisture and light interception using permanently installed theta probe access tubes. The remaining portions were sub-divided randomly to permit non-destructive and destructive measurements of crop growth.

Non-destructive measurements were repeated fortnightly between thinning of maize (30 days after sowing; DAS) and final harvest. Two plants per row were labelled on each side of the tree row to enable repeated measurements, providing a total of 32 plants per plot. Smallest and largest basal stem diameters, height to the tip of the youngest leaf, height to the top of the canopy and the numbers of green, yellow and dead leaves were recorded.

Destructive measurements were made at 60 DAS and maturity (105 DAS at Thika and 135 DAS at Naro Moru). Above-ground fresh and dry weights and leaf number were determined 1, 3, 5 and 7 m from the tree row in the agroforestry plots, or from the central row in the sole maize plots on both the northern and southern sides of the plots. Two plants per row were sampled, giving a total of 16 per plot. The shoots were severed at ground level and the number of leaves recorded. The entire shoot including leaves, stems and cobs was weighed and placed in labelled paper bags. The samples were dried at 70 °C for one week to determine dry weight.

Biomass and grain yield at maturity were determined for each plot. Cob number and shoot and grain dry weight were determined on a row-by-row basis to establish the effect of distance from the tree row. Plant number per row was determined before excising the plants at ground level. Cobs and stover and were weighed separately. Cobs from two representative plants per row were weighed, placed in labelled bags and dried at 70 °C for one week. Grain dry weight was determined after shelling the cobs. Total grain dry weight for all plants in each row was determined by multiplying the grain dry weight:cob fresh weight ratio for the sub-sample by the total fresh weight of cobs from all plants in the same row. Stover fresh weight was determined on a row-by-row basis before sub-sampling two representative plants per row. These were weighed to determine fresh weight before being dried at 70 °C for one week. Total stover dry weight per row was determined by multiplying the dry:fresh weight ratio for the sub-sample by total fresh biomass for the same row.

2.6. Light interception

Incident and intercepted photosynthetically active radiation were measured at 10 d intervals using a Sunfleck Ceptometer (Delta-T Devices, Cambridge, UK). This interval was chosen to establish temporal trends without causing excessive disturbance. Measurements were made around midday above and below the trees and crop for maize rows 1, 3, 5 and 7 on both sides of the tree row in all plots. PAR measurements were made perpendicular to the tree row between trees 9 and 10. Equivalent measurements were made for 10 rows in the sole maize plots.

2.7. Statistical analysis

The results were analysed by Analysis of Variance using Genstat 5 Release 6.1 (Rothamsted Research, Harpenden, UK).

3. Results

3.1. Tree height and stem diameter

Height increased in all species between September 2000 and July 2002 (p < 0.001; Fig. 1b), but was smallest in *P. fortunei* at both sites (p < 0.001). *G. robusta* was tallest at Thika, whereas *A. acuminata* was tallest at Naro Moru until October 2001;



Fig. 1. Timecourses of (a) mean basal trunk diameter and (b) mean tree height for *G. robusta*, *A. acuminata* and *P. fortunei* at Thika and Naro Moru, Kenya, between September 2000 and July 2002; (c) mean daily air temperature and monthly rainfall. Vertical bars in (a) and (b) show single standard errors of the mean.

thereafter, *G. robusta* was slightly, but not significantly, taller. The altered ranking may have resulted from infestation of *A. acuminata* by defoliating insects, probably *Nodonota irazuensis* or *Apis melifera*, as found in Uganda (Nyeko et al., 2002); this greatly increased leaf fall and retarded growth.

Height generally increased significantly during the rainy seasons (p < 0.01; Fig. 1c), although there was no marked increase in *P. fortunei* during the 2001 short rains at Thika, perhaps because heavy rain in January and March caused flooding and anaerobic soil conditions. Height increases were negligible during the dry season (June–October), when temperatures were relatively low; this effect was more pronounced at Thika. Differences between species were greater at Thika (p < 0.05; Fig. 1b). Height differed between species (p < 0.001) and sites (p < 0.05), and the site × species interaction was significant (p < 0.05).

Basal stem diameter increased markedly during the rainy seasons but showed smaller increases during the dry season (Fig. 1a). At Naro Moru, basal diameter was greatest in P. fortunei after December 2001 and smallest in G. robusta throughout the observation period; the reverse was true at Thika. In contrast to height, for which substantial species differences persisted throughout the observation period, the differences in basal diameter were smaller and decreased with time. The renewed increase in basal diameter in P. fortunei before the short rains preceded those for the other tree species. The effect of flooding on basal diameter was smaller than that on height in P. fortunei. Although differences between species in basal diameter were not significant, those between sites and the site \times species interaction were significant (p < 0.01 and 0.001).

