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Light interception and utilization in relay intercrops of wheat and cotton

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Abstract

In China, a large acreage of cultivated land is devoted to relay intercropping of winter wheat and cotton. Wheat is sown in strips with interspersed bare soil in October and harvested in June of the next year, while cotton is sown in the interspersed paths in the wheat crop in April and harvested before the next wheat sowing in October. This paper addresses the question how strip width and number of plant rows per strip of wheat or cotton affect light interception (LI) and light use efficiency (LUE) of both component crops.

Field experiments were carried out in three consecutive years: 2002, 2003 and 2004. Light interception and productivity were estimated in monocultures of wheat and cotton and four intercropping designs differing in strip and path width as well as number of rows per strip. The intercrop systems were identified by the number of rows per strip of wheat and cotton, respectively, as 3:1, 3:2, 4:2 and 6:2. Total light interception over a season was calculated from LAI measurements, using a model for light interception in a row crop. The spatial distribution and diurnal course of light in intercrops were also measured with sensors.

Wheat monocrops intercepted 618 MJ m^{-2} photosynthetically active radiation (PAR) from 18 March to harvest in 2002, 337 MJ m^{-2} from 29 April to harvest in 2003, and 457 MJ m^{-2} from 13 April to harvest in 2004. Averaged over 3 years, wheat in the four intercrops (3:1, 3:2, 4:2 and 6:2, respectively) intercepted 83, 71, 73 and 75% as much PAR as the sole wheat. From sowing to harvest, cotton monocrops intercepted 491 MJ m^{-2} PAR in 2002, 426 MJ m^{-2} in 2003, and 415 MJ m^{-2} in 2004. Cotton in the four intercrops (3:1, 3:2, 4:2 and 6:2, respectively) intercepted 73, 93, 86 and 67% as much PAR as the sole cotton. LUE of wheat was 2.12 ± 0.14 g total dry matter MJ^{-1} PAR during the reproductive period, while that of cotton was 1.33 ± 0.02 g dry matter MJ^{-1} PAR over the whole growing period. No differences in LUE of wheat or cotton were found between systems.

The analysis indicates that the high productivity of intercrops, compared to monocultures, can be fully explained by an increase in accumulated light interception per unit cultivated area. The component crops are thus complementary in their interception of light over space and time. The model results indicate that light interception can be modified by choice of the number of crop rows per strip and strip width. The best distribution of light is attained in systems with narrow strips, a high proportion of border rows, and high planting densities of cotton. Suggestions for system improvement are given.

Keywords: Leaf are index (LAI); Light use efficiency (LUE); Photosynthetic active radiation (PAR); Intercropping; Competition

1. Introduction

China has three cotton growing areas, and in one of those, the Yellow River valley, the majority of the cotton (1.4 million ha) is grown in relay intercropping with wheat. In relay intercropping, wheat is sown in autumn and harvested in early summer of the following year. Space is left open in the wheat crop to enable sowing of cotton before the harvest of wheat, resulting in a strip-based wheat crop that covers the land incompletely. From the sowing of cotton in April, until the harvest of wheat, in June, the cotton and wheat are growing simultaneously, competing for light, water and nutrients; especially in the border rows. During this phase, which lasts about 7 weeks, the wheat crop shades the cotton plants that are still in the seedling stage. After wheat is harvested, the whole space is available for cotton, and the gaps that appear after the wheat harvest have to be bridged by the expanding leaf canopy

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of cotton. The spatio-temporal architecture of the relay intercropping system determines the pattern of light capture of both component crops.

Light interception (LI) and light use efficiency (LUE) characterize resource capture and use efficiency of cropping systems, including intercrops. In field crops, there is often a linear relationship between cumulative intercepted PAR and accumulated biomass. The slope of this relationship is called the light use efficiency (Monteith, 1977; Russell et al., 1989). Improved productivity can result from either greater interception of solar radiation, a higher light use efficiency, or a combination of the two (Willey, 1990). Light interception is sometimes increased as a result of growing two species together in one field, either as a result of a lengthening of the period of soil coverage (temporal advantage), or as a result of a more complete soil cover (spatial advantage) (Keating and Carberry, 1993). Resource use efficiency is not likely to be much affected in intercropping systems with component crops that differ in growing period, since competition between component crops is weak (Fukai and Trenbath, 1993).

In a wheat–cotton intercropping system, wheat is cropped in strips with a spare path for intercropping cotton. After wheat is harvested, the cotton crop is initially also strip structured because the plants need time to expand the canopy and bridge the space freed up by the harvested wheat. The whole cropping season includes three phases: (i) a wheat phase; (ii) an intercropping phase and (iii) a cotton phase (Fig. 1). Different relay intercropping designs are used in practice and their spatial configuration has been characterized by the number of wheat rows per strip and the number of cotton rows per strip; 3:1, 3:2, 4:2 and 6:2 (Zhang et al., 2007). Yield analyses demonstrated high land equivalent ratios: 1.28 in the 6:2 system, and 1.39 in each of the other three systems. To what extent the increased productivity of relay intercropping of wheat and cotton is determined by light interception, by light use efficiency, or by a combination of these two is unknown.

The fractions of the incoming PAR which are absorbed by canopies of component crops in intercrop systems mainly depend on leaf area index and canopy structure (Spitters and Aerts, 1983; Lantinga et al., 1999; Bastiaans et al., 2000). Although the principles are understood, Willey (1990) noted that it is a challenge to determine light capture by component crops in intercrops. Measurement is difficult, especially over a whole growing season, but several modeling approaches are available to estimate light interception in heterogeneous canopies. Wilkerson et al. (1990) describes an empirical approach based on a competitive factor and an ‘area of influence’. Detailed three-dimensional light interception models have also been developed (Whitfield, 1986; Gijzen and Goudriaan, 1989; Rohrig et al., 1999). A simplified approach, based on a block-shaped strip crop structure, was developed by Goudriaan (1977) and further elaborated by Pronk et al. (2003). This approach is used here to calculate light distribution in wheat–cotton intercrops, because it truthfully represents the geometry of this system (Fig. 1; cf. Fig. 1 in Zhang et al., 2007).

The objectives of this study are: (i) to characterize the spatial distribution of PAR in a cotton–wheat intercrop system, based

