Understorey microclimate and crop performance in a *Grevillea robusta*-based agroforestry system in semi-arid Kenya

J.E. Lott [a,1], C.K. Ong [b,2], C.R. Black [a,*]

[a] *Plant and Crop Sciences Division, University of Nottingham, Sutton Bonington Campus, Loughborough, LE12 5RD, UK*
[b] *World Agroforestry Centre, PO Box 30677, Nairobi, Kenya*

ABSTRACT

The influence of dispersed trees on microclimatic conditions, gas exchange and productivity of maize (*Zea mays* L.) in a *Grevillea robusta*-based agroforestry system in semi-arid Kenya was examined to test the hypothesis that the benefits of shade seen in savannah ecosystems may be outweighed by competition for below-ground resources. Meristem temperature, cumulative thermal time, intercepted radiation, spatial distribution of shade and gas exchange were determined for maize grown as sole crops, in an agroforestry system, or under shade nets providing 25 or 50% reductions in incident radiation to discriminate between effects of shade and below-ground competition. The major benefit of shade was to reduce exposure to the supra-optimal temperatures experienced in many tropical regions, and which are predicted to become increasingly common by climate change models. However, although trees decreased photosynthetic photon flux density (*PPFD*) incident on understorey maize by *ca.* 30%, the yield reduction was much greater than in the 25% shade net treatment in four seasons providing contrasting rainfall. Maize yield was unaffected by 50% artificial shade in the driest season (168 mm) but decreased with increasing shade when rainfall was high (628 mm). Shade reduced meristem temperature and delayed flowering by 5–24 days depending on treatment and seasonal rainfall. Thermal time to flowering in the agroforestry system doubled from 600 to 1200 °C day as rainfall decreased. Photosynthetic and transpiration rates for understorey maize were similar to the 25 and 50% shade treatments when rainfall was high, but were *ca.* 10% of those for unshaded sole maize in dry seasons. *PPFD*-saturated photosynthetic rate was initially similar in all treatments but fell sharply in the agroforestry system as the season progressed. Radiation conversion coefficients did not differ between unshaded sole and understorey maize. The results suggest that the ameliorative influence of tree shade was greater in low rainfall seasons, as in savannah systems, but that potential benefits were outweighed by below-ground competition. This may be managed by root-pruning trees.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Predictions suggest that climatic conditions will become more variable and extreme in much of the arid, semi-arid and sub-humid tropics (Rosenzweig et al., 2004; IPCC, 2007), particularly in Africa (Orindi and Murray, 2005). Simulations suggest that East Africa will experience increased temperature, a 5–20% increase in rainfall between December and February and decreased rainfall between June and August by 2050 (Hulme et al., 2005). Cash crops such as tea and coffee, usually grown as monocultures, are expected to be most affected by increased temperature, while drought is expected

to cause widespread famine. Gregory and Ingram (2000) suggested that smallholder farmers may combat climate change by reverting to more natural systems which provide beneficial ecological functions. This suggestion is particularly pertinent for farmers who lack financial or material resources to adopt technological solutions such as irrigation (Eakin, 2000). Previous studies suggest that trees in semi-arid savannahs in East Africa increase understorey productivity by improving microclimate and redistributing water from relatively wet to drier soil horizons (Burgess et al., 1998; Ludwig et al., 2003).

Microclimatic variation has a major impact on crop performance as extremes affect growth, development and yield in a wide range of species (Slingo et al., 2005). Previous studies suggest there are thresholds for temperature and atmospheric saturation deficit, above which physiological and developmental processes and yield become increasingly vulnerable (Challinor et al., 2005; Porter and Semenov, 2005). Air temperature is important as excessively hot conditions during critical developmental stages may greatly

reduce yield; thus, temperatures exceeding 30 °C may induce pollen sterility and reduce seed or fruit yield (Porter and Semenov, 2005). Shade from overstorey trees may ameliorate microclimatic conditions for understorey crops, increasing growth and productivity (Gregory and Ingram, 2000). For example, the optimal range for Arabica coffee is 18–21 °C and shade helps to keep plants cooler during the day and warmer at night (Lin, 2007). Temperatures above 20–24 °C greatly reduce net photosynthesis, with values approaching 0 at 34 °C (Cannell, 1976); development and ripening of fruit in coffee are also accelerated above 23 °C, leading to loss of quality (Camargo, 1985). There is concern that future temperature increases may severely affect coffee production and quality, while some staple crops such as rice are already widely grown at temperatures close to the upper limit of their optimal range (Peng et al., 2004). As any further increase would seriously affect the viability of these important food and cash crops, it is vital to develop effective and economically feasible strategies to protect smallholder farmers from the damaging impact of climate change.

Agroforestry may provide a financially viable way of protecting crops in areas where microclimatic factors regularly exceed the optimal range (Lin, 2007). The importance of microclimate in determining crop performance is well documented and has been incorporated into simulation models to predict crop yield over a wide range of environments (Ong et al., 1996, 2006, 2007). However, our understanding of the impact of trees on the microclimate experienced by understorey crops, their physiological responses and on yield is incomplete (Ong et al., 2006, 2007). Early studies of the influence of trees on understorey microclimate focussed on alley cropping (Corlett et al., 1992; McIntyre et al., 1996) or trees grown as shelter belts (McNaughton, 1988; Brenner et al., 1995); few have attempted to characterise the influence of dispersed overstorey trees (Vandenbelt and Williams, 1992; Jonsson et al., 1999; Lott et al., 2000a,b; Muthuri et al., 2005, 2009).

There is good evidence that trees in savannah systems benefit understorey vegetation. Belsky et al. (1989, 1993) found that scattered *Adansonia digitata* and *Acacia tortilis* trees enhanced the growth of understorey vegetation in Kenya by reducing incident solar radiation, air and soil temperature and atmospheric saturation deficit, while Kinyamario et al. (1995) reported that shade improved water status, gas exchange and water use efficiency in the understorey grasses, *Themeda triandra* and *Panicum maximum*. However, attempts to reproduce these benefits by introducing agroforestry in similar environments have often been disappointing (Lott et al., 2000a,b; Muthuri et al., 2005; Ong et al., 2006, 2007). Ong and Leakey (1999) concluded that the potential benefits of microclimatic amelioration are often negated by decreases in soil water supplies caused by interception losses from the tree canopy and depletion of available soil moisture. Trees may affect microclimate in ways that either improve or reduce understorey crop yield; thus, Kater et al. (1992) and Kessler (1992) reported that shade under scattered *Parkia biglobossa* and *Vitellaria paradoxa* trees reduced sorghum and millet yields in the Sahel, while Vandenbelt and Williams (1992) and Jonsson et al. (1999) found that temperature amelioration and improved soil fertility more than offset the influence of shade on understorey crops. In semi-arid Kenya, Huxley et al. (1994) reported that maize yields were up to 80% greater on the downwind side of tree lines than in unsheltered maize, while Huxley et al. (1989) found that maize yield in a *Cassia*/maize system was greatly improved by shade from trees during the afternoon in low rainfall seasons. These studies are by no means the only ones to report benefits of shade for crop growth and yield, although the precise nature of the microclimatic changes remains unclear. Effects on the thermal and radiation environment of understorey crops are likely to be key factors.

This paper describes the influence of dispersed trees on understorey microclimate, focussing on temperature and solar radiation and associated effects on gas exchange, conversion coefficient for solar radiation and yield in maize in semi-arid Kenya. The hypothesis was that benefits of microclimatic amelioration for understorey crops by trees may be negated by competition for limited natural resources.

2. Materials and methods

2.1. Site description and experimental design

The Complementarity In Resource Use on Sloping land (CIRUS) trial was located at ICRAF's Machakos Research Station, Kenya (1°33′S, 37°8′E, 1560 m a.s.l.) on a moderately steep south-westerly slope. Experimental design, management and analytical procedures are described by Ong et al. (2000). Climate and soil are typical of the area. Rainfall is bimodal, with rainy seasons extending from March to June (long rains) and October to December (short rains); little rain is received between July and September. Mean rainfall during the short and long rains between 1963 and 1971 was 414 and 359 mm, with an annual average of 782 mm; monthly potential evaporation ranges between 95 and 165 mm, with an annual total of 1450 mm (Ong et al., 2000). Climate is relatively cool, with annual mean, minimum and maximum temperatures of 20.1, 13.8 and 23.2 °C; monthly mean relative humidity ranged from 56% during the day to 96% at night.

CIRUS examined the extent of complementarity between *Grevillea robusta* (A. Cunn., grevillea) and maize (*Zea mays* L. Katumani composite) in their use of water, nutrients and light. The 0.6 ha site had no cropping history before being cleared of scrubby vegetation dominated by *Acacia* species. The soil was a well-drained, shallow to moderately deep sandy clay loam characterised as a Khandic Rhodustalf overlying petroplinthite (murram) and contained five horizons. The stone-free upper layer was sub-divided into till (0–40 cm), sub-surface (40–80 cm) and clay (80–100 cm) layers; a mixed clay/gravel layer and saprolite (eroded gneiss bedrock) were present at 100–120 and 120–160 cm. Nutrient content and other soil parameters were not limiting for maize and plot size was 20 m × 20 m (Ong et al., 2000). A balanced incomplete block design with four replicates of three treatments was used i.e.:

- Cg: contour-planted sole maize grown at inter- and intra-row spacings of 1 m × 0.3 m.
- Td: contour-planted sole trees grown at a 3 m × 4 m spacing with 35 trees per plot (833 trees ha^{-1}).
- CTd: identical to Td except that maize was grown as an understorey crop; planting densities were identical to the Cg and Td treatments.

Three-month-old grevillea seedlings were planted in October 1991 and maize was grown continuously from the 1994 long rains (L94) onwards. A strip of vetiver grass (*Vetiver zizanoides* L.) was contour-planted across the centre of all plots to control erosion and cut to a height of 10–15 cm at 7–14 days intervals to limit competition with trees and crops. Plots were separated by grass paths and no fertiliser or organic residues were applied. Trees were managed to produce single stems and maintain leaf area index between 0.25 and 0.50 by removing the longer side branches 21 months after planting (6 June 1993) and at subsequent annual prunings. 1 m deep trenches were dug around plots containing trees before each cropping season to sever roots extending into adjacent plots. Measurements were made during the 1994 and 1995 long cropping seasons (L94 and L94) and 1994/1995 and 1995/1996 short cropping seasons (S94/95 and S95/96).