The timecourses for DBH (data not shown) resembled those for basal stem diameter, being greatest for *G. robusta* at Thika and *P. fortunei* at Naro Moru (39.5 and 44.1 mm, respectively) by the end of the observation period. The differences in DBH between species and sites and the species \times site interaction were all significant (p < 0.001, <0.004 and <0.001, respectively).

Daily mean increments for basal stem diameter and height varied between seasons (p < 0.001 and 0.009, respectively; Fig. 2a and b), being much lower during the dry season. The mean values for both variables differed between the two cropping seasons for *G. robusta* and *A. acuminata* (p < 0.009 and < 0.01,

respectively), but not for *P. fortunei*. No significant species differences were apparent during the dry season. The smallest and largest seasonal mean daily increments in height were found in *G. robusta* (0.02 cm d⁻¹, 2001 dry season and 0.89 cm d⁻¹, 2002 long rains at Thika). The corresponding values for stem diameter were 0.009 mm d⁻¹ in *G. robusta* (2001 dry season) and 0.17 mm d⁻¹ in *A. acuminata* (2001 long rains). Mean growth rates for basal stem diameter and height over the entire observation period were greater at Naro Moru than at Thika for all species (Fig. 2c); this trend was more pronounced for height than for basal diameter, but was not statistically significant.

3.2. Leafing phenology

P. fortunei showed the most dramatic phenophases of the species examined (Fig. 3a-c), as leaf cover declined sharply during the dry season. At Naro Moru, leaf fall began before the end of the long rains (early May) and extended through most of the dry season until early September. Leaf fall was greatest in June and July, and by August most trees had lost all their leaves. At Thika, leaf fall began four weeks later, in late June, perhaps because the higher rainfall increased water supplies. Extensive leaf fall also occurred during early February and March 2001 and May 2002 after heavy rain caused flooding (Figs. 1c and 3c). Rainfall was more intense and flooding more severe in May 2002 than in 2001. In contrast to the normal pattern of leaf fall between June and September, the leaves abscinded while still green. There was no flooding at Naro Moru during February/March 2001, and hence no leaf fall; this began in late April and early May.

Leaf flushing in *P. fortunei* commenced in September at Naro Moru (Fig. 3b), one month before the short rains began, during a period of low soil moisture resulting from the limited rainfall during the preceding long rains (Fig. 1c). Leaf flushing and expansion were greatest between November and December, during the period of greatest rainfall. Flushing began to decline in March and ceased in most trees by July. The periods of intense flushing coincided with periods of low leaf fall, thereby increasing leaf cover. A similar trend was observed at Thika, although flooding greatly reduced flushing during February/March 2001 and May 2002. However, flushing recommenced within two weeks once the surface water drained away.



Fig. 2. Seasonal mean daily increments for (a) basal trunk diameter and (b) tree height; (c) mean daily increase in basal trunk diameter and tree height between September 2000 and July 2002 for *G. robusta*, *A. acuminata* and *P. fortunei* at Thika and Naro Moru, Kenya. SR, LR and DS, respectively, denote the short and long rains and dry season. Vertical bars show double standard errors of the mean.

In *A. acuminata*, leaf flushing increased during both rainy seasons and decreased during the dry seasons, particularly between July and September (Fig. 3b) when soil moisture declined to 14% (Muthuri, 2004). Leaf fall occurred during the dry season between August and October 2001 at both sites, but was more intense at Naro Moru, perhaps due to the presence of defoliating insects. Although these were also present at Thika, infestation was delayed until late September, reducing its duration and intensity. Despite the absence of defoliators during the same period in 2002, leaf fall again occurred,



Fig. 3. Timecourses 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.

although at a much lower intensity. However, most trees exhibited leaf fall within two weeks of heavy rainfall at Thika in May 2002 (p < 0.001). Unlike *P. fortunei*, the leaves of *A. acuminata* underwent extensive chlorosis prior to abscission. Leaf fall ceased when flooding receded. Leaf flushing in *A. acuminata* began following the onset of both the short and long rains. Its intensity was initially low, but reached a maximum around the middle of the rainy season. Flushing decreased between February and March and was lowest in August and September, at the end of the dry season. The timing and intensity of the phenophases in *A. acuminata*, therefore, appear to be determined by environmental factors, particularly rainfall.