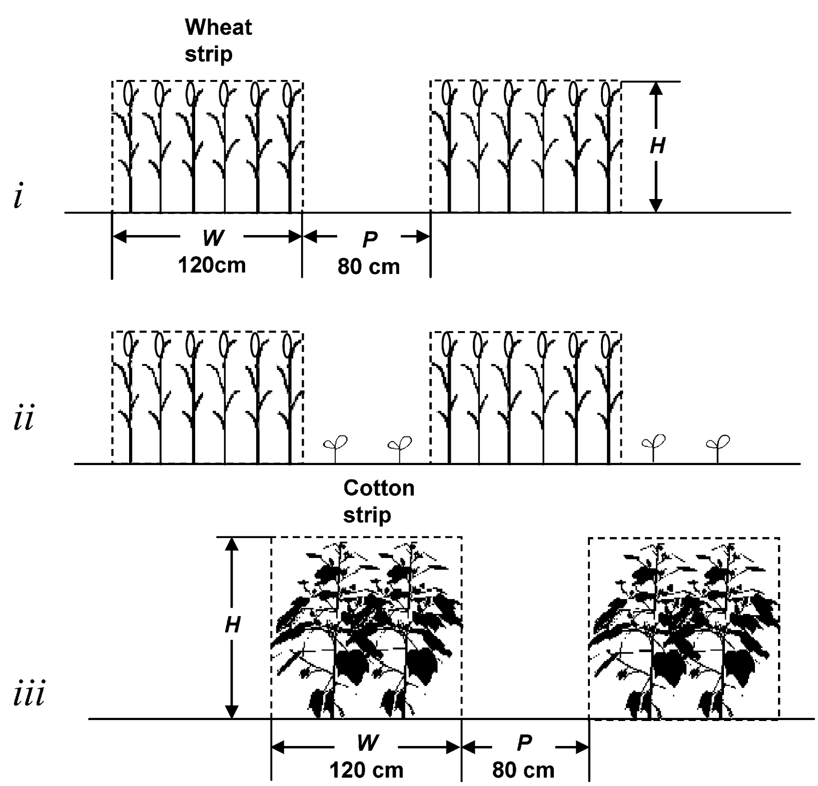

Fig. 1. Conceptual representation of the cross-row profile of a wheat–cotton relay intercrop as used in calculations of radiation interception by cotton and wheat with the row crop model (6:2 system). Crop phases: (i) wheat phase from February/March to end of April; (ii) intercropping phase from end of April to middle of June; (iii) cotton phase from middle of June to October.

on measurements during the intercropping phase; (ii) to estimate PAR interception by component crops and by both monocultures over a growing season, using a model for light interception in a row crop; (iii) to calculate LUE, based on the relationship between dry matter accumulation and cumulative intercepted radiation; (iv) to explore options for improving cropping arrangements and geometry. Null hypotheses that pertain to this work are: (i) all systems have the same light capture; (ii) all systems have the same light use efficiency. Clearly, given the high LER of these systems (Zhang et al., 2007), one of these hypotheses must be incorrect.

2. Materials and methods

2.1. Field experiments

Field experiments were conducted in 2001/2002, 2002/2003 and 2003/2004 at the Cotton Research Institute (CRI), Anyang, Henan province, China, 36°07′N and 116°22′E. The experiments comprised six cropping systems with wheat (*Triticum aestivum* L.) and cotton (*Gossypium hirsutum* L.), two of which were monocultures, while four were intercropping systems. The four intercropping patterns were characterized by the number of wheat and cotton rows that were alternated: three wheat rows:one cotton row (3:1), three wheat rows:two cotton rows (3:2), four wheat rows:two cotton rows (4:2), and six wheat rows:two cotton rows (6:2). Just as in the monoculture, distance between wheat rows in a strip was 20 cm. Systems that contained wheat strips with a larger number of wheat rows were also characterized by a larger gap-width between wheat strips. Consequently, the row length density of wheat (RLD_w) was very similar among intercropping systems, varying between 50% (3:2) and 60% (3:1 and 6:2) of the row length density of wheat in monoculture (Table 1). Gaps between wheat strips were planted with either one cotton row (3:1) or two cotton rows (all other systems). The planting of two cotton rows in the gap results in an uneven distribution of cotton rows, with a distance of 40 cm between the rows planted in the same gap and distances varying from 80 cm (3:2) to 160 cm (6:2) between adjacent cotton rows planted in neighbouring gaps. The resulting row length density of cotton (RLD_c) in intercropping systems was 1.00 m/m^2 in the 3:1 and 6:2 systems, 1.33 m/m^2 in the 4:2 system and 1.67 m/m^2 in the 3:2 system, compared to 1.25 m/m^2 in monoculture (row distance 80 cm). Detailed information on the design parameters of all systems is given in Tables 1 and 2. Maps of the various systems are given in Fig. 1 of Zhang et al. (2007). The development of cotton in different systems is described by Zhang et al. (2008b). Wheat development is expressed according to Zadoks et al. (1974).

Table 1
Geometry of wheat and cotton strips at three growth phases in wheat–cotton relay intercropping systems

Cropping system	Width of single unit (cm)	Wheat phase		Intercrop phase		Cotton phase	
		Wheat rows[a]	Wheat rows lost[a]	Gap-width between wheat rows (cm)	Distance of cotton to nearest wheat row (cm)	Cotton rows[a]	Distance between cotton rows[b] (cm)
Sole wheat	20	1	0	–	–	0	–
Sole cotton	80	0	4	–	–	1	80
3:1	100	3	2	60	30	1	100
3:2	120	3	3	80	20	2	40/80
4:2	150	4	3.5	90	25	2	40/110
6:2	200	6	4	100	30	2	40/160

[a] A single unit is defined as one complete cotton plus wheat strip. Wheat rows lost is the number of rows (20 cm width per row) that is omitted in comparison to wheat monoculture, in order to leave space for cotton.
[b] Row distance is uniform in cotton monoculture and in the 3:1 system and alternating (narrow-wide) in the other intercrop systems.

Table 2
Parameters describing density, strip width, path width and maximum plant height of component crops in wheat–cotton strip intercropping systems, as used in the model for calculating light interception

Intercropping pattern	Row length density[a]		Parameters of a strip structured canopy					
	Wheat (m m^{-2})	Cotton (m m^{-2})	Wheat (before wheat harvest)			Cotton (after wheat harvest)		
			W[b] (cm)	P[c] (cm)	H[d] (cm)	W (cm)	P (cm)	H (cm)
3:1	3	1	60	40	65	80	20	90
3:2	2.5	1.67	60	60	65	120	0	90
4:2	2.67	1.33	80	70	65	120	30	90
6:2	3	1	120	80	65	120	80	90
Monoculture	5	1.25	20	0	65	80	0	90

[a] Total row length of a component crop per unit intercrop area (m m^{-2}, or rows per meter cross-row).
[b] Strip width of each crop. For wheat, strip width is defined as the product of the number of rows and row space (20 cm). For cotton, row width is defined by taking 40 cm at each side of a cotton row.
[c] The width of the unplanted path between the strips of a crop.
[d] Maximum height of wheat and cotton. Two-weekly measurements of height were used in model calculations.

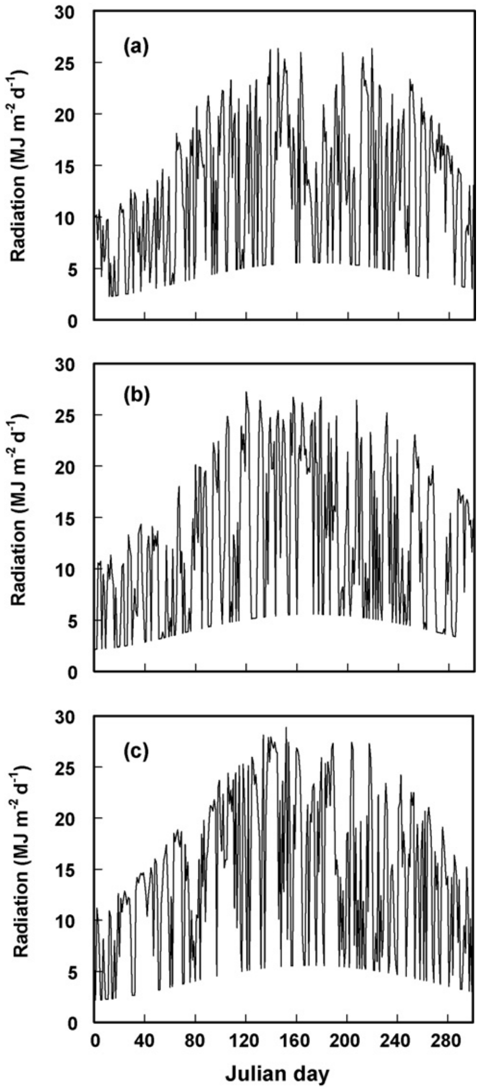

Fig. 2. Seasonal trends in estimated daily global radiation at Anyang, China, in 2002 (a), 2003 (b) and 2004 (c).