2.2. Shade treatments

To distinguish effects of shade from those induced by below-ground competition with trees, shade treatments were established in the sole crop plots using spectrally neutral netting (Lowes of Dundee, UK) to reduce incident radiation by 25 or 50%; 3 m × 4 m enclosures were supported 80 cm above the ground and raised as the crops grew taller. The unshaded, 25 and 50% shade treatments are hereafter termed Cg 0%, Cg 25% and Cg 50%. Meristem temperature and gas exchange were measured for plants in the central three rows in each enclosure; four randomly selected plants from each row were used for growth analysis at maturity.

2.3. Crop growth

The timing of floral initiation, anthesis, silking and physiological maturity, and hence duration of the vegetative, reproductive and grain-filling phases, was determined from non-destructive observations at 16 locations in the 12 m^2 area bounded by four adjacent trees (hereafter referred to as 'cell') in all replicates of the CTd treatment and equivalent locations for sole maize. Floral initiation was determined by daily inspection of the inflorescences of four randomly selected plants per plot until tassle primordia were present for at least 75% of plants. Anthesis and silking were defined as occurring when spikelets emerged from the leaf whorl and silks (stigmata) appeared from the husk. Physiological maturity was defined by the formation of a black layer at the pedicel of at least one grain per cob (Daynard and Duncan, 1969), or when 90% of the leaf area had fully senesced when CTd maize failed to set grain. Destructive analyses were made at maturity for randomly selected plants from each sampling location in all plots to determine fresh and dry (constant weight at 70 °C) weights for leaves, stems, cobs and grain.

2.4. Climatic and microclimatic conditions

Rainfall 20 m from the nearest trees was measured daily using an automatic tipping-bucket gauge. Copper/constantan thermocouples coated with high thermal conductivity epoxy resin to prevent penetration by water were used to determine soil and stem meristem temperatures for maize in all treatments; the lead wires were wrapped in reflective foil and supported above the soil to minimise thermal errors. Four thermocouples were used to measure soil (2 cm depth) and meristem temperature at the same locations as the solarimeters and maize plants used for non-destructive growth analysis. Meristem temperature was assumed to be identical to soil temperature until 45 days after sowing, when stem elongation began; thermocouples were subsequently inserted directly into the meristem. Soil temperature initially provides a reliable measure of meristem temperature in cereals as this remains below the soil surface until stem elongation begins (Norman et al., 1984).

Incident short-wave solar radiation and photosynthetic photon flux density (PPFD) were recorded 2 m above the trees and beneath their canopy at distances of 0.3 and 2.5 m from the trunk (Ong et al., 2000). Interception by tree and crop canopies was determined using unscreened tube solarimeters (Delta-T Devices, Cambridge, UK) referenced against incident values outside the experimental area. Solarimeters mounted horizontally in groups of three were used to integrate interception by adjacent crop rows or concentric rings around individual trees; these were placed immediately above the ground for Cg 0% and CTd maize and 100 cm above ground level for Td grevillea. Full details are given by Ong et al. (2000).

Daily mean fractional interception (f) was calculated from hourly values for incident and transmitted solar radiation as

$$f = 1 - \left(\frac{S_t}{S}\right) \tag{1}$$

where S and S_t represent daily total incident and transmitted solar radiation for the tree, crop or combined canopies. Ground-level measurements in the CTd system provided values for combined interception by maize and grevillea. To calculate interception by CTd maize, estimates of interception by grevillea, and hence the quantity of radiation received by understorey maize, were required. As the number of solarimeters and datalogger channels available precluded direct measurement of interception by grevillea in the CTd treatment, values were derived from measurements for the Td system by calculating a correction factor (p) to account for the differing height of solarimeters above ground level and hence distance from the base of the tree canopy in these treatments (Ong et al., 2000). p corresponds to the slope of the linear correlation passing through the origin between mean values for the CTd and Td treatments before crop emergence and after harvest. The correction factor was applied as follows:

$$S_{t(CTdt)} = \frac{S_{t(Td)}}{p} \tag{2}$$

$$S_{t(CTdm)} = S_{t(CTd)} - \frac{S_{t(Td)}}{p} \tag{3}$$

where $S_{t(CTdt)}$, $S_{t(Td)}$, $S_{t(CTdm)}$ and $S_{t(CTd)}$ represent transmitted radiation beneath CTd grevillea, Td grevillea, CTd maize and combined grevillea and maize canopies in the CTd treatment.

2.5. Gas exchange

A CIRUS 1 infrared gas analyser (PP Systems, Hitchin, Herts, UK) was used to determine gas exchange by the youngest mature leaf of maize during L95 and S95/96. Measurements were made four times daily at 2 h intervals commencing at 1000 h on four occasions during each season. The cuvette was outlined on the sampled leaves using a fine permanent marker pen to allow successive measurements for the same area. PPFD response curves were constructed around midday using a light source and 11 spectrally neutral filters placed in turn between the light source and chamber. Leaves were equilibrated for 90 s before making the measurement and each curve required ca. 20 min to complete. Measurements were repeated for four plants in each treatment.

2.6. Statistical analysis

Results were analysed by split-plot analysis of variance using Genstat 5 (Rothamsted Research, Harpenden, Herts, UK). Main treatment effects were tested against between-plot variation. Inspection of residual plots to test for normality and homogeneity showed there was no need to transform data before analysis.

3. Results

3.1. Crop yield

Above-ground biomass and grain yield were greatly reduced in CTd maize relative to Cg 0% maize in three of the four seasons examined ($P < 0.05$; Table 1). Shoot biomass approached 50% of that for Cg 0% maize only when rainfall was well above average (628 mm in S94/95 vs. long-term mean of 414 mm), but grain yield was 36% of that for Cg 0% maize. Biomass and grain yield were greater in the shade net treatments than in CTd maize ($P < 0.05$) for all except grain yield in Cg 50% maize in S94/95. Biomass in the shade net treatments

Table 1
Seasonal rainfall, above-ground biomass and grain yield for maize grown under 0, 25 and 50% artificial shade (Cg 0%, Cg 25% and Cg 50%) or in the CTd agroforestry system.

Season	Rainfall (mm)	Above-ground biomass (t ha^{-1})				Grain yield (t ha^{-1})			
		Cg 0%	Cg 25%	Cg 50%	CTd	Cg 0%	Cg 25%	Cg 50%	CTd
L94	199	3.17a	3.28a	3.32a	0.37b	1.80a	1.71a	1.70a	0.06b
S94/95	628	3.28a	2.34b	2.34b	1.48c	2.17a	1.26b	0.91b	0.82b
L95	302	4.12a	3.44a	2.27b	0.17c	1.79a	1.27a	0.58b	0.08c
S95/96	317	3.21a	3.26a	2.60a	0.25b	1.53a	1.70a	1.28a	0.02b

Values for biomass and grain yield for specific seasons followed by different letters differ significantly ($P < 0.05$).

did not differ significantly from Cg 0% maize in L94 and S95/96, but was lower in Cg 50% than in Cg 0% maize in L95 and S94/95 ($P < 0.05$). Further consideration of the seasonal timecourses of leaf area index and above-ground biomass, and harvest index and land equivalent ratios at maturity, are provided by Lott et al. (2000b).

3.2. Meristem temperature and thermal time

Shade had a substantial effect on the seasonal mean diurnal timecourses for meristem temperature (Fig. 1). The mean diurnal range for Cg 0% maize varied from 10 °C in S94/95 to 20 °C in S95/96; the corresponding minimum and maximum ranges for CTd maize were 9 °C in L94 and 13 °C in L95. Mean maximum meristem temperature for CTd maize was 2.5–6.0 °C lower than for Cg 0% maize depending on season. Daytime meristem temperature in Cg 25%

maize was higher than for CTd maize in L94 and S94/95 ($P > 0.05$), highlighting the substantial shading effect of trees, although their moderating influence declined in L95 and S95/96 when daytime values for CTd maize were greater than for Cg 25% and Cg 50% maize ($P < 0.001$). Fig. 2 shows the proportion of the total seasonal number of hours when meristem temperature was sub-optimal, optimal or supra-optimal. Temperature was sub-optimal (<28 °C) for a large proportion of all seasons and there was little benefit of shade in L94 and S94/95, whereas extensive exposure to supra-optimal temperatures (>34 °C) occurred in Cg 0% and CTd maize in L95 and, especially, S95/96. Fig. 2e shows that meristem and air temperature were similar at *ca.* 20 °C but meristem temperature increasingly exceeded air temperature as the latter increased.