G. robusta displayed the least episodic phenophases of the species examined. As there were no detectable incidences of leaf fall, changes in canopy size resulted primarily from leaf flushing, which coincided with the onset of the rains in mid-March and late September at both sites and continued for approximately 3.5 months. Branches retained leaves of different age, ranging from very young (light green with a soft texture) to much older leaves. *G. robusta* exhibited increased flushing during periods of flooding at Thika in January 2001 and May 2002, in contrast to *P. fortunei* and *A. acuminata* which shed leaves. *G. robusta* maintained the greatest leaf cover during both rainy seasons, although a slight reduction occurred during the dry season between July and September. This did not result from leaf fall and visual observations indicated that the leaves lost turgidity and decreased in size, reducing canopy area. This effect reflected the sharp reduction in soil moisture from 30% in May to 13% in September (Muthuri, 2004). There were no detectable differences in leaf fall, flushing or canopy cover between sites.

3.3. Crop height and stem diameter

Height increased in all treatments until 90 DAS at both sites (p < 0.001; Fig. 4c and d). At Thika, treatment effects were apparent between 30–90 DAS



Fig. 4. Timecourses of basal stem diameter and height for maize grown as a sole crop or in agroforestry systems containing *G. robusta*, *A. acuminata* or *P. fortunei* at Thika and Naro Moru, Kenya, during the 2001–2002 short cropping season. Vertical bars marked 1 and 2 show SED values for comparing species and time.

(p < 0.05), but not at 105 DAS. In the agroforestry treatments, maize was shortest under *G. robusta* and tallest under *A. acuminata* until 75 DAS (p < 0.001). Comparison of means tests showed the difference between *G. robusta* and all other treatments was significant (p < 0.05), but that the other three treatments did not differ significantly. At Naro Moru, height tended to be greatest under *A. acuminata* and smallest under *P. fortunei*, although the differences were not significant. Overall, the effects of time and site on height were significant (p < 0.001 and 0.05). Similar patterns were observed during the 2002 long rains except that height and basal diameter were greater at Thika (184.7 cm and 25.7 mm, respectively) than at Naro Moru (101.7 cm and 23.4 mm; Muthuri, 2004).

Basal stem diameter increased initially during the 2001–2002 short rains but then decreased (p < 0.001; Fig. 4a and b); these changes were greater at Naro Moru (p < 0.01). These changes were significant between 30 and 60 DAS at Naro Moru and 30–75 DAS at Thika (p < 0.05). Maximum basal stem diameter at Thika was 19.3 mm in sole maize, compared to 30.7 mm in the *G. robusta* treatment at Naro Moru. Treatment effects on the basal diameter of maize were insignificant at both sites. However, comparison of means tests revealed significant differences between *G. robusta* and all other treatments at Thika (p < 0.05); the differences between the other three treatments were not significant. No significant treatment effects were detected at Naro Moru.



Fig. 5. Influence of distance from the tree row on basal stem diameter and plant height averaged from measurements made between 30 and 100 DAS for maize grown as a sole crop or in agroforestry systems containing *G. robusta*, *A. acuminata* or *P. fortunei* at Thika and Naro Moru during the 2001–2002 short cropping season. Vertical bars marked 1 and 2 show SED values for comparing species and distance from tree rows.

Height and basal stem diameter decreased with increasing proximity to the tree row at Naro Moru (p < 0.01; Fig. 5), particularly in the two rows adjacent to the trees. The effect of tree species was also significant (p < 0.001). At Thika, suppression of maize growth was greatest in the *G. robusta* system, with *P. fortunei* having no detectable effect. However, height was increased in the crop rows adjacent to *A. acuminata* (p < 0.05), and was generally greatest in the first four rows in this system, followed successively by the sole maize, *P.*

fortunei and G. robusta treatments. Although the overall effect of distance from the tree row on crop height and stem diameter was not significant at Thika, analysis of individual treatment means revealed significant effects in the A. acuminata and G. robusta treatments (p < 0.05). Species × - distance from the tree row interactions were also found for height and basal diameter (p < 0.001) during the 2002 long rains, when trends similar to those observed during the 2001–2002 short rains were obtained (Muthuri, 2004).



Fig. 6. Grain yield, above-ground biomass and harvest index of maize grown as a sole crop or in agroforestry systems containing *G. robusta*, *A. acuminata* or *P. fortunei* at Thika and Naro Moru, Kenya, during the 2001–2002 short and 2002 long cropping seasons. Vertical bars show single standard errors of the mean.

3.4. Above-ground biomass, grain yield and harvest index

During the 2001–2002 short rains, grain yield was reduced in the agroforestry treatments relative to sole maize at both sites (Fig. 6a; p < 0.001). Grain yield was greatest for sole maize at both sites, followed successively by the P. fortunei, A. acuminata and G. robusta treatments at Thika and the P. fortunei, G. robusta and A. acuminata systems at Naro Moru. Maximum biomass and grain yields at Thika were 1.95 and 0.65 t ha^{-1} , compared to 5.5 and 2.37 t ha^{-1} at Naro Moru (Fig. 6a and c). Harvest index was consistently lower in the agroforestry systems than in sole maize (Fig. 6e), suggesting that competition had a greater impact on grain yield than on biomass production. This effect was greatest under G. robusta at Thika and A. acuminata at Naro Moru. Harvest index was lower, although not significantly, at Thika than at Naro Moru.