2.2. Determination of above-ground dry matter

To assess the aboveground biomass, 1-m long row sections were sampled every 2 weeks in each plot. The number of rows sampled depended on the intercropping design, such that each row in a ''minimum combination'' (i.e. one whole wheat strip plus the adjacent cotton strip) was included in the sample. Wheat samples were taken from 18 March to 10 June 2002, from 20 April to 11 June 2003, and from 13 April to 31 May 2004. Cotton samples were taken from 14 June to 18 September 2002, from 29 May to 15 September 2003, and from 17 June to 7 September 2004. First, the number of plants was counted, then a subsample of plants was randomly selected for further analyses; the wheat subsample consisted of twenty plants while the cotton subsample consisted of 10 seedlings during early growth and 3 plants later on. The samples were oven-dried at 65 °C to constant weight to determine dry matter (DM). Detailed results on dry matter and yield are presented by Zhang et al. (2007).

2.3. Light interception

2.3.1. Incoming radiation

In 2002–2004, daily global solar radiation was derived from sunshine hours, using Angstrom's equation (1924) with coefficients applicable to China (Zhou et al., 2005). Sunshine hours were measured at the experimental site. Daily incoming global radiation in 2002–2004 is presented in Fig. 2. Photosynthetically active radiation (PAR) was computed as 50% of global radiation.

In 2004, global solar radiation was measured with a pyranometer (LI-200SZ, LI-COR, Lincoln, NE, USA) and datalogger (CR10X, Campbell Sci., Logan UT). A comparison of daily incoming global radiation estimated with Angstrom's formula and measured with a pyranometer was made using data collected in 2004 (Fig. 3). The association yielded a coefficient of determination (R^2) of 0.84, a bias of -0.6 MJ m^{-2} d^{-1}, and a RMSE (root mean square error between observed and estimated values) of 2.9 MJ m^{-2} d^{-1}. Based on this result, the estimates with the Angstrom equation were deemed adequate.

2.3.2. Measurement of leaf area index

Leaf area index of wheat was determined by using the same samples as used for determining DM weight. The number of plants per m row length over the width of one wheat strip plus the adjacent cotton strip (a ''minimum combination'' to represent the whole crop), was counted. Homogenized plant density, i.e. density of one component species expressed per unit intercropping area, was then calculated by dividing the counted number of plants by the total sample area. Next, length and width of each leaf were determined on a sample of 10–12 plants from each plot. The sample consisted of 12 plants in each of the intercropping systems, equally divided over the different rows (2 per row in the 6:2 system, 3 per row in the 4:2 system, and 4 per row in the 3:1 and 3:2 systems), and of 10 plants in sole wheat. Following Miralles and Slafer (1991), leaf area was calculated as

$$\text{area} = 0.835 \times \text{length} \times \text{width}$$

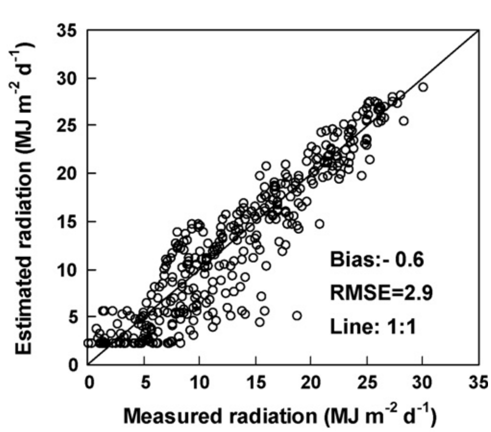

Fig. 3. Relationship between measured and estimated global radiation at Anyang, China, in 2004, as measured with a pyranometer (*x*-axis) and as estimated from measured sunshine hours using Angstroms equation (*y*-axis).

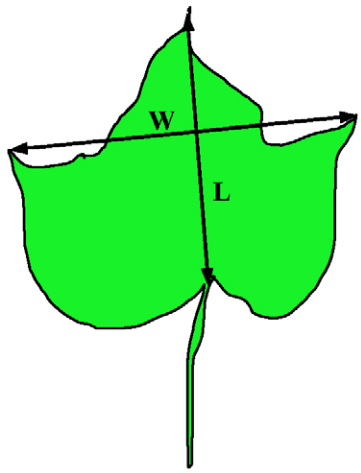

Fig. 4. Leaf length was measured from the point of attachment of the petiole to the leaf tip. Width was measured as the greatest cross-leaf distance perpendicular to the line connecting the leaf tip and the point of attachment of the leaf to the petiole.

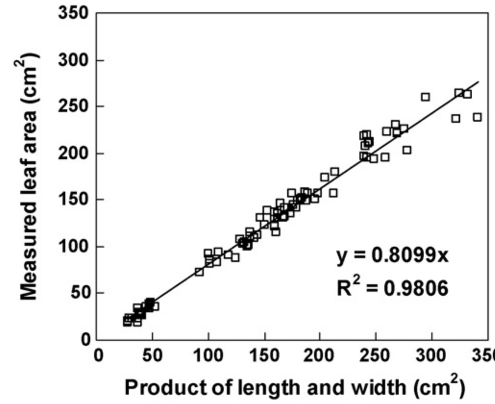

Fig. 5. Relationship between measured leaf area and product of leaf length and width in cotton.

The total leaf area per plant was determined, and LAI (m^2 leaf area per m^2 ground area) was determined by multiplying plant density (plants per m^2 ground area) with leaf area per plant (m^2 leaf area per plant). Leaf area index (LAI) was expressed as m^2 leaf per m^2 total mono- or intercrop area. In intercrops, the leaf area of a component crop was thus ''homogenized'' over the whole area of the intercrop.

Leaf area index of cotton was also based on the two weekly sampling for dry weight measurements. Length and width of each leaf were measured as indicated in Fig. 4, and leaf area was then estimated as

$$\text{area} = c \times \text{length} \times \text{width}$$

The coefficient c was estimated by collecting 59 leaves of four plants on 20 August 2004 and 29 leaves of two plants on 26 August 2004 from two cultivars 'CRI45' and '33B'. Maximum length and maximum width of all leaves of the sampled plants were measured and the areas of the individual leaves were measured with a Leaf Area Meter (AM200, ADC BioScientific Ltd., UK). The coefficient c was estimated as the slope of a regression through the origin, using measured leaf area as y-variable and the product of length and width of the leaf as x-variable. A good linear relationship through the origin was found ($R^2 = 0.98$). The estimate of the coefficient c was 0.81 ± 0.006 (Fig. 5).