Fig. 3 shows cumulative thermal time above a base temperature of 8 °C for all treatments and seasons; dashed lines indicate mean
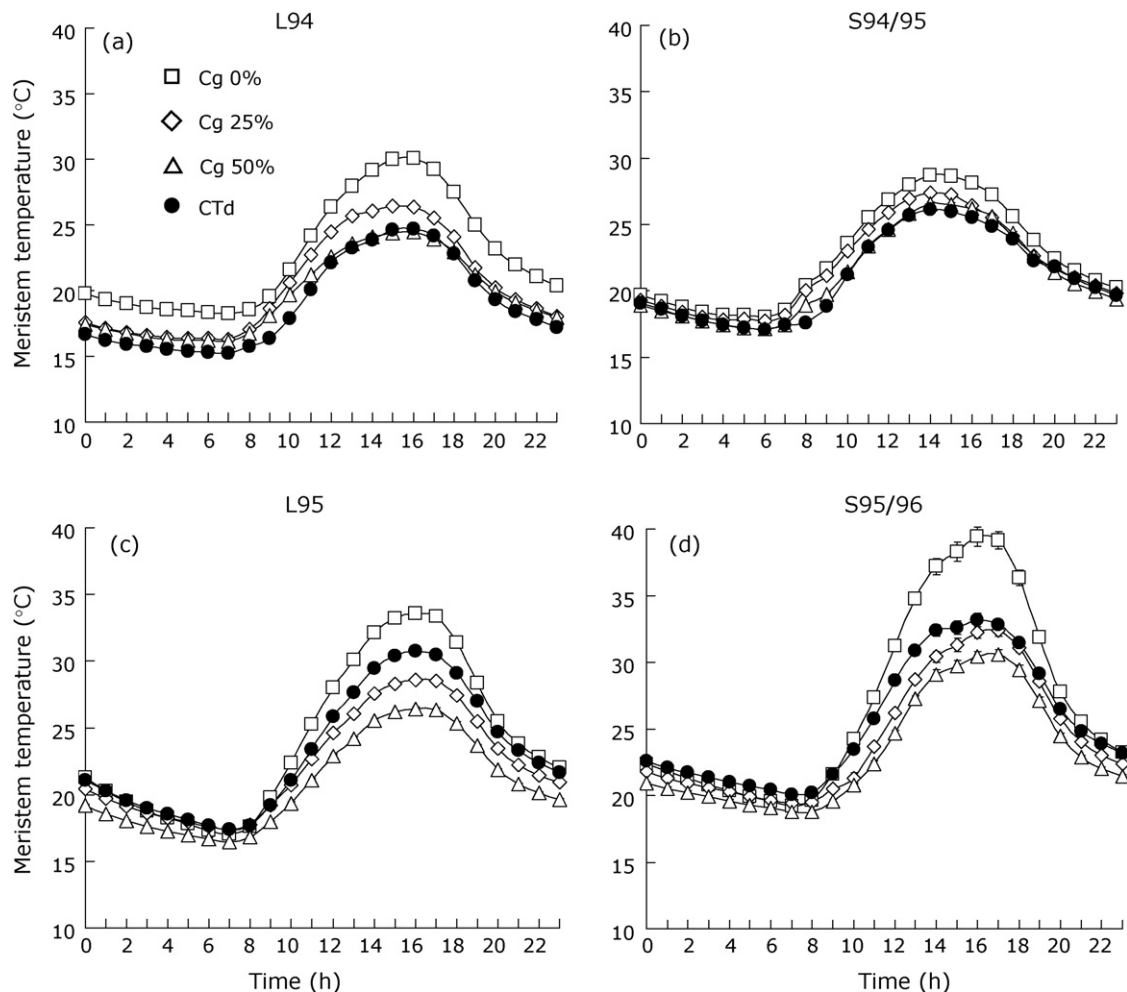

Fig. 1. Seasonal mean diurnal timecourses of meristem temperature for maize grown under 0, 25 and 50% artificial shade (Cg 0%, Cg 25% and Cg 50% treatments) or in the CTd agroforestry system during the L94 and L95 long and S94/95 and S95/96 short cropping seasons. Double standard errors of the mean are shown where these are larger than the symbols.
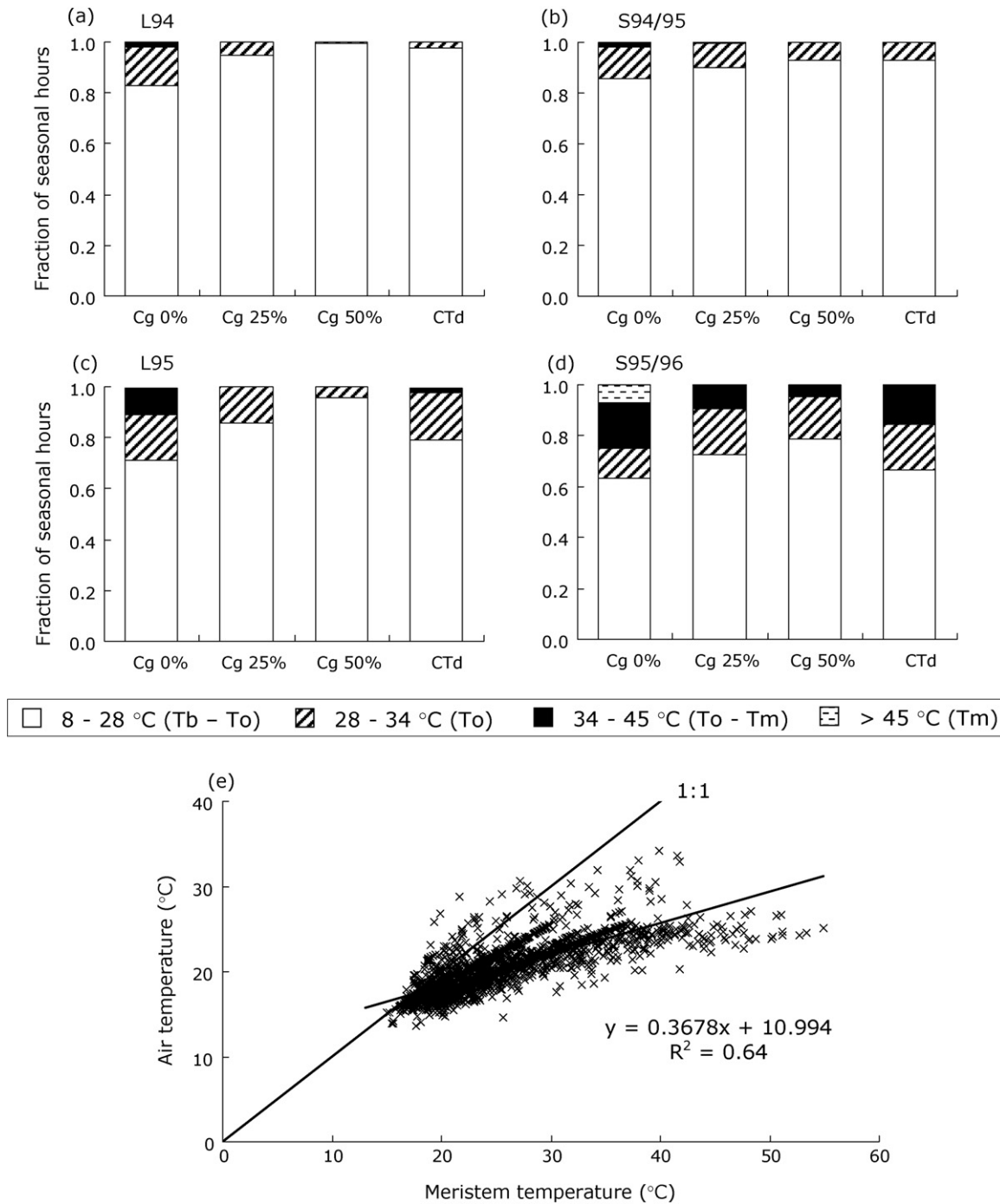
Fig. 2. (a–d) Fraction of seasonal total hours within the sub-optimal (8–28 °C), optimal (28–34 °C) and supra-optimal (34–45 °C) temperature ranges and above the maximum temperature for meristem activity (45 °C) for maize grown under 0, 25 and 50% artificial shade (Cg 0%, Cg 25% and Cg 50% treatments) or in the CTd agroforestry system during the L94 and L95 long and S94/95 and S95/96 short cropping seasons. T_b, T_o and T_m denote minimum, optimum and maximum temperatures for meristem activity. (e) Relation between hourly mean values for meristem and air temperatures in all seasons.

flowering dates and the thermal duration (°C day) of vegetative growth. Thermal time accumulated most rapidly in S94/95, as shown by the steeper gradient of the correlations and shorter chronological time needed to reach 1200 °C day because meristem temperature was consistently closer to the optimum than in other seasons (Fig. 2). Cumulative thermal time values were greatest for Cg 0% maize and lowest for Cg 50% and CTd maize in L94 ($P < 0.05$), but were greatest for CTd maize and lowest for Cg 50% and Cg 25% maize in subsequent seasons. Flowering occurred later in CTd than in sole maize in terms of both chronological and thermal time, by

24 days and 600 °C day in S95/96; differences between shade net treatments never exceeded 5 days or 80 °C day.

3.3. Solar radiation

Mean diurnal timecourses for solar radiation incident upon maize over an 11 day period (26 November–6 December 2004) centred on anthesis (60 DAS) in S94/95 show that values decreased with increasing shade in the shade net treatments, while those for CTd maize were intermediate between the Cg 25% and Cg 50%
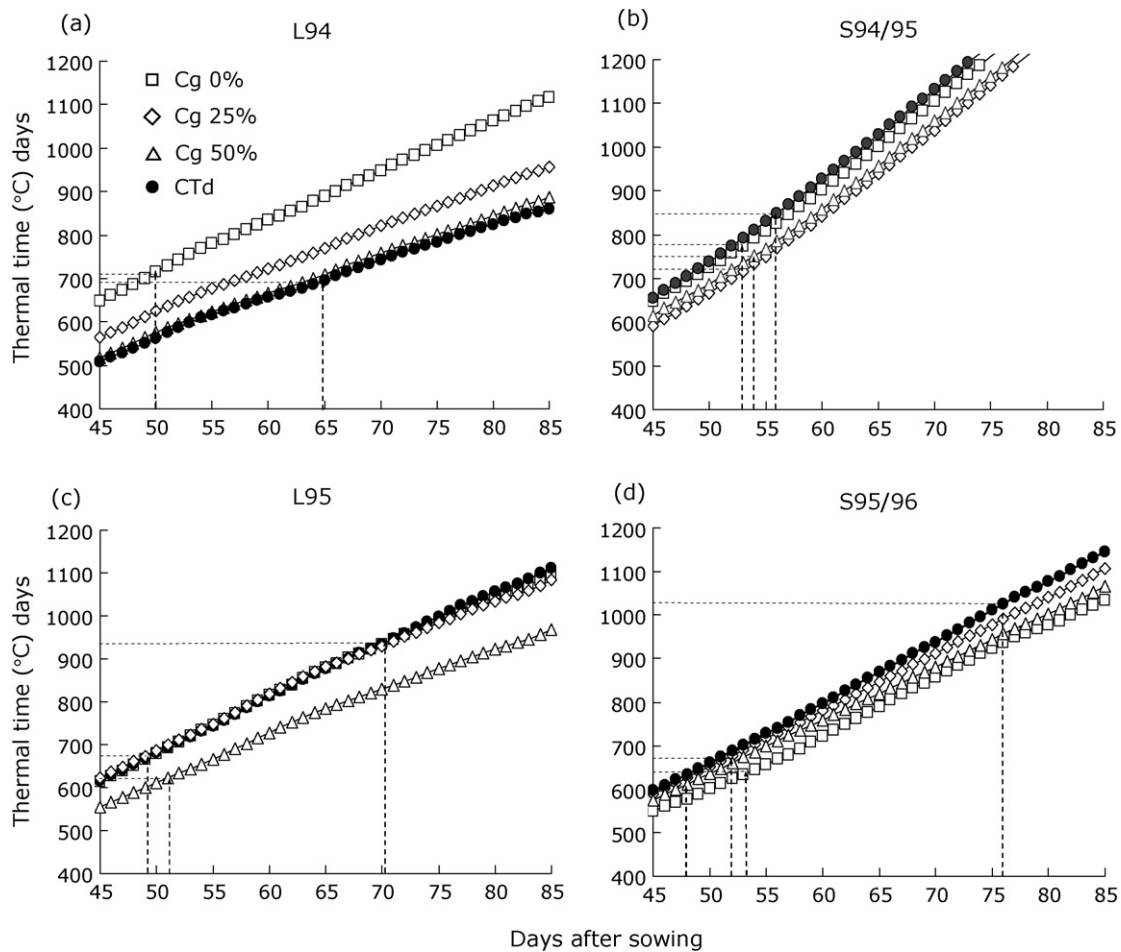
Fig. 3. Relationship between cumulative thermal time and chronological time for maize in all treatments and growing seasons. Dashed lines indicate timing of flowering in days and associated thermal time required.