During the 2002 long rains, the values for all variables were significantly greater at Thika than at Naro Moru (p < 0.001; Fig. 6b, d and f). The influence of tree species was significant for grain yield and harvest index at Thika (p < 0.001), but not for biomass. Comparison of means tests revealed significant differences between *G. robusta* and the other tree species (p < 0.05), but not between the other three treatments. At Naro Moru, treatment effects were detected for harvest index and biomass (p < 0.002), but not for yield. Biomass was lower in the *P. fortunei* treatment (p < 0.05).

Table 1 shows grain yield and biomass in the agroforestry treatments expressed as a percentage of the values for sole maize during the 2001–2002 short

Table 1 Grain yield and above-ground biomass of maize in the agroforestry treatments at Thika and Naro Moru expressed as a percentage of the corresponding values for sole maize during the 2001–2002 short rains

| Species | Above-ground biomass (percentage of sole maize) | | Grain yield (percentage of sole maize) | | |
|--------------|---|-------|--|-------|--|
| | Naro Moru | Thika | Naro Moru | Thika | |
| G. robusta | 93 | 79 | 86 | 64 | |
| A. acuminata | 89 | 97 | 79 | 99 | |
| P. fortunei | 96 | 107 | 95 | 100 | |

rains. At Thika, grain yield was reduced under G. robusta (64% of sole crop; p < 0.001) but no detectable effect was apparent in the A. acuminata and P. fortunei systems. Biomass followed a similar trend, being lower in the G. robusta treatment (79% of sole crop; p < 0.001) than in the *P. fortunei* and *A*. acuminata systems (107% and 97%, respectively). At Naro Moru, grain yields in the P. fortunei, G. robusta and A. acuminata treatments were 95%, 86% and 79% of the sole crop values, and a broadly similar trend was observed for biomass; the effect of tree species was significant (p < 0.01). The reductions in grain yield and biomass were smaller at Thika than at Naro Moru for A. acuminata and P. fortunei, whereas the converse applied for G. robusta; however, these differences were not statistically significant.

3.5. Light interception

Shading decreased with distance from the tree row in all agroforestry treatments at Naro Moru and in the *G. robusta* and *A. acuminata* systems at Thika during the 2001–2002 short rains (Table 2). The effects of species and distance from the tree row were significant (p < 0.01 and 0.05, respectively), particularly for maize rows 1 and 2 (p < 0.001). Light interception by *G. robusta*, *A. acuminata* and *P. fortunei* 1 m from the

Table 2

Fractional interception (%) of PAR incident upon understorey maize at various distances from the tree row at Thika and Naro Moru, Kenya during tasselling in the 2001/02 short and 2002 long cropping seasons

| Season | Site | Species | Distance from tree row (m) | | | |
|-----------------------------|-----------|--------------|-------------------------------|----|---|---|
| | | | 1 | 2 | 3 | 5 |
| October 2001– March 2002 | Naro Moru | G. robusta | 40 | 8 | 0 | 0 |
| | | A. acuminata | 38 | 6 | 0 | 0 |
| | | P. fortunei | 42 | 9 | 0 | 0 |
| | Thika | G. robusta | 31 | 7 | 0 | 0 |
| | | A. acuminata | 28 | 7 | 0 | 0 |
| | | P. fortunei | 3 | 1 | 0 | 0 |
| April–August 2002 | Naro Moru | G. robusta | 43 | 11 | 0 | 0 |
| | | A. acuminata | 40 | 10 | 0 | 0 |
| | | P. fortunei | 5 | 0 | 0 | 0 |
| | Thika | G. robusta | 35 | 8 | 0 | 0 |
| | | A. acuminata | 30 | 7 | 0 | 0 |
| | | P. fortunei | 3 | 0 | 0 | 0 |

tree row was 40%, 38% and 42%, respectively, at Naro Moru, compared to 31%, 28% and 3% at Thika during the 2001–2002 short rains. There was little change in interception by *G. robusta* and *A. acuminata* between the 2001–2002 short and 2002 long rains. However, in sharp contrast to the former season, interception by *P. fortunei* at Naro Moru was greatly reduced for much of the 2002 long rains by sustained leaf fall. No significant differences between sites were detected.