2.3.3. Calculation of light interception

Cumulative light interception was computed from daily incoming radiation and the calculated fraction of intercepted radiation. The fraction of PAR intercepted daily, both for wheat and cotton, was calculated with the strip crop model of Goudriaan (1977), based on measurements of leaf area index, and parameters describing the geometry of the system (strip width; path width) and the height of the plants (Table 2). For each of the three phases of the relay intercropping it was assumed that this strip-path geometry existed (Fig. 1). During phase i (Fig. 1), the wheat rows constitute the strips (three, four or six wheat rows per strip) and the empty spaces between the strips are the paths. During phase ii, the reproductive wheat forms the strips, while the cotton seedlings occupy the path. During phase iii, the cotton rows constitute the strips (one or two cotton rows per strip) while the paths are formed by the harvested wheat strips. Dimensions are given in Table 2. Light interception in monocultures was calculated on the assumption of a homogeneous canopy.

$$f_i = 1 - \exp(k_i L_i) \quad (1)$$

where f_i is the fraction of light intercepted by the canopy, L_i the leaf area index, and k_i is the light extinction coefficient, for crop i. The value of k_i is taken to be 0.7 for wheat (Yunusa et al., 1993; Olesen et al., 2004) and 0.95 for cotton (Sadras, 1996).

Light interception by the wheat canopy was estimated from pseudo-stem erection (Zadoks scale 30) until harvest in 2002; from the beginning of anthesis (Zadoks scale 60) until harvest in 2003, and from flag-leaf sheath extension (Zadoks scale 41) until harvest in 2004, using LAI measurements made in named periods.

The output of the model is the time course of the cumulative light interception by each component crop.

The equations for light interception in a strip crop are (Goudriaan, 1977; Pronk et al., 2003):

$$f_{\text{int},i} = f_i - \frac{(f_i - f_{\text{comp},i})(S_{\text{p},i} - S_{\text{s},i})}{1 - \exp(k_i L_{\text{comp},i})} \quad (2)$$

$$f_{\text{comp},i} = \frac{W_i}{W_i + P_i}(1 - \exp(k_i L_{\text{comp},i})) \quad (3)$$

$$L_{\text{comp},i} = L_i \frac{W_i + P_i}{W_i} \quad (4)$$

$$S_{\text{p},i} = a_i + (1 - a_i)\exp(-k_i L_i) \quad (5)$$

$$S_{\text{s},i} = b_i \exp(-k_i L_{\text{comp},i}) + (1 - b_i)\exp(-k_i L_i) \quad (6)$$

$$a_i = \frac{\sqrt{H_i^2 + P_i^2} - H_i}{P_i} \quad (7)$$

$$b_i = \frac{\sqrt{H_i^2 + W_i^2} - H_i}{W_i} \quad (8)$$

where int refers to intercropping, and i is a component crop in the intercrop: wheat or cotton. $f_{\mathrm{int},i}$ is the fraction of light intercepted by a component crop with reference to the radiation incident on the whole intercropping system, f_i the proportion of incoming light intercepted by crop i in monoculture, and $f_{\mathrm{comp},i}$ is the proportion of light incident per unit of component crop area in an intercrop that is intercepted by that component crop. W_i and P_i are widths of the crop strip and the path for wheat or cotton, which are taken to be constants (Table 2), and H_i is plant height, which is input to the model according to interpolation between two-weekly measurements. L_i represents the LAI of species i in the monocrop, while $L_{\mathrm{comp},}$ represents the LAI of species i per unit area of strip in the intercrop. $S_{\mathrm{p},i}$, $S_{\mathrm{s},I}$, and a_i and b_i are intermediate variables (Pronk et al., 2003). Following Goudriaan (1977) and Pronk et al. (2003), no corrections are made for border rows.

During the intercropping phase, the young cotton plants are shaded by the wheat crop. The fraction of light interception by cotton in this phase is therefore proportional to the amount of light transmitted to the strip with cotton seedlings.

$$f'_{\mathrm{int,c}} = S_{\mathrm{p,w}} f_{\mathrm{int,c}} \quad (9)$$

where $f'_{\mathrm{int,c}}$ is LI of cotton during intercropping period, $f_{\mathrm{int,c}}$ is Eq. (2) for the cotton crop, and $S_{\mathrm{p,w}}$ is calculated according to Eq. (5) for the wheat crop.

2.3.4. Calculation of light use efficiency

LUE was calculated by regressing measured cumulative dry matter on estimated cumulative intercepted PAR, for each plot, year and system separately.

2.4. Measurement of cross-row profiles and diurnal course of radiation in intercrops

Direct measurements of radiation intensity in different intercrops were made to characterize the radiative environment at different positions in the canopy and at different times of day. Horizontal, cross-row profiles of transmitted photosynthetically active radiation (PAR, 0.4–0.7 μm) in intercrops were determined by placing a 1.0 m long quantum meter (LI-190SB line quantum sensor, LI-COR, Lincoln, NE, USA), at different positions along a transect across the rows. Sensors were placed at soil level and parallel to the crop rows. Measurements were carried out in the centre of the wheat strip, underneath the border wheat rows, midway between cotton and wheat rows, underneath cotton rows and in the centre of the cotton strip. Moreover, a reading was taken above the canopy. Placement of sensors in the 4:2 system is illustrated in Fig. 6. Measurements were made at noon on three dates (1 May, 26 May, and 12 June 2002) in the beginning, middle and end of the intercrop phase, during which the intercrop consists of a fully developed wheat canopy plus cotton seedlings in the paths between the wheat strips. The measurements illustrate the distribution of light in the path between wheat strips in different intercrop patterns. They were not used for calculating cumulative light interception.

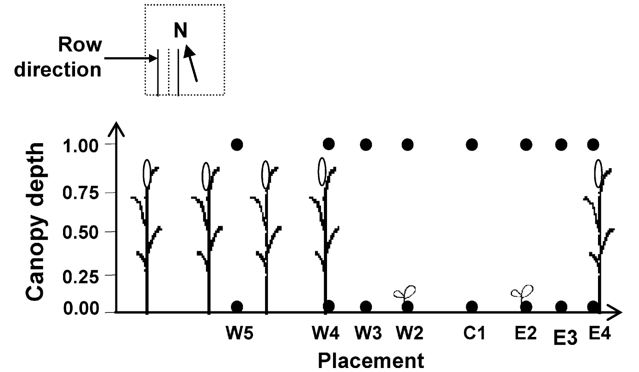

Fig. 6. Setting of PAR sensors in the wheat–cotton strip intercropping system (4:2). Letters refer to the orientation: west (W), central (C) and east (E), and the numbers indicate the sequence from the centre position of the cotton strip to the centre of the wheat strip.

The diurnal course of PAR was measured by individual quantum sensors (LI-190SZ, LI-COR, Lincoln, NE, USA) on 29 May and 12 June 2003, and on 6 May and 9 June 2004. Measurements were made while both wheat and cotton were present in the intercrop. Two measurements were made per hour. Hourly averages were recorded with a datalogger (CR23X, Campbell Sci., Logan, UT). Data were not collected in all treatments simultaneously because of the limited number of PAR sensors.