treatments (Fig. 4a). Values for CTd maize were calculated on the assumption that shading was uniform within cells bounded by four trees, although the discontinuity of the tree canopy caused substantial spatial variation depending on proximity to trees (Fig. 4b) and solar angle. As the site had a slope ranging between 18 and 22%, shadows from trees exceeded their projected canopy area (shown as circles), even at solar noon. Radiation incident upon CTd maize was greatest under the uphill side of the tree canopy and in the upper central quadrant in each cell, and lowest towards the centre of cells between the canopies of adjacent trees.

Fractional interception (*f*) in S94/95 (Fig. 5a) increased rapidly in Cg 0% maize to reach 0.4 at flowering, the time of maximum leaf area index (1.6 *vs.* 1.2 for Cg and CTd maize; Lott et al., 2000b); this was maintained for *ca.* 30 days before declining rapidly as the leaves senesced. *f* values for Td grevillea gradually increased to reach a maximum of 0.4 by the end of the season. Values for the combined tree and crop canopies in the CTd system exceeded those for the Td and Cg 0% systems (*P* < 0.05) but followed a similar timecourse to Cg 0% maize, attaining a maximum of 0.54; the decline during the final 30 DAS was smaller. The seasonal mean *f* value for Cg 0% maize (0.26; Table 2a) was slightly lower than for Td grevillea (0.29); the value for the combined tree and crop canopies in the CTd system (0.39) was 50% greater than that for Cg 0% maize.

Daily incident radiation often exceeded 20 MJ m^{-2} day^{-1} and total incident radiation during the 123 day period S94/95 season was 2432 MJ m^{-2}. Cumulative intercepted radiation by the tree and crop canopies in the CTd system was much greater than in the

Cg 0% and Td treatments after 15 DAS (Fig. 5b) and treatment differences increased with time; values were consistently lowest for CTd maize (CTdm). Total seasonal interception was greater in the CTd treatment (952 MJ m^{-2}) than in the Td and Cg 0% systems (718 and 630 MJ m^{-2}; *P* < 0.05; Table 2a). Maize in the CTd system intercepted 261 MJ m^{-2}, 27% of the total. Seasonal mean conversion coefficients for intercepted radiation (*e*), calculated as the ratio between above-ground biomass at final harvest and cumulative seasonal intercepted radiation, were lower for Cg 0% and CTd maize than for Td grevillea and the combined tree and crop canopies in the CTd system (*P* < 0.05; Table 2a). Seasonal mean values for maize were lower than those for the period before flowering.

3.4. Gas exchange and conversion coefficients in maize

Fig. 6 shows diurnal timecourses for photosynthetic photon flux density (*PPFD*), net photosynthesis (*A*), transpiration (*E*) and leaf conductance (*g*$_s$) at anthesis (55 DAS) in S95/96. *PPFD* was greatest for Cg 0% maize and lowest for Cg 50% maize (*P* < 0.05). *A*, *E* and *g*$_s$ tracked the timecourses of *PPFD* in all treatments, although values for CTd maize were less than half those for Cg 0% maize (*P* < 0.05). Fig. 7 shows the influence of shade on *A* and *E* for maize during the high rainfall S94/95 season (628 mm; Fig. 7a–d) and much drier L95 season (302 mm; Fig. 7e–h). *PPFD* declined with increasing shade in the shade net treatments and decreased for CTd maize as the tree canopy grew larger, particularly in L95. The trees initially had little effect on *A* and *E* in CTd maize relative to Cg 0% maize in
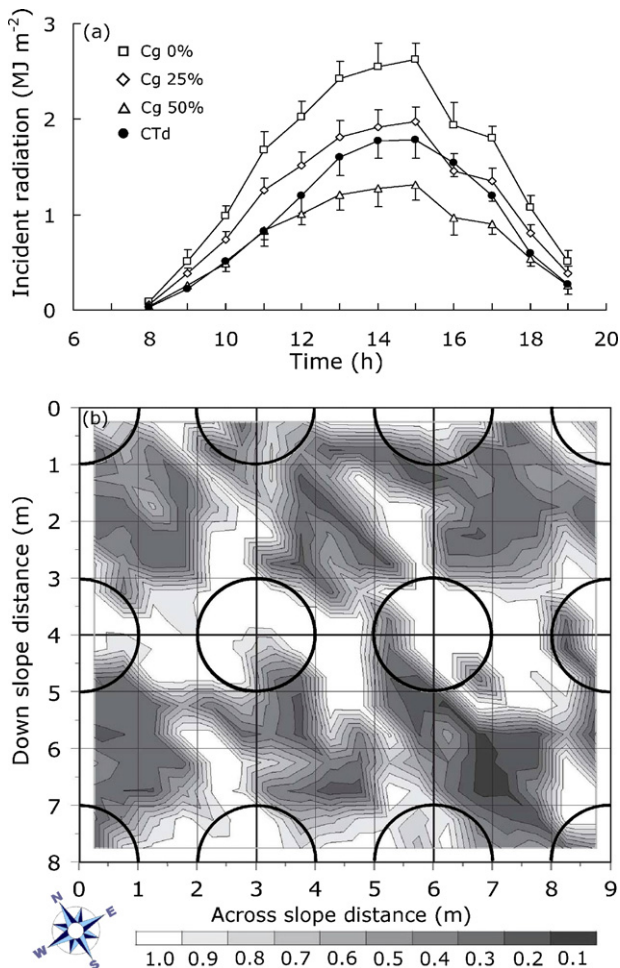
Fig. 4. (a) Mean diurnal timecourses of short-wave radiation incident on maize in the Cg 0%, Cg 25%, Cg 50% and CTd treatments and (b) spatial variation in short-wave radiation incident on understorey maize in the CTd treatment at solar noon (1100 h local time) for an 11 day period (26 November–6 December 2004) centred around anthesis (60 DAS) during the S94/95 season. Single standard errors of the mean are shown in (a); circles in (b) represent projected area of the tree canopy.

S94/95 (Fig. 7a–d), but values for both variables decreased as the season progressed, although neither fell below 60% of those for Cg 0% maize. This pattern reflects the timecourses of f (Fig. 5a), which was initially comparable for Cg 0% and CTdm maize but increased more rapidly with time in the former. In L95, A and E for CTd maize decreased sharply from levels similar to Cg 50% maize at 41 DAS to *ca.* 10% of Cg 0% maize at 94 DAS (Fig. 7e–h). A and E values for CTd maize were generally similar to Cg 25% and Cg 50% maize in S94/95 (Fig. 7a) but were much lower in L95, suggesting that gas exchange was restricted by the limited water supplies and associated water stress.

PPFD response curves in S95/96 were initially similar for all sole maize treatments, although the *PPFD*-saturated A value (A_{sat}) for Cg 50% maize was lower than for Cg 0% maize at 25 and 43 DAS ($P < 0.05$; Fig. 8). A_{sat} for CTd maize was much lower than in all sole maize treatments at 43 DAS and negligible by 85 DAS, when plants were *ca.* 30 days into their grain filling period and approaching maturity. Senescence reduced photosynthetic competence for all except Cg 50% maize, as shown by the *ca.* 40% reduction in A_{sat} for Cg 0% and Cg 25% maize between 43 and 85 DAS; the corresponding value for Cg 50% maize at 85 DAS was comparable to that at 43 DAS, suggesting that lower tissue temperatures in this treatment delayed senescence. The sharp step in the response for CTd maize at *ca.* 1350 mmol m^{-2} s^{-1} *PPFD* at 85 DAS reflects the
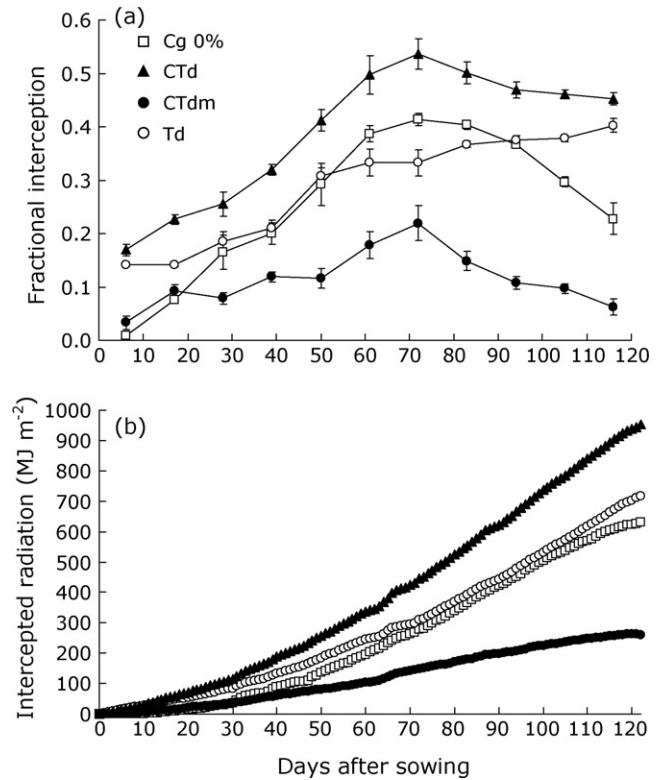