4. Discussion

4.1. Tree growth

The growth patterns of trees have important implications for resource capture and use, and hence the extent of inter-specific competition and compatibility within specific environments and systems. The tree species examined here exhibited differing growth rates. The height and basal diameter of A. acuminata at Naro Moru and Thika were slightly greater than reported for two-year-old trees in Uganda (Okorio, 2000), whereas the corresponding values for G. robusta were lower than in Uganda. By contrast, in modelling study, Zomer (1993) predicted a total standing biomass of 273 t ha⁻¹ for Himalayan alder (Alnus nepalensis) grown in an intercropping system with large cardamom in eastern Nepal at a plantation age of 25 years. Tree heights for G. robusta at Machakos, Kenya (Lott et al., 2000a) were similar to those observed in the present study for trees of the same age. The timecourses of increments of tree height and stem diameter at Machakos were also comparable to the present study. Increases in trunk diameter at Machakos were characterised by a surge during the rainy seasons followed by decline during the dry season; a similar pattern was apparent at both sites in the present study (Fig. 1a), although mean daily growth rates were greater during the long rains than the short rains, as occurred at Machakos.

Stem diameter and height increments for *P. fortunei* were greater during both rainy seasons than during the dry season (Fig. 1a and b). Height increments were smaller than in a study in North Carolina, USA, in which 12-month-old saplings propagated from shoot cuttings reached a height of 1.8 m (Bergmann, 1998), compared to 1.3 m at Naro Moru. However, DBH at

the Carolina and Naro Moru sites was comparable (3.05 versus 2.85 cm). Observations in China under similar rainfall conditions (mean of 720 mm year⁻¹ versus 856 and 800 mm year⁻¹ at Thika and Naro Moru, respectively) showed that seven-year-old trees reached a mean height of 16 m and a DBH of 35 cm (Newman et al., 1997), substantially greater than at Naro Moru. However, the trees at Naro Moru were only two years old, and *P. fortunei* makes little growth during the first year after planting (Bergmann, 1998).

Periods of flooding reduced growth in *P. fortunei* and, to a lesser extent, *A. acuminata*, perhaps because inundation of air-filled pores in the soil matrix with water restricted oxygen exchange with the atmosphere and exposed the roots to anaerobic conditions (Kozlowski, 1997). Moreover, the aerobic organisms typical of well-drained soils are replaced under flooded conditions by anaerobes, particularly bacteria, which cause denitrification and reduction of oxides of Mn, Fe and S, leading to accumulation of toxic compounds such as sulphides (Kozlowski, 2002). Stem dieback similar to that seen in *P. fortunei* has been reported in a Louisiana coastal marsh dominated by *Spartina alterniflora* (Webb et al., 1995).

4.2. Leafing phenology

Woody species fall into four phenological groups (Williams et al., 1997). Evergreen species retain a full canopy throughout the year and leaf turnover is continuous; brevi-deciduous species exhibit brief reductions in canopy size which never exceed 50% and do not occur every year; semi-deciduous species show reductions in canopy density of at least 50% every year; while deciduous trees are leafless for at least one month every year (Eamus and Prichard, 1998). Deciduousness may be regarded as a seasonal response to unfavourable environmental factors and an adaptation to drought.

The leaf fall pattern for *P. fortunei* resembles that reported for the exotic species, *Senna spectabilis* and *Gliricidia sepium*, at Machakos, Kenya, which shed their leaves during the dry season preceding the short rains (Broadhead et al., 2003). However, leaf fall in *P. fortunei* occurred earlier, at the end of the long rains. Leaf fall in *P. fortunei* also differed from the indigenous species examined by Broadhead et al. (2003), which showed reduced leaf cover during both dry seasons. The pattern exhibited by *P. fortunei* is perhaps not surprising as it is also an exotic, supporting the view that the main contrast in leaf cover dynamics is between indigenous and exotic species (Broadhead et al., 2003).

The onset of leaf flushing in P. fortunei at the end of the dry season may have resulted from exploitation of residual water in the soil or, more probably, within the trees as this event occurred when soil moisture content was low (ca. 15%), in agreement with previous work (Williams et al., 1997). This observation suggests that stored water within the trees was used to support the onset of flushing. It may be argued that, because leaf fall reduces transpiration and soil moisture content was relatively high when leaf fall occurred, absorption continued, increasing the quantity of stored water within the tree. This view is supported by evidence that flushing during dry periods may result from rehydration of trees following reductions in transpiration induced by leaf fall (Borchert, 1994).