3. Results

3.1. Dynamics of leaf area index

The homogenized LAI of wheat in intercrops was lower than in monoculture (Fig. 7a, c and e). The LAI of wheat in intercrops was closely associated with the row length density, i.e. generally highest in the 3:1 and 6:2 systems ($\mathrm{RLD_w}$ = 3 m/m^2; Table 2), lowest in the 3:2 system ($\mathrm{RLD_w}$ = 2.5 m/m^2), and intermediate in the 4:2 system ($\mathrm{RLD_w}$ = 2.67 m/m^2). Thus, the LAI of wheat in intercropping systems was to a large extent determined by the relative width of the space left for cotton.

The LAI of cotton peaked around 105 DAS (days after sowing) in all systems, 5–10 d after cotton 'cut-out' (Fig. 7b, d and f). The rate of increase in leaf area in the intercropping systems after the wheat harvest was lowest in systems with a low row length density of cotton, such as the 3:1 and 6:2 systems ($\mathrm{RLD_c}$ = 1 m/m^2), and highest in the system with the greatest $\mathrm{RLD_c}$ (3:2; $\mathrm{RLD_c}$ = 1.67 m/m^2). Maximum LAIs of intercropped cotton in the 3:1 and 6:2 systems were much lower than in monoculture, reflecting the low row length density of cotton in these systems. The maximum LAIs of the 3:2 and 4:2 systems were at least as high as in monoculture, indicating that the high row length densities in these intercrops, compared to cotton monoculture (Table 2), made up for the initial, shade-induced, delay in the growth of LAI.

3.2. Light interception

The course of cumulative light interception by wheat and cotton in the six different systems, estimated with the row crop

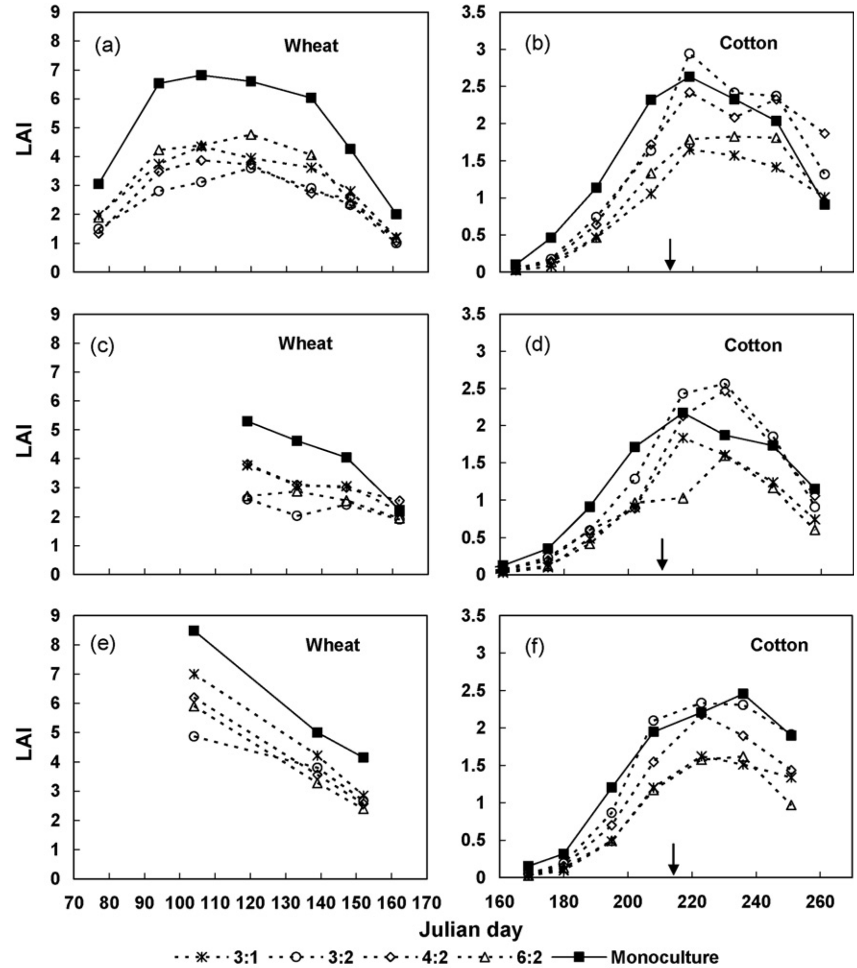

Fig. 7. Growth pattern of leaf area index (LAI) for wheat and cotton in 2002 (a and b), 2003 (c and d) and 2004 (e and f). Filled symbols indicate the monocultures of wheat or cotton. Arrows indicate the dates of cotton 'cut-out' (31 July 2002, 29 July 2003 and 1 August 2004).

model, is given for 3 years LAI and light data in Fig. 8. Monoculture wheat intercepted more light than wheat in intercrops. Wheat in the 3:1 system captured more light than wheat in the other three intercropping systems, due to the combination of a high row length density and a high proportion of border rows. Differences in light interception among the systems were consistent over the 3 years. The LI course of cotton showed an initial delay in all intercropping systems, compared to monoculture, and this delay was never fully made up for. From the harvest of wheat onwards, the LI increased faster in the 3:2 and 4:2 than in the 3:1 and 6:2 systems, reflecting differences among these systems in RLD and LAI.

The total amount of light intercepted by wheat in the different systems is given for all 3 years separately (Fig. 9a, c and e). PAR intercepted by wheat in intercrops from stem elongation to harvest ranged from 422 to 491 MJ m^{-2} in 2002, corresponding to 68–79% of the LI in the monocrop for the same period (618 MJ m^{-2}) over the same period. Differences between cropping systems were significant ($P < 0.01$) except for the 3:2 and 4:2 system in 2002, which were similar ($P = 1.0$), and the 3:2, 4:2 and 6:2 system in 2004 (no significant differences; $P = 0.57$–0.95). Averaged over the 3 years, the PAR intercepted by wheat differed significantly among all systems ($P < 0.05$) except between the 4:2 and 6:2 system ($P = 0.2$). For wheat, the amount of LI in the 3:1, 6:2, 4:2 and 3:2 systems was 83, 75, 74 and 71% of that in wheat monoculture, respectively. The lowest LI of wheat was found in the 3:2 system, being the intercrop with the lowest row length density of wheat. Light interception by wheat was significantly higher in the 3:1 system than in the 6:2 system. In both configurations 60% of the area was planted with wheat, i.e. the row length density was 60% of that in the monoculture, but in the 3:1 system the unplanted area was distributed over twice as many gaps, resulting in a much smaller gap width and twice as many border rows that were able to intercept sideways incident radiation (Zhang et al., 2007).