Fig. 5. (a) Seasonal timecourses of fractional interception (f) of short-wave radiation by unshaded sole maize (Cg 0%), sole grevillea (Td), grevillea and maize in the CTd treatment and maize in the CTd system (CTdm); (b) cumulative intercepted radiation during the S94/95 short growing season.

limited water supplies, which may have promoted rapid stomatal closure and cessation of photosynthetic activity during construction of the response curves. As *PPFD* is the primary rate-limiting factor for A below *ca.* 200 μmol m^{-2} s^{-1}, the slope of the tangent to the response curve in this region provides a measure of the instantaneous radiation conversion coefficient (e_i). Values did not differ between treatments at 23 DAS, but declined dramatically with time in CTd maize ($P < 0.001$; Table 2a); values for sole maize tended to increase with increasing shading intensity but did not differ significantly.

4. Discussion

4.1. Thermal amelioration

A key question is whether thermal amelioration by trees improves the performance of understorey vegetation in semi-arid areas, particularly in view of the predicted impact of climate change (Rosenzweig et al., 2004; Slingo et al., 2005; Lin, 2007; Ong et al., 2007). In this study, shade from trees reduced mean maximum meristem temperature in maize by between 2.5 and 8 °C (Fig. 1), consistent with observations that overstorey trees reduce the maximum temperature experienced by coffee in Mexico by *ca.* 2.5 °C (Lin, 2007). The decline in temperature moderation in CTd maize with time (Fig. 1) relative to the shade net treatments occurred because increasing tree height and removal of the lower branches increased distance between the ground and tree canopy to over 2 m, enhancing understorey air-flow. As the timecourses are seasonal means, maximum temperature would have been greater, and hence more damaging, on some days than others in each season. Shading may be beneficial when crops frequently experience supra-optimal temperatures (Khalifa and Ong, 1990; Lin, 2007), as is well documented for agroforestry

Table 2
(a) Above-ground biomass at final harvest, total seasonal intercepted short-wave radiation, seasonal mean fractional interception (f), radiation conversion coefficient (e) for the Cg 0%, Td and CTd treatments and maize in the CTd system, and e between planting and flowering for maize in the Cg 0% and CTd systems during the S94/95 season; (b) instantaneous radiation conversion coefficients (e_i) calculated from PPFD response curves constructed on 23, 43 and 85 DAS during the S94/95 season.

(a)

Treatment	Above-ground biomass (t ha^{-1})	Intercepted radiation (MJ m^{-2})	f	e (g MJ^{-1})	e up to flowering (g MJ^{-1})
Cg 0%	3.28	630	0.26	0.52	1.04
Td	5.07	718	0.29	0.71	–
CTd	6.65	952	0.39	0.70	–
CTdm	1.48	261	0.11	0.57	0.88

(b)

Treatment	e_i (μmol CO$_2$ m^{-2} s^{-1} mmol PPFD m^{-2} s^{-1})			SED
	23 DAS	43 DAS	85 DAS	
Cg 0%	0.059	0.056	0.046	0.004
Cg 25%	0.058	0.064	0.051	0.004
Cg 50%	0.060	0.066	0.065	0.002
CTd	0.054	0.027	0.002	0.011

SED denotes the standard error of the difference between means.

systems (Jonsson et al., 1999; Ong et al., 2006, 2007). Ovalle and Avendano (1987) found that maximum soil temperatures in an *Acacia* woodland were 3–10 °C lower than in the open, consistent with Fig. 1.

Temperature is an important rate-modifier for developmental processes, as these increases linearly between a base temperature where these processes begin and an optimum where they reach their maximum rate, before declining to a maximum temperature above which they cease (Black and Ong, 2000). Relationships between the timing and duration of key developmental events and

accumulated thermal time may be used to assess the influence of thermal amelioration on understorey vegetation. As temperature is the primary determinant of development in the absence of other stress factors, the thermal duration of specific developmental stages should be similar for plants exposed to differing temperature environments under otherwise comparable conditions (Ong and Monteith, 1985). As air temperature in the East African highlands, including Machakos, is more favourable for crop growth than at lower altitudes, meristem temperature persistently exceeded the optimum only during sustained drought in S95/96,
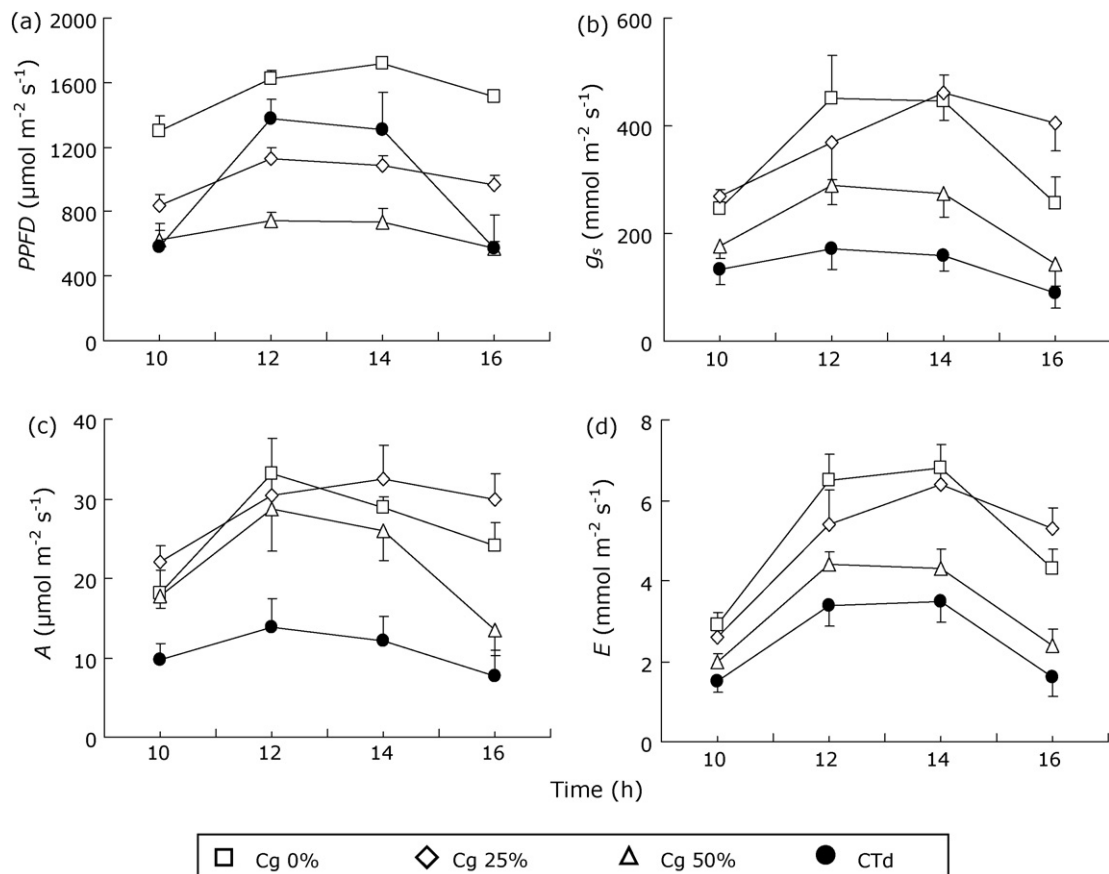