After shedding their leaves, the stems of P. fortunei had three distinct segments. That nearest the soil surface was compact, green and apparently alive, while the central section was pale green, hollow and usually the site of new growth when flushing began. The smaller apical section was dry and hollow. Prior to the onset of leaf flushing, this portion rehydrated and changed from its initial dry, brown appearance to a light green fleshy stem from which buds developed. However, the apical portion rarely recovered following flooding; in such cases, leaf flushing occurred from the stem section immediately below the apical segment. Kozlowski (1997) reported similar shoot dieback and decreases in cambial activity in response to waterlogging. The flushing of A. acuminata and G. robusta at the start of each rainy season suggests this process was triggered by environmental factors such as increased soil moisture.

Flooding may affect shoot phenology through various mechanisms including suppression of leaf initiation and expansion, reduced internode elongation, chlorosis, leaf senescence and abscission (Kozlowski, 1997, 2002). Flooding alters the internal hormonal balance, often increasing ethylene synthesis. In the present study, most leaves of *A. acuminata* became chlorotic and senescent within one week of flooding and were subsequently shed. By contrast, the

leaves of *P. fortunei* did not undergo complete chlorosis before being shed. Thus, although flooding induced leaf fall in both species, this may have been achieved by different mechanisms, or perhaps by similar mechanisms expressed differently in each species. This may reflect the fact that flooding tolerance varies greatly between species, genotype and rootstock, and is influenced by plant age, timing and duration of flooding, condition of the floodwater, e.g. moving or stagnant, and site characteristics (Kozlowski, 1997). Broadhead et al. (2003) also reported extensive leaf fall during periods of high soil water content, but suggested that waterlogging was not the primary cause as soil moisture barely reached field capacity.

4.3. Crop performance

Maize grown at Thika performed much better during the 2002 long rains than during the 2001-2002 short rains, perhaps because di-ammonium phosphate (DAP) fertiliser was applied during the second season to increase phosphate supplies. The occurrence of Pdeficiency during the first season was apparent from the characteristic purple colouration of the leaves. By contrast, the first maize crop at Naro Moru performed much better than the second, possibly due to the greater rainfall. The delayed emergence in the second season resulting from removal of seed by squirrels necessitated replacement and increased variability; the lower temperatures between June and September at Naro Moru also delayed crop maturation. Although diammonium phosphate was applied at Naro Moro during the second season, the limited rainfall negated its beneficial influence. Maize yields were, therefore, greater at Thika than at Naro Moru during the second season, whereas the reverse applied during the first season (Fig. 1c).

The presence of trees affected maize growth and yield to an extent dependent on tree species and location. Muchiri et al. (2002) reported that the impact of trees on resource availability increases with tree size but decreases with distance from the tree row. The present results support this view. The reduced biomass and grain yields in the agroforestry treatments relative to sole maize demonstrate the existence of competition, as reported by Namirembe (1999). Crop yields differed between agroforestry treatments, but were C.W. Muthuri et al. / Forest Ecology and Management 212 (2005) 23-39

never higher than for sole maize except in the A. acuminata system at Thika during the second season. Positive interactions between A. acuminata and associated crops have been reported previously. For example, in Uganda, A. acuminata benefited associated crops when grown as upperstorey trees or hedgerows (Peden et al., 1993); this effect may have originated from its ability to fix atmospheric nitrogen, which may have been transferred via the soil to associated crops. In India, Sharma and Sharma (1997) reported that nitrogen-fixing trees such as A. nepalensis enhanced N and P cycling by increasing litter production, thereby promoting the release of these nutrients. This species, therefore, appears well suited for improving soil fertility and restoring degraded lands. However, the observation that A. acuminata impaired crop performance at Naro Moru concurs with findings that maize yield was reduced by 26% by boundary plantings of this species at Kifu, Uganda under more humid conditions (mean annual rainfall, 1240 mm; Okorio, 2000). Nevertheless, Zomer (1993) reported that agroforestry systems containing mixtures of alder and large cardamom were suitable for reclaiming marginal or wastelands for productive use as well as meeting a range of farmers' needs. Future studies should, therefore, investigate the value of integrating crops other than maize which are of economic importance to farmers and perform well at the study sites, for example, onions and ginger, into systems containing A. acuminata.

Ong et al. (2000) reported that grain yield in maize was unaffected by G. robusta at densities of 600-800 trees ha⁻¹ for the first three years after planting, but was greatly reduced in subsequent years, leading to crop failure in dry seasons. This observation was supported by Lott et al. (2000b), who showed that above-ground biomass and grain yield in understorey crops were not affected by G. robusta during the first four cropping seasons, but were then greatly reduced as the trees became increasingly dominant. In the present study, the trees reduced biomass and crop yield by 14-36%, particularly in rows adjacent to the trees, even when these were only 2.5 years old. These observations corroborate evidence that 20-month-old G. robusta trees reduced maize yield by 29% at Kifu, Uganda (Okorio, 2000). Otengi et al. (2000) reported similar competitive interactions between G. robusta hedgerows and maize at Laikipia, Kenya. However,

shoot and root pruning of trees may reduce competition for water, nutrients and light and increase crop yield in agroforestry systems (Namirembe, 1999). Although the present study did not examine the impact of pruning, the results for *G. robusta* suggest that the extent of competition is site-dependent as its competitive influence was less at Naro Moru than at Thika.