The amount of PAR intercepted in monoculture cotton from sowing at the end of April to the open boll stage (September) was 491 MJ m^{-2} PAR in 2002, 426 MJ m^{-2} in 2003, and 415 MJ m^{-2} in 2004 (Fig. 9b, d and f). LI in monoculture was always significantly higher than in intercrops, except for LI in the 3:2 system in 2002, which was not significantly lower than LI in the monoculture. LI in the 6:2 system was in each of the 3 years the lowest of all intercropping systems, though not significantly different from the 3:1 system in 2002. LI of cotton in the 3:2 system was always the highest of the intercrops,

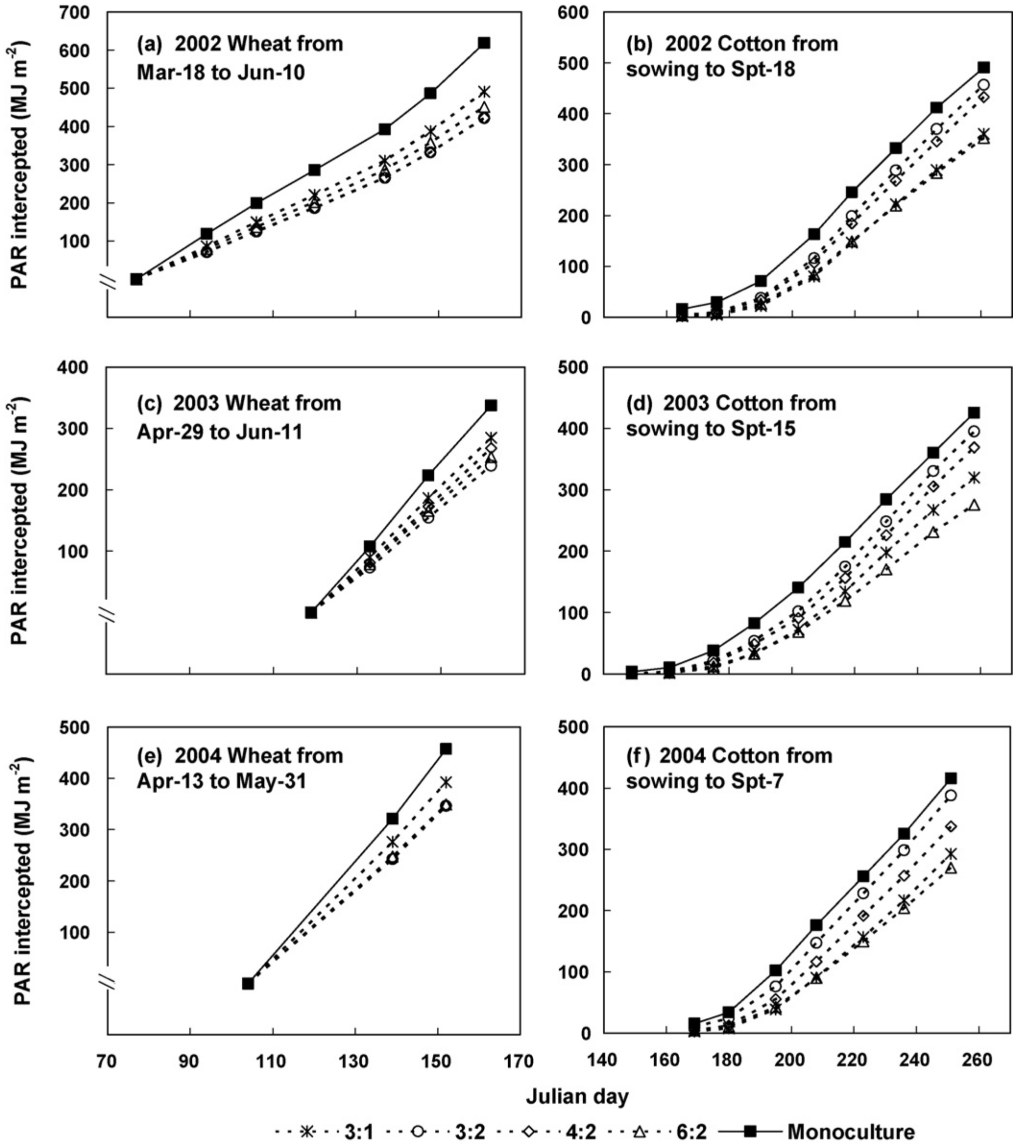

Fig. 8. Time course of estimated cumulative light interception in sole wheat and cotton and in intercrops during the LAI measurement periods from 2002 to 2004.

though not significantly different from the 4:2 system in 2002 and 2003. The 4:2 and 3:1 system held intermediate positions, whereby in each of the 3 years LI was significantly higher in the 4:2 than in the 3:1 system. Averaged over 3 years, the LI in the 3:2, 4:2, 3:1 and 6:2 systems amounted to 93, 86, 73 and 67% of the monoculture. The higher planting densities in the 3:2 and 4:2 systems helped to minimize the losses in LI, but did not compensate fully for the reduction that resulted from the delay in canopy closure in intercrops. The 3:1 and 6:2 system, having a row length density below that of the monoculture, never reached full light interception and, as a result, intercepted considerable less radiation. The even distribution of cotton rows in the 3:1 system resulted in a smaller reduction in LI than the comparatively uneven row distribution in the 6:2 system.

3.3. Light use efficiency

The LUE of wheat was estimated as the slope of a fitted linear relationship between intercepted PAR and DM for each plot and each year and system. ANOVA of LUE values, taking into account data collected in all the 3 years, showed that wheat in intercrops and monoculture did not significantly differ in LUE ($P = 0.74$). Differences between years were significant ($P = 0.004$). The interaction between cropping systems and years was borderline significant ($P = 0.058$), indicating that the effects of weather (temperature, humidity, and light) were different among systems.

The LUE of wheat from stem elongation to harvest in 2002 ranged from 2.71 to 3.43 g DM MJ^{-1} PAR in different systems (Table 3). LUE was significantly higher in the monoculture than in the intercrops in 2002 ($P = 0.02$). Averaged over 3 years, the LUEs of wheat for the intercrops and the monoculture ranged from 1.94 to 2.29 g DM MJ^{-1} PAR during the reproductive period, without significant differences between systems.

The LUE of cotton in intercropping systems did not significantly differ from that in monoculture in 2002–2004 except for a lower value in the 6:2 system in 2003 and 2004 (Table 3). Averaged over 3 years, the LUE of cotton in