Fig. 6. Diurnal timecourses for (a) PPFD, (b) stomatal conductance (g_s), (c) net photosynthesis (A) and (d) transpiration (E), for maize grown under 0, 25 or 50% artificial shade or in the CTd treatment at 55 DAS during S95/96. n = 4; single standard errors of the mean are shown where larger than the symbols.
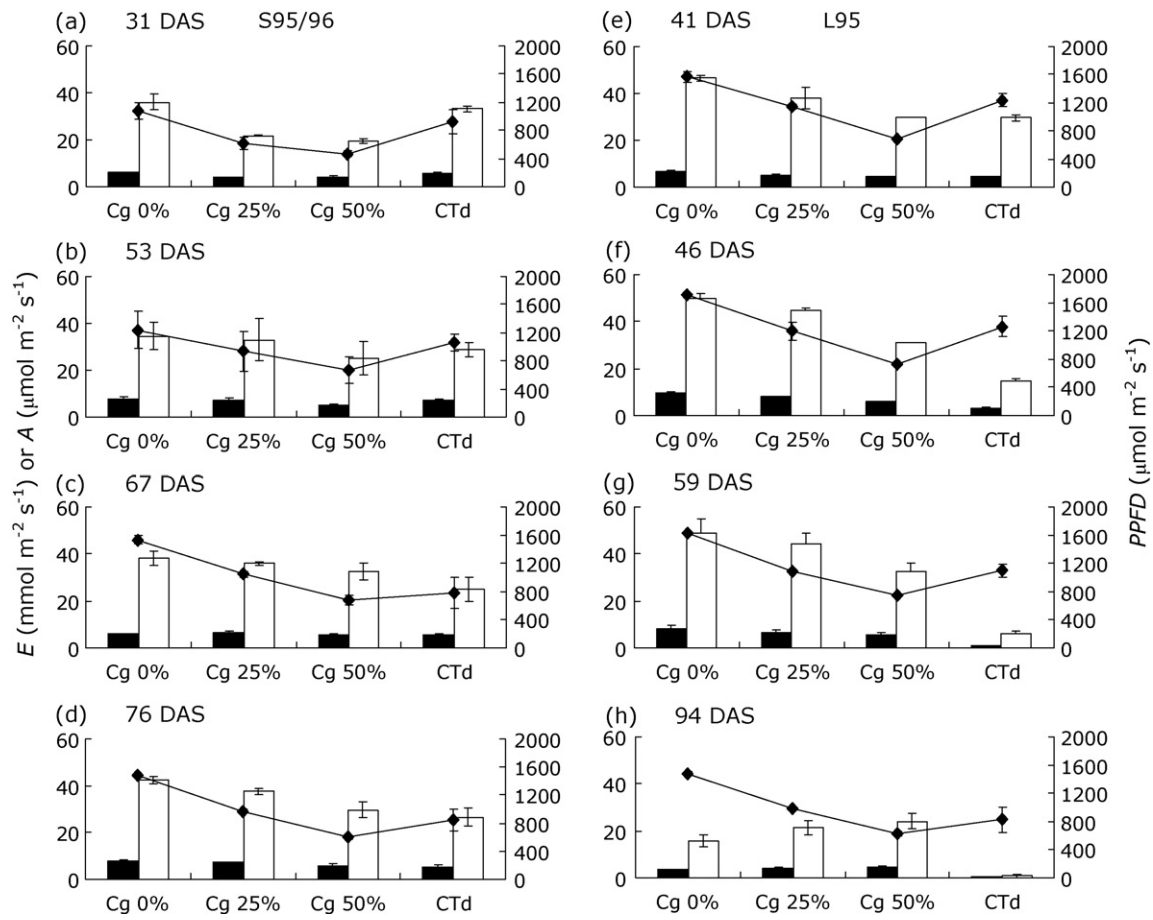
Fig. 7. Photosynthetic photon flux density (*PPFD*), net photosynthesis (*A*) and transpiration (*E*) for maize grown under 0, 25 or 50% artificial shade (Cg 0%, Cg 25% and Cg 50%) or in the CTd treatment for four dates during S95/96 and L95. Values are means for measurements made at 1000, 1200, 1400 and 1600 h local time. $n = 4$; double standard errors of the mean are shown. ◆, open bars and solid bars respectively denote *PPFD*, *A* and *E*.

although supra-optimal temperatures were experienced to some extent in all seasons (Figs. 1 and 2). Similarly, Lin (2007) found that maximum temperature exceeded the optimum for coffee by 4–8 °C depending on season and intensity of shade throughout the daytime period.

Thermal time analysis revealed that flowering was delayed by 5 days by the lower temperatures experienced by CTd maize when water was not limiting (S94/95), but by 15–24 days in seasons when flowering occurred after available soil moisture had been depleted (Fig. 3; Lott et al., 2003), resulting in crop failure (Table 1). Flowering occurred later in CTd than in Cg 0% maize in terms of both chronological and thermal time and this effect increased as the trees grew larger and more competitive, whereas differences between shade net treatments never exceeded 5 days or 80 °C day. Results from the shade net treatments are consistent with previous studies (Belsky et al., 1993; Belsky, 1994), while the differing responses to natural and artificial shade of similar intensity suggest that the delayed flowering of CTd maize resulted from below-ground competition. In contrast to savannah systems where shading was most beneficial under low rainfall conditions (Belsky et al., 1993), below-ground competition negated the benefits of temperature amelioration in the present study. Van Noordwijk and Ong (1999) concluded that the contrast between savannah and agroforestry systems occurs because water use per unit of tree shade is greater in the latter.

Moderation of understorey temperature is not always beneficial; for example, thermal amelioration by agroforestry is unimportant on the Deccan plateau in India as temperatures during the cropping season are favourable for crop growth (Corlett et al., 1992), while Brenner et al. (1995) attributed the reduced productivity of millet downwind of windbreaks in Niger relative to unsheltered crops to increased soil and leaf temperatures. These observations highlight the difficulty of predicting the impact of tree shade on understorey crops under differing climatic conditions. Bhatt et al. (1991) attempted to characterise the suitability of trees for agroforestry in semi-arid areas by determining energy exchange by their canopies; species which lost most energy by radiative transfer and transpiration were regarded as being suited to environments where air temperatures are high and were suggested to benefit understorey crops by reducing thermal load, improving their growth, development and yield. Moderation of soil temperature is also important for seedling survival, soil water status, litter decomposition and N-mineralisation (Kirschbaum, 1995). Further studies to identify tree species providing appropriate microclimatic amelioration in dryland areas are essential, although there are inherent risks in attempting to define suitability on the basis of specific microclimatic factors.

4.2. Radiation interception and conversion coefficients for maize

Our conclusion that microclimatic amelioration may improve the performance of understorey crops concurs with studies of African savannah systems (Belsky et al., 1989, 1993) and coffee plantations in Mexico (Lin, 2007), although evidence for agroforestry systems is inconsistent. Kater et al. (1992) and Kessler (1992) reported that sorghum and millet yields in the Sahel were correlated with incident radiation under the tree canopy, while Jonsson et al. (1999) concluded that microclimatic amelioration
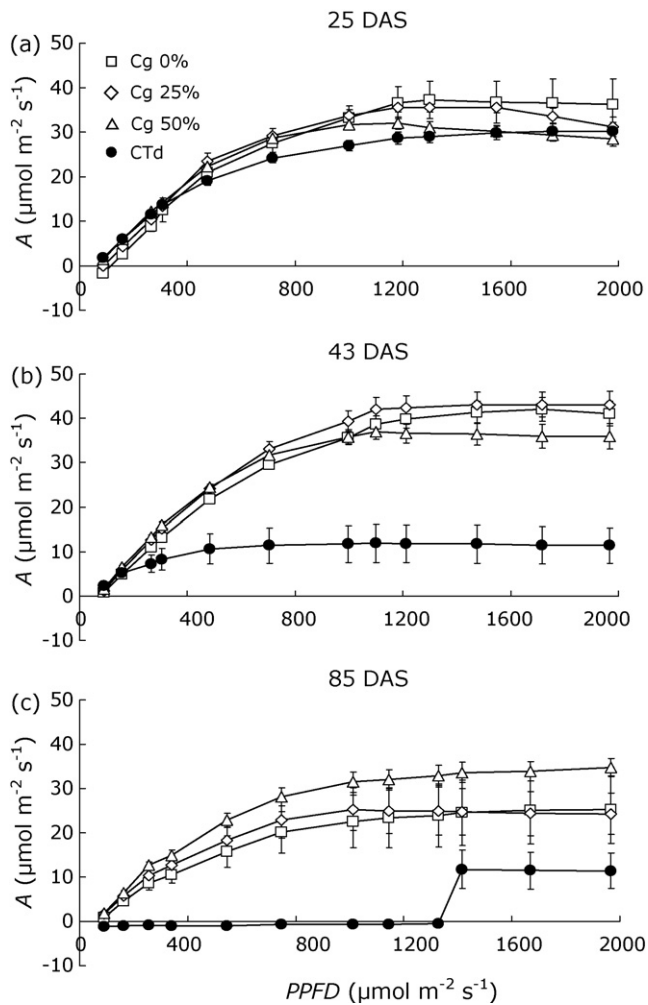
Fig. 8. *PPFD* response curves for net photosynthesis (*A*) for maize grown in the Cg 0%, Cg 25%, Cg 50% and CTd treatments during S95/96. *n* = 4; double standard errors of the mean are shown.

and enhanced soil fertility may exceed the potentially detrimental influence of shade in the Sahel. By contrast, studies using root barriers to segregate tree and crop roots suggest that shading is less important than below-ground competition (Corlett et al., 1992; Jose et al., 2000). In the present study, diurnal and cumulative solar radiation incident upon maize were reduced to an extent related to shading intensity (Fig. 4a, Table 2a), consistent with previous studies of coffee (Lin, 2007). The low *f* values for Cg 0% maize (Table 2a) suggest that canopy size was restricted by below-ground resources or population density as seasonal mean values for short duration tropical cereals under favourable water and nutrient supply conditions are typically *ca.* 0.5 (Squire, 1990; Black and Ong, 2000). The seasonal mean *f* value for the tree and crop canopies in the CTd system was 50% greater than for Cg 0% maize, suggesting potential for spatial complementarity, although the yield of CTd maize was greatly reduced (Table 1). The observation that total radiation interception was greater in the CTd system than in sole stands supports reports that resource capture is increased by agroforestry (Ong et al., 1996, 2006, 2007). As *f* depends on canopy architecture and tree phenology, factors which affect crop growth and canopy structure may influence the values obtained.

As shade decreased seasonal total radiation received by CTd maize by *ca.* 30% in S95/96, its photosynthetic characteristics might be expected to be intermediate between Cg 25% and Cg 50%

maize if these attributes are affected only by shade. However, substantial variation in photosynthetic competence was apparent within and between seasons. Thus, *A* and *E* for CTd maize were comparable to all sole maize treatments at the first measurement date in S95/96 and L95, but then decreased (Fig. 7). The *PPFD*-saturated *A* value for CTd maize at 25 DAS in S95/96 (30 mol m^{-2} s^{-1}; Fig. 8) was intermediate between the Cg 25% and Cg 50% treatments, whereas the equivalent value at 43 DAS (12 mmol m^{-2} s^{-1}) was *ca.* 30% of that for Cg 0% maize and occurred at *ca.* 500 as opposed to *ca.* 1100 mmol m^{-2} s^{-1}. Similarly, maximum g_s, *A* and *E* values for CTd maize at 55 DAS in S95/96 were 30–40% of those for Cg 0% maize and lower than in both shade net treatments (Fig. 6). Maximum values for all gas exchange variables are comparable to those reported for the same maize variety at another site in semi-arid Kenya (Muthuri et al., 2009). These observations suggest that the performance of CTd maize was limited by reductions in both *PPFD* and photosynthetic competence, as reflected by its almost complete failure in both seasons (Table 1).