Reductions in maize yield adjacent to Paulownia were minimal, in contrast to previous evidence that grain yield was reduced in Paulownia-based agroforestry systems (Chirko et al., 1996). The most likely explanation for this contrast is that the trees were 2.5 years old in the present investigation, compared to 11 years in the previous study. This view is consistent with work by Yin and He (1997), who found that effects on crop yield depended on tree density and rotation length. Substantial yield advantages have been reported for Paulownia/wheat systems in China resulting from temporal separation of resource capture, especially light, because wheat is generally sown in autumn (November), following leaf fall in Paulownia, and reaches maturity prior to renewed flushing of the trees in the following spring (May; Newman et al., 1997). This observation suggests that crops grown in Paulownia-based agroforestry systems in Kenya may perform better during the short rains as this is when it sheds its leaves. This view appears to be true for both sites, particularly at Thika where temperatures are favourable for the cultivation of maize during this period. However, the adoption of better-adapted crops at Naro Moru might also be advantageous during this season.

Newman et al. (1997) reported that maize yields were reduced by 32% relative to sole crops when intercropped with *P. fortunei* during the summer in China, whereas the yield of ginger was 34% greater than in sole crops. This observation suggests that crop yields in *Paulownia*-based systems may be increased if shade-tolerant C3 species such as ginger are substituted for shade-intolerant C4 species such as maize. As vegetable crops are widely grown at Naro Moru, it is possible that such crops might be grown successfully under Paulownia. Several practices used to reduce the impact of shading and improve compatibility in *Paulownia*/wheat systems in China might also be exploited in East African environments, including management of tree form, row spacing and orientation, and leafing phenology (Chirko et al., 1996). Moreover, segregation of tree and crop roots would avoid below-ground competition for water and nutrients. This could be achieved using the root pruning approaches adopted in other agroforestry systems, implying that further development and implementation of effective tree management practices to reduce competition and enhance complementarity are worthy of further investigation in semi-arid environments.

5. Conclusions

A. acuminata and P. fortunei proved suitable for semi-arid areas and hence offer viable alternatives to G. robusta. However, further studies are needed to determine how tree/crop interactions change as the trees mature. The efficacy of management practices such as shoot and root pruning in reducing competitive interactions and enhancing complementarity also requires further clarification. The possibility of substituting vegetable crops for conventional field crops as the trees grow larger and shading intensity increases should also be explored. Other deciduous tree species, including non-indigenous species, should be tested to broaden the farmers' choice and reduce problems associated with their reluctance to accept new tree species and technologies. Although previous studies suggest that the indigenous species, Melia volkensii, may be suitable (Broadhead et al., 2003), other species need to be tested as Melia retains its foliage during the long rains, offering little scope for temporal separation of resource use at this time.