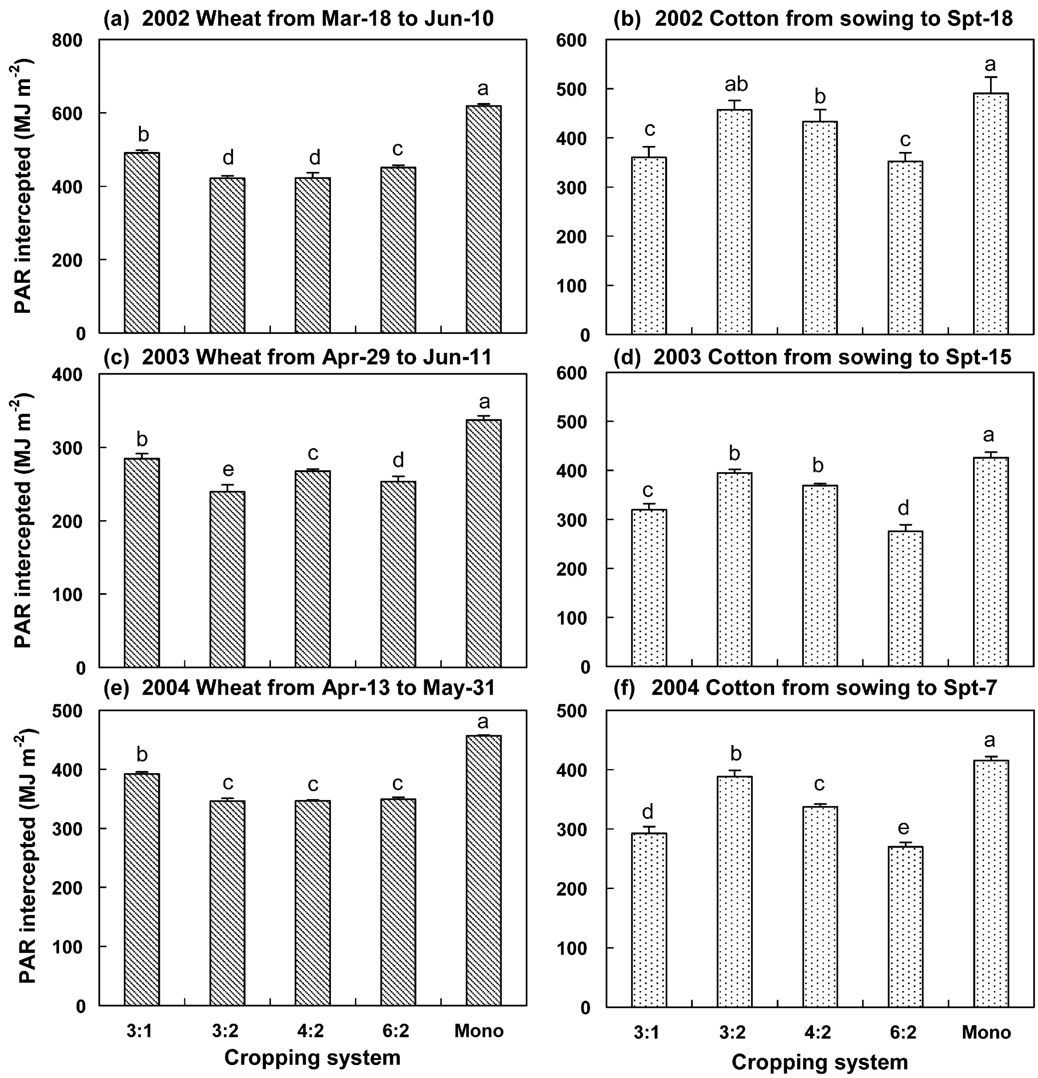

Fig. 9. Amount of PAR intercepted by wheat and cotton in the intercropping systems and the monocultures (mono) during the measuring periods in 2002–2004.

intercropping systems and the monoculture did not differ significantly ($P > 0.05$), ranging from 1.26 to 1.39 g DM MJ^{-1} PAR.

3.4. Spatial distribution and diurnal course of PAR

During the intercropping phase, PAR density varied considerably across the rows in the system (Fig. 10). At the middle of the wheat strip (W5) the fraction of light transmitted at soil level ranged from 0.17 ± 0.05 to 0.09 ± 0.03, which was slightly higher than in the monoculture of wheat (0.06 ± 0.01). From the wheat border row (E4 or W4) to the cotton row (E2 or W2; C1 in the 3:1 system), the fraction of transmitted light increased considerably, but still light intensities were considerably lower than in the monoculture cotton. Averaged from May 1 to June 12, the fraction of light transmitted by the monoculture of cotton was 0.87 ± 0.03. In the intercropping systems, measured close to the cotton row, the fraction of light transmitted was 0.32 ± 0.06 in the 3:1 system, 0.47 ± 0.07 in the 3:2 and 4:2 systems, and 0.50 ± 0.06 in the 6:2 system, illustrating the strong reduction in light intensity compared to the monoculture cotton. The differences between intercropping systems illustrate the effect of gap width between the wheat rows on shading, with comparatively strong shading in the 3:1 system, and relatively mild shading in the 6:2 system.

Diurnal courses of PAR density are shown in Fig. 11. During the intercropping phase, the lowest PAR densities occurred in the middle of the wheat strips (W5; Fig. 11b and c), due to the high leaf area index of the wheat. Low PAR densities between the cotton rows (position C1; Fig. 11a) and in the cotton rows (position E2; Fig. 11b and c) illustrate the severe shading effects of wheat on cotton seedlings. The differences in light interception between monoculture and intercrops diminished towards the end of the intercropping period as cotton LAI increased especially in monoculture. The PAR density reaching cotton had a minimum in the morning in the east rows (E2; Fig. 11a–c) and in the afternoon in the west rows (W2; Fig. 11d), illustrating the effect of north-south oriented rows on the diurnal course of the shade cast by the wheat plants.

Table 3
Light use efficiency (LUE) of wheat and cotton in intercropping systems and monoculture in 2002–2004

Year	Cropping system	LUE		
		Wheat		Cotton
		From stem elongation to harvest (g DM MJ (PAR)$^{-1}$)	During reproductive period	From sowing to boll open
2002	3:1	2.71 b	2.58 a	1.37 a
	3:2	2.83 b	2.59 a	1.29 a
	4:2	2.85 b	2.65 a	1.55 a
	6:2	2.85 b	2.36 a	1.55 a
	Monoculture	3.43 a	3.21 a	1.33 a
	S.E.	0.16	0.30	0.12
2003	3:1	n.d.	2.05 a	1.16 ab
	3:2		2.28 a	1.23 ab
	4:2		1.90 a	1.20 ab
	6:2		2.02 a	1.04 b
	Monoculture		1.41 b	1.32 a
	S.E.		0.14	0.07
2004	3:1	n.d.	1.77 ab	1.44 ab
	3:2		1.99 a	1.46 ab
	4:2		1.64 ab	1.31 ab
	6:2		1.45 b	1.20 b
	Monoculture		1.96 ab	1.52 a
	S.E.		0.16	0.08
Mean	3:1	n.d.	2.13 a	1.32 a
	3:2		2.29 a	1.33 a
	4:2		2.06 a	1.35 a
	6:2		1.94 a	1.26 a
	Monoculture		2.19 a	1.39 a
	S.E.		0.13	0.05

The same letter in the same column subdivision means no significant difference according to $LSD_{0.05}$.
n.d. = not determined.

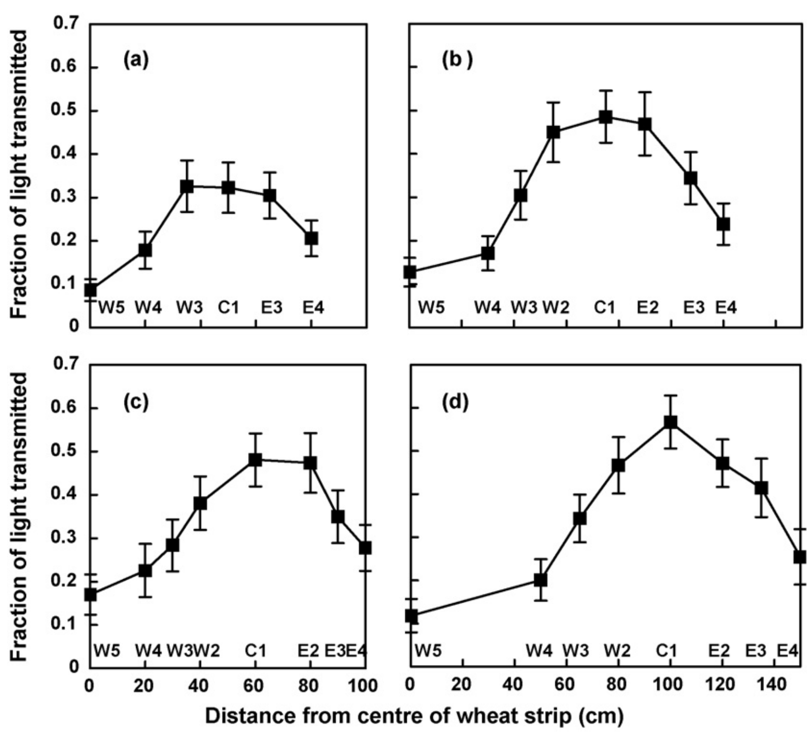

Fig. 10. Fraction of light transmitted at different placements in intercropping systems during the intercropping period (averages of data collected on 1 May, 26 May and 12 June 2002). (a) 3:1, (b) 4:2, (c) 3:2 and (d) 6:2.