The finding that the instantaneous radiation conversion coefficient (e_i) for maize was comparable for all treatments at 23 DAS in S95/96, but declined dramatically with time in CTd maize (Table 2a), suggests that the photosynthetic competence of CTd maize was increasingly limited by below-ground competition. Consistent with this observation, long-term *e* values were greater for the period before flowering than the equivalent seasonal values (Table 2a), substantiating reports highlighting the importance of maturation and senescence in determining the values obtained (Squire, 1990; Stirling et al., 1990; Black and Ong, 2000; Ong et al., 2007). Seasonal values were greatest in treatments containing grevillea (*ca.* 0.7 g MJ^{-1}) and within the estimated range for forest ecosystems (Black and Ong, 2000; Ong et al., 2007; Muthuri et al., 2009). Muchow (1989) reported seasonal means of 1.2 and 0.8 g MJ^{-1} for irrigated and drought-stressed maize, while values for tropical C4 cereals may reach 2.5 g MJ^{-1} under favourable conditions (Squire, 1990). The seasonal *e* values for Cg 0% and CTd maize in S94/95 (0.52 and 0.63 g MJ^{-1}) are therefore low, perhaps because planting density, chosen to maximise yield under conditions of limited rainfall, was sub-optimal in this unusually wet season. The importance of microclimate in determining crop performance is well documented (Ong et al., 1996, 2006, 2007; Black and Ong, 2000) and microclimatic and physiological variables have been included in simulation models to improve predictions of growth for a wide range of crops and environments (Spitters, 1990; Overman and Scholtz, 2002).

4.3. Balancing trade-offs between microclimatic amelioration and competition

As the trees in agroforestry systems are initially short and their canopy is small during the establishment phase, they experience competition from associated crops (Lott et al., 2000a; Ong et al., 2007) but become less reliant on current rainfall as their deep rooting, perennial habit increasingly enables them to exploit deep moisture reserves (Ong et al., 2000, 2006, 2007; Lott et al., 2003). Although trees eventually become the dominant component, competition with crops during establishment may permanently affect their growth potential (Lott et al., 2000a). Once established, the trees may buffer understorey crops against climatic extremes, reducing their transpiration rates and minimising water stress (Khalifa and Ong, 1990; Ong et al., 2006, 2007; Lin, 2007). Thus, studies of a system containing 100-year-old *Acacia tortilis* trees in northern Tanzania showed that understorey grasses benefitted from hydraulic lift by tree roots up to 10 m from the trunk in a relatively wet year but not in a drier year (Ludwig et al., 2003),

suggesting that the beneficial influence of shade trees was limited by competition for water during drought seasons. Other reports suggest that more natural agroecosystems providing greater levels of shade for understorey crops may cope more effectively with global warming than over-simplified agricultural systems (Gregory and Ingram, 2000; Lin, 2007).

However, these potential benefits are not realised when below-ground competition is severe. Much effort has been devoted to identifying species which are deep-rooting or whose leafing phenology provides temporal complementarity with crops (Broadhead et al., 2003a,b; Ong et al., 1999, 2006, 2007; Muthuri et al., 2005, 2009). Full spatial complementarity is difficult to achieve in semi-arid environments as trees may use deep soil water reserves during drought periods but often exploit surface water reserves after rainfall (Ong et al., 2006, 2007). Temporal complementarity provided by deciduous or semi-deciduous trees may offer a better solution as below-ground interactions are limited by the asynchronous demand for resources by trees and crops associated with their differing leafing phenologies. Trees which shed their leaves before the rainy season do not initially compete with understorey crops, although these may subsequently benefit from partial shade and increased soil organic matter content and fertility (Broadhead et al., 2003a,b; Ong et al., 2006, 2007). Selection criteria for *G. robusta* provenances in East Africa initially focussed on stem height, diameter and straightness, wood density, growth rate and crown diameter (Esegu and Odoul, 1992; Kallinganire and Hall, 1993), although Broadhead et al. (2003a,b) suggested that traits which improve complementarity are more appropriate. Harwood and Owino (1992) suggested that sparse and narrow crowns and deep rooting habit are desirable attributes.

4.4. Tree management

Tree pruning before planting crops is a viable management option to enforce complementarity by limiting competition during crop establishment and providing potential benefits during the cropping season. In bimodal rainfall areas, shoot pruning would most appropriately precede the season of more reliable rainfall to limit competition when crop yield is potentially greatest (Ong et al., 2006, 2007). Pruning represents a compromise between limiting tree production and promoting crop growth, although there is scope to limit adverse effects on trees while providing favourable understorey conditions; for example, tree canopies with different shapes may transpire at similar rates but have differing above-ground interactions with crops. Further studies are needed to evaluate the impact of shoot pruning on water use and tree and crop productivity.

Competition may also be limited by root pruning (Onyewotu et al., 1994; Muthuri et al., 2005; Ong et al., 2006, 2007), although this labour-intensive practice is justifiable only when trees offer attractive economic returns in the form of fruit, timber or carbon credits and long payback periods (Ong et al., 2007; TIST, 2008; Muthuri et al., 2009). Root pruning has been used successfully in densely populated upland areas in Bangladesh (Hocking, 1998) and may become increasingly attractive as farm size decreases throughout the tropics. An alternative strategy is to separate competitive trees from crops to minimise the interface between them, although this may not be possible on smallholder farms (Ong et al., 2006, 2007). Planting arrangements must take account of physical factors such as prevailing wind, solar angle, aspect and economic factors. This is particularly pertinent in the context of rapidly increasing human and livestock populations and consequent pressure on scarce rural resources at a time when climate change seems certain to further restrict their availability and impose additional stress on staple crops already grown at the upper limit of their optimum temperature range (Lin, 2007; Ong et al., 2007).

4.5. Crop selection

Although attributes which improve complementarity are important, the search for such traits must not compromise economic potential. Complementarity may be enhanced by appropriate practices, including low tree densities and management to improve economic value, without compromising crop yield. Thus, farmers in eastern Kenya have adopted intensive parkland systems containing the fast-growing indigenous species, *Melia volkensii*, to provide high value timber within 5–8 years and fodder during the dry season without apparent loss of crop yield (Stewart and Bromley, 1994). Crops grown in agroforestry systems are almost inevitably the species and cultivar best suited to the prevailing climatic conditions as sole crops, even though they may be inappropriate for the modified understorey microclimate. Any developmental delay associated with moderation of the thermal environment or reduced water supplies in the crop rooting zone may make it necessary to choose shorter duration varieties, particularly when consecutive cropping seasons are separated by only a few weeks. Crop varieties which establish rapidly and develop extensive root systems may compete more effectively with trees for below-ground resources, although such attributes may be undesirable during tree establishment when competition may permanently affect tree growth. By characterising understorey environments for the various stages within the life-span of agroforestry systems and predicted future climate change for specific regions, it may be possible to recommend specific crop species and cultivars suited for use at each stage.

5. Conclusions

Our findings show that the ameliorative influence of tree shade on understorey microclimate was greater in low rainfall seasons, as in savannah ecosystems, but that potential benefits were outweighed by below-ground competition although this may be managed by root pruning, as has been successfully demonstrated in environments similar to those projected for East Africa by current climate change models. Detailed information regarding these conflicting interactions is vital to facilitate the design of systems which maximise microclimatic benefits and minimise competition to combat the increased air temperature and unreliability of rainfall predicted by current climate change scenarios. Although the planting density of trees may be manipulated to maximise microclimatic benefits, system productivity and economic returns, crop yield must be maintained to support farmers during the long payback periods typical of agroforestry systems. The crop component is likely to continue to be planted at its optimum density as a sole crop and the trees at sub-optimal densities, even when this does not make most effective use of available resources. Further research is needed to establish optimal tree and crop densities and management practices and the extent to which these should be adjusted as systems mature.

References

Belsky, A.J., 1994. Influence of trees on savannah productivity: test of shade, nutrients, and tree grass competition. Ecology 75, 922–932.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S., Mwonga, S.M., 1989. The effects of trees on their physical, chemical and biological environments in semi-arid savanna in Kenya. J. Appl. Ecol. 26, 143–155.

Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M., Ali, A.R., 1993. Comparative effects of isolated trees on their understorey environments in high- and low-rainfall savannas. J. Appl. Ecol. 30, 143–155.

Bhatt, R.K., Misra, L.P., Pathak, P.S., 1991. Diurnal variation in transpiration and energy exchange in some tree species from a semi-arid region. Range Manage. For. 12, 79–84.

Black, C.R., Ong, C.K., 2000. Utilisation of light and water in tropical agriculture. Agric. For. Meteorol. 104, 25–47.

Brenner, A.J., Jarvis, P.G., Vandenbeldt, R.J., 1995. Tree-crop interactions in a Sahelian windbreak system. 2. Growth response of millet in shelter. Agric. For. Meteorol. 75, 235–262.

Broadhead, J.S., Black, C.R., Ong, C.K., 2003a. Tree leafing phenology and crop growth in semi-arid agroforestry systems. Agrofor. Syst. 58, 137–148.

Broadhead, J.S., Ong, C.K., Black, C.R., 2003b. Tree phenology and soil water in semi-arid agroforestry systems. For. Ecol. Manage. 180, 61–73.

Burgess, S.S.O., Adams, M.A., Turner, N.C., Ong, C.K., 1998. The redistribution of soil water by tree root systems. Oecology 115, 306–311.

Camargo, A.P., 1985. O clima e a cafeicultura no Brasil. Inf. Agropec. 11, 13–26.

Cannell, M.G.R., 1976. Crop physiological aspects of coffee bean yield—a review. Kenya Coffee 41, 245–253.

Challinor, A.J., Wheeler, T.R., Slingo, T.M., Hemming, D., 2005. Quantification of physical and biological uncertainty in the simulation of yield of a tropical crop using present-day and doubled CO_2 climates. Philos. Trans. R. Soc. B 360, 2085–2094.

Corlett, J.E., Ong, C.K., Black, C.R., Monteith, J.L., 1992. Above- and below-ground interactions in a leucaena/millet alley cropping system. II. Light interception and dry matter production. Agric. For. Meteorol. 60, 73–91.

Daynard, T.B., Duncan, W.G., 1969. The black layer and maturity in corn. Crop Sci. 9, 473–476.