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References

- Bergmann, B.A., 1998. Propagation method influences first year field survival and growth of *Paulownia*. New Forests 16, 1– 264.
- Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75, 1437–1449.
- Broadhead, J., Ong, C.K., Black, C.R., 2003. Tree phenology and water availability in semi-arid agroforestry systems in Kenya. Forest Ecol. Manage. 180, 61–73.
- Caru, M., Becerra, C.M., Sepulveda, M., Cabello, A.D., 2000. Isolation of infective and effective Frankia strains from root nodules of *Alnus acuminata* (Betulaceae). World J. Microbiol. Biotechnol. 16, 647–651.
- Chirko, C.P., Gold, M.A., Nguyen, P.V., Jiang, J.P., 1996. Influence of direction and distance from trees on wheat yield and photosynthetic photon flux density (Q(p)) in a *Paulownia* and wheat intercropping system. Forest Ecol. Manage. 83, 171–180.
- Eamus, D., 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. Trends Ecol. Evol. 14, 11–16.
- Eamus, D., Prichard, H., 1998. A cost-benefit analysis of leaves of four Australian savanna species. Tree Physiol. 18, 537–545.
- Jaetzold, R., Schmidt, H., 1983. Farm Management Handbook of Kenya, vol. II. Natural Conditions and Farm Management Information in East Kenya, Ministry of Agriculture, Nairobi, Kenya, 311 pp.
- Kozlowski, T.T., 1997. Response of woody plants to flooding and salinity. Tree Physiology Monograph No. 1, pp. 1–29.
- Kozlowski, T.T., 2002. Physiological–ecological impacts of flooding on riparian forest ecosystems. Wetlands 22, 550–561.
- Lott, J.E., Howard, S.B., Ong, C.K., Black, C.R., 2000a. Long-term productivity of a *Grevillea robusta*-based overstorey agroforestry system in semi-arid Kenya. 1. Tree growth. Forest Ecol. Manage. 139, 175–186.
- Lott, J.E., Ong, C.K., Black, C.R., 2000b. Long-term productivity of a *Grevillea robusta*-based overstorey agroforestry system in semi-arid Kenya. II. Crop growth. Forest Ecol. Manage. 139, 187–201.
- Muchena, F.H., Wamicha, W.N., Njoroge, C.R.K., 1978. Detailed survey of the Jomo Kenyatta College of Agriculture and Technology, Juja (Kiambu District). Soil Survey Report No. D13, Kenya Soil Survey, 51 pp.
- Muchiri, M.N., Pukkala, T., Miina, J., 2002. Optimising the management of maize—*Grevillea robusta* fields in Kenya. Agroforestry Syst. 56, 13–25.
- Muthuri, C.W., 2004. Impact of agroforestry on crop performance and water resources in semi-arid central Kenya. Ph.D. thesis, Jomo Kenyatta University of Agriculture and Technology, Kenya, 292 pp.
- Namirembe, S., 1999. Tree management and resource utilisation in agroforestry systems with *Senna spectabilis* in the drylands of Kenya. Ph.D. thesis, University of Wales, Bangor, UK, 206 pp.
- Newman, S.M., Bennett, K., Wu, Y., 1997. Performance of maize, beans and ginger as intercrops in *Paulownia* plantations in China. Agroforestry Syst. 39, 23–30.

- Nyeko, P., Edwards-Jones, G., Day, R.K., Raussen, T., 2002. Farmers' knowledge and perceptions of pests in agroforestry with particular reference to *Alnus* species in Kabale District, Kenya. Crop Prot. 21, 929–941.
- Okello, B.D., O'Connor, T.G., Young, T.P., 2001. Growth, biomass estimates, and charcoal production of *Acacia drepanolobium* in Laikipia, Kenya. Forest Ecol. Manage. 142, 143–153.
- Okorio, J., 2000. Light interception and water use in boundary planting agroforestry systems. Ph.D. thesis, Reading University, UK, 230 pp.
- Ong, C.K., Black, C.R., Wallace, J.S., Khan, A.A.H., Lott, J.E., Jackson, N.A., Howard, S.B., Smith, D.M., 2000. Productivity, microclimate and water use in *Grevillea robusta*-based agroforestry systems on hillslopes in semi-arid Kenya. Agric. Ecosyst. Environ. 80, 121–141.
- Otengi, S.B.B., Stigter, C.J., N'ganga, J.K., Mungai, D.N., 2000. Wind protection in a hedged agroforestry system in semi-arid Kenya. Agroforestry Syst. 50, 137–156.
- Peden, D.G., Byeenkya, S., Wajja, N., Okorio, J., 1993. Increased production with *Alnus acuminata* in Uganda. Agroforestry Today 5, 5–8.

- Rao, M.R., Nair, P.K.R., Ong, C.K., 1998. Biophysical interactions in tropical agroforestry systems. Agroforestry Syst. 38, 3–49.
- Sharma, R., Sharma, E., 1997. Cardamom, mandarin and nitrogenfixing trees in agroforestry systems in India's Himalayan region. I. Litterfall and decomposition. Agroforestry Syst. 35, 239–253.
- Webb, E.C., Mendelssohn, I.A., Wilsey, B.J., 1995. Causes for vegetation dieback in a Louisiana salt marsh: a bioassay approach. Aquat. Bot. 51, 281–289.
- Williams, R.J., Myers, B.A., Muller, W.J., Duff, G.A., Eamus, D., 1997. Leaf phenology of woody species in a North Australian tropical savannah. Ecology 78, 2542–2558.
- Wu, Y.Y., 1996. Paulownia agroforestry in China—a contribution to adaptive research. Ph.D. thesis, Silsoe College, Cranfield, UK, 114 pp.
- Yin, R., He, Q., 1997. The spatial and temporal effects of *Paulownia* intercropping—the case of northern China. Agroforestry Syst. 37, 91–109.
- Zomer, R., 1993. Site index and biomass productivity estimates for Himalayan alder-large cardamom plantations: a model agroforestry system of the middle hills of eastern Nepal. Mountain Res. Dev. 13, 235–255.