Eakin, H., 2000. Smallholder maize production and climatic risk: a case study from Mexico. Clim. Change 19–36.

Esegu, O.F.I., Odoul, P.A., 1992. Baseline selection of Grevillea robusta in Western Kenya. In: Harwood, C.E. (Ed.), Grevillea robusta in Agroforestry Systems: Proceedings of International Workshop. ICRAF, Nairobi, pp. 183–188.

Gregory, P.J., Ingram, J.S.I., 2000. Global change and food and forest production: future scientific challenges. Agric. Ecosyst. Environ. 82, 3–14.

Harwood, C.E., Owino, F., 1992. Design of a genetic improvement strategy for Grevillea robusta. In: Harwood, C.E. (Ed.), Grevillea robusta in Agroforestry Systems: Proceedings of International Workshop. ICRAF, Nairobi, pp. 141–150.

Hocking, D., 1998. Trees in wetland rice fields: a successful tree management technology developed through participatory action research in Bangladesh. Agrofor. Today 10, 4–6.

Hulme, M., Dherty, T., Ngara, T., New, M., Lister, D., 2005. African climate change: 1900–2100. Clim. Change 17, 145–168.

Huxley, P.A., Pinney, A., Akunda, E., Muriya, P., 1994. A tree/crop interface orientation experiment with a Grevillea robusta hedgerow and maize. Agrofor. Syst. 26, 23–45.

Huxley, P.A., Pinney, A., Gutama, D., 1989. Development of Agroforestry Research Methodology Aimed at Simplifying the Study of Potential Tree/Crop Mixtures. Final Report, Project No. 1-432-60005613, ICRAF, Nairobi, 109 pp.

IPCC, 2007. Climate change and water. In: Bates, B., Kundzewitz, Z., Wu, S., Palutikov, J. (Eds.), Intergovernmental Panel for Climate Change. Technical Paper VI. 200 pp. http://www.ipcc.ch/ipccreports/tp-climate-change-water.htm.

Jonsson, K., Ong, C.K., Odongo, J.C.W., 1999. Influence of scattered nere and karite trees on microclimate, soil fertility and millet yield in Burkina Faso. Expl. Agric. 35, 39–53.

Jose, S., Gillespie, A.R., Seifert, J.R., Biehle, D.J., 2000. Defining competition vectors in a temperate alley cropping system in midwestern USA; 2. Competition for water. Agrofor. Syst. 48, 41–59.

Kallinganire, A., Hall, J.B., 1993. Growth and biomass production of young Grevillea robusta provenances in Rwanda. For. Ecol. Manage. 62, 73–84.

Kater, L.J.M., Kante, S., Budelman, A., 1992. Karite (Vitellaria paradoxa) and nere (Parkia biglobosa) associated with crops in south Mali. Agrofor. Syst. 18, 89–105.

Kessler, J.J., 1992. The influence of karite (Vitellaria paradoxa) and nere (Parkia biglobosa) on sorghum production in Burkina Faso. Agrofor. Syst. 17, 97–118.

Khalifa, F.M., Ong, C.K., 1990. Effect of supra-optimal temperatures on germination of pearl millet (Pennisetum glaucum (L) R.BR.) hybrids. Ann. Arid Zone 29, 279–288.

Kirschbaum, M.U.F., 1995. The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. Soil Biol. Biochem. 27, 753–760.

Kinyamario, J.I., Trlica, M.J., Njoka, T.J., 1995. Influence of tree shade on plant water status, gas exchange, and water use efficiency of Panicum maximum Jacq and Themeda triandra Forsk. in a Kenya savanna. Afr. J. Ecol. 33, 114–123.

Lin, B.B., 2007. Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. Agric. For. Met. 144, 85–94.

Lott, J.E., Howard, S.B., Black, C.R., Ong, C.K., 2000a. Long term productivity of a Grevillea robusta-based agroforestry system in Kenya. I. Tree growth. For. Ecol. Manage. 139, 175–186.

Lott, J.E., Howard, S.B., Black, C.R., Ong, C.K., 2000b. Long term productivity of a Grevillea robusta-based agroforestry system in Kenya. II. Crop growth and system productivity. For. Ecol. Manage. 139, 187–201.

Lott, J.E., Khan, A.A.H., Black, C.R., Ong, C.K., 2003. Water use by trees and crops in a Grevillea robusta-based overstorey agroforestry system in semi-arid Kenya. For. Ecol. Manage. 180, 45–59.

Ludwig, F., Dawson, T.E., Kroon, H., Berendse, F., Prins, H.H.T., 2003. Hydraulic lift in Acacia tortilis trees on an East African savanna. Oecology 134, 293–300.

McIntyre, B., Riha, S.J., Ong, C.K., 1996. Light interception and evapotranspiration in hedgerow agroforestry systems. Agric. For. Meteorol. 81, 31–40.

McNaughton, K.G., 1988. Effects of windbreaks on turbulent transport and microclimate. Agric. Ecosyst. Environ. 22, 17–39.

Muchow, R.C., 1989. Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment. II. Effects of water deficits. Field Crops Res. 20, 207–219.

Muthuri, C.W., Ong, C.K., Black, C.R., Ngumi, V.W., Mati, B.M., 2005. Tree and crop productivity in Grevillea. Alnus and Paulownia-based agroforestry systems in Kenya. For. Ecol. Manage. 212, 23–39.

Muthuri, C.W., Ong, C.K., Craigon, J., Mati, B.M., Ngumi, V.W., Black, C.R., 2009. Gas exchange and water use efficiency of trees and crops in agroforestry systems in semi-arid Kenya. Agric. Ecosyst. Environ. 129, 497–507.

Norman, M.J.T., Pearson, C.J., Searle, P.G.E., 1984. The Ecology of Tropical Food Crops. Cambridge University Press, Cambridge, UK, pp. 103–109.

Ong, C.K., Leakey, R.R.B., 1999. Why tree-crop interactions in agroforestry appear at odds with tree-grass interactions in tropical savannahs. Agrofor. Syst. 45, 109–129.

Ong, C.K., Monteith, J.L., 1985. Influence of light and temperature on pearl millet. Field Crops Res. 11, 141–160.

Ong, C.K., Anyango, S., Muthuri, C.W., Black, C.R., 2007. Water use and water productivity of agroforestry systems in the semi-arid tropics. Ann. Arid Zone 46, 255–284.

Ong, C.K., Black, C.R., Muthuri, C.W., 2006. Modifying forests and agroforestry for improved water productivity in the semi-arid tropics. CAB Reviews: Perspectives in Agriculture, Veterinary Science. Nutr. Nat. Resour. 65, 1–19.

Ong, C.K., Black, C.R., Marshall, F.M., Corlett, J.E., 1996. Principles of resource capture and utilisation of light and water. In: Ong, C.K., Huxley, P.A. (Eds.), Tree–Crop Interactions in Agroforestry Systems: A Physiological Approach. CAB International, Wallingford, UK, pp. 73–158.

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, 1–21.

Ong, C.K., Deans, J.D., Wilson, J., Mutua, J., Khan, A.A.H., Lawson, E.M., 1999. Exploring below ground complementarity using sap flow and root fractal techniques. Agrofor. Syst. 44, 87–103.

Onyewotu, L.O.Z., Ogigirigi, M.A., Stigter, C.J., 1994. A study of the competitive effects of Eucalyptus camendulensis shelterbelts on an adjacent millet (Pennisetum typhoides) crop. Agric. Ecosyst. Environ. 51, 281–286.

Orindi, V.A., Murray, L.A., 2005. Adapting to Climate Change in East Africa: A Strategic Approach. Gatekeeper Series No. 117, International Institute for Environment and Development, London, UK, 25 pp.

Ovalle, C., Avendano, J., 1987. Interactions of the tree layer with the herbaceous understorey layer in the plant-communities of Acacia caven in Chile. 1. Tree influence on the botanical composition, production and phenology of the herbaceous stratum. Acta Oecol. 8, 385–404.

Overman, A.R., Scholtz Jr., R., 2002. Mathematical Models of Crop Growth and Yield. Marcel Decker, New York, USA, 344 pp.

Peng, S., Huang, J., Sheehy, J.E., Laza, R.C., Visperas, R.M., Zhong, X., Centeno, G.S., Khush, G.S., Cassman, K.G., 2004. Rice yields decline with higher night temperature from global warming. PNAS 27, 9971–9975.

Porter, J.R., Semenov, M.S., 2005. Crop responses to climatic variation. Philos. Trans. R. Soc. B 360, 2021–2035.

Rosenzweig, C., Strzepek, K.M., Major, D.C., Iglesias, A., Yates, D.N., McCluskey, A., Hillel, D., 2004. Water resources for agriculture in a changing climate: international case studies. Global Environ. Change 14, 345–360.

Slingo, J.M., Challinor, A.J., Hoskins, B.J., Wheeler, T.R., 2005. Introduction: food crop in a changing climate. Philos. Trans. R. Soc. B 360, 1983–1989.

Spitters, C.J.T., 1990. Crop growth models: their usefulness and limitations. Proceedings of Sixth Symposium on the Timing of Field Production of Vegetables, Acta Hortic. 267, 349–368.

Squire, G.R., 1990. The Physiology of Tropical Crop Production. CAB International, Wallingford, UK, 236 pp.

Stewart, M., Bromley, T., 1994. Use of Melia volkensii in semiarid agroforestry systems in Kenya. Commonw. For. Rev. 73, 128–131.

Stirling, C.M., Williams, J.H., Black, C.R., Ong, C.K., 1990. The effect of timing of shade on development, dry matter production and light use efficiency in groundnut (Arachis hypogaea L.) under field conditions. Aust. J. Agric. Res. 41, 633–644.

TIST, 2008. Planting Trees and Improving Agriculture for Better Lives. In: http://www.tist.org/.

Vandenbelt, R.J., Williams, J.H., 1992. The effect of soil surface temperature on the growth of millet in relation to the effect of Faidherbia albida trees. Agric. For. Meteorol. 60, 93–100.

Van Noordwijk, M., Ong, C.K., 1999. Can the ecosystem mimic hypotheses be applied to farms in African savannahs? Agrofor. Syst. 45, 131–158.