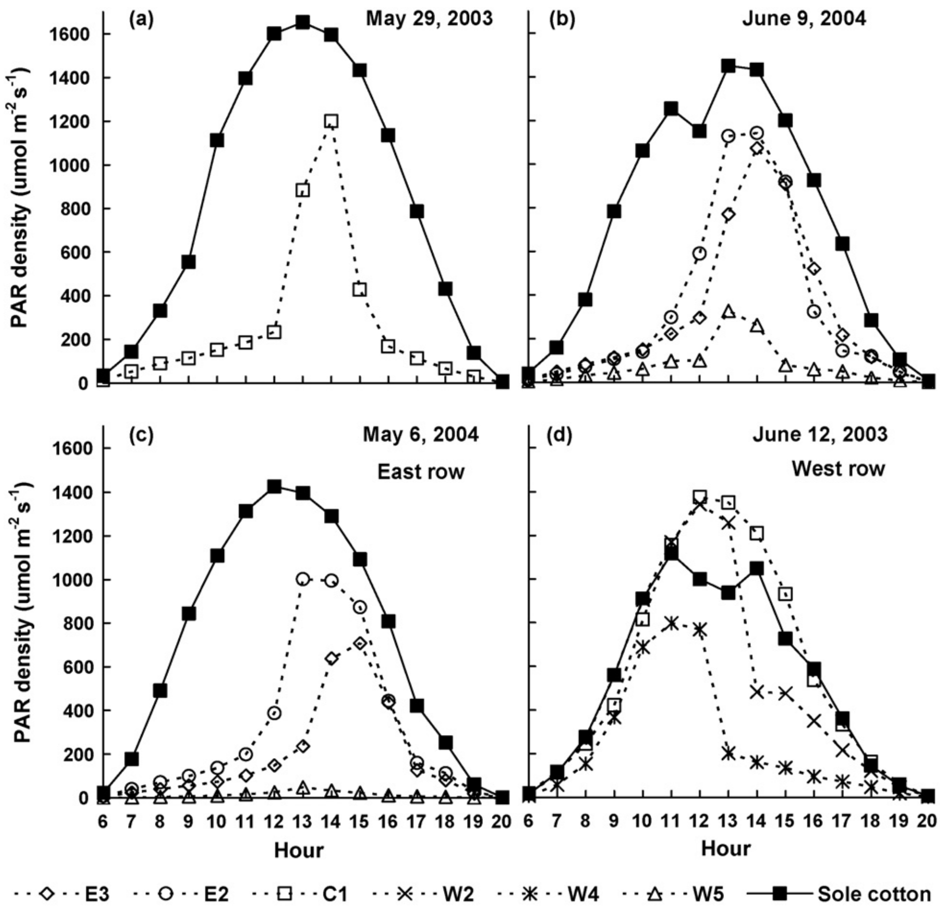

Fig. 11. Daily courses of PAR density at soil surface at different placements in wheat–cotton intercrop systems and in monoculture in 2003 and 2004. The measurements taken in sole cotton were underneath cotton rows. (a) 3:1, (b) 4:2, (c) 6:2 (positions within the cotton strip to the east of the centre of the cotton strip) and (d) 6:2 (positions within the cotton strip to the west of the centre of the cotton strip).

4. Discussion and conclusions

Averaged over 3 years, wheat in the four intercrops (3:1, 3:2, 4:2 and 6:2, respectively) intercepted 83, 71, 73 and 75% as much PAR as the sole wheat. Cotton in the four intercrops (3:1, 3:2, 4:2 and 6:2, respectively) intercepted 73, 93, 86 and 67% as much PAR as the sole cotton. Total light capture by a wheat monocrop from stem elongation after the winter until harvest is in the order of 600 MJ m^{-2}, while that of a sole cotton crop from sowing to harvest is in the order of 400–500 MJ m^{-2}. Thus, the relay intercropping of wheat and cotton increases the total capture of radiation, compared to monocultures of either crop. As no consistent differences in light use efficiency were found between monocrops and intercrops nor between the different intercropping systems, the increased light capture in intercrops can be held solely responsible for the high land equivalence ratios in wheat cotton relay intercropping.

In theory, other systems could show a similar advantage in light capture, e.g. the cultivation of a winter fodder crop between the wheat strips until the sowing of cotton, or the cultivation of a full wheat crop, part of which is harvested as fodder prior to the sowing of cotton. Currently, such systems are not compatible with the socio-economic conditions in the North China cotton production region (Zhang and Li, 1997). Relay cultivation is a common tool to press multiple crops in a single growing season, when the temperature sum barely suffices completion of the development. In the Yellow River region, corn is also often sown in the maturing wheat prior to wheat harvest. This practice allows a better labour distribution in time and it ensures an advanced start of the corn crop and a sufficient temperature sum to let it reach maturity. As the corn is more tolerant of lower temperatures and shading than cotton, the wheat crop does not need to be reduced to a strip cultivation to allow corn to be sown into the wheat.

The advantage with respect to light acquisition does not apply another resource, nitrogen. Analyses of nitrogen economy in wheat–cotton relay intercropping (Zhang et al., 2008a), demonstrate that intercropped cotton requires a greater nitrogen uptake per unit lint yield than monoculture cotton. This disadvantage is mainly due to a lower harvest index in intercropped cotton, as a result of a delayed development and fruit formation in intercrops (Zhang et al., 2008b). This delay is likely caused by the lower temperature experienced by seedlings in intercrops, as a result of shading by wheat.

It cannot be ruled out that the presence of wheat could also have small benefits for the early growth of cotton seedlings. For instance, due to shading, and providing a barrier against wind, the presence of wheat strips could diminish the evaporative demand for cotton seedlings and alleviate heat and drought stress on hot days. However, such a slight positive effect, if it exists, is dominated by negative effects of shading and cooling on development, and a reduction of the water availability in the field, due to water use by the wheat crop.

4.1. Light use efficiency of wheat and cotton

Light use efficiencies of both wheat and cotton were not affected by intercropping. This is consistent with the literature, which indicates that the LUE of dominant component crops is generally not affected in intercropping systems. Examples include millet in millet/groundnut intercrops (Willey, 1990), sorghum in sorghum/groundnut intercrops (Matthews et al., 1991), and maize in maize/cowpea intercrops (Watiki et al., 1993). The LUE of groundnut was 46% higher in an intercrop with millet than in a groundnut monocrop (Willey, 1990) and it was substantially increased also in an intercrop with sorghum (Matthews et al., 1991) probably due to the greater efficiency of C3 plants at lower light intensity. The LUE of cowpea was not affected when it was grown in an intercrop with corn (Watiki et al., 1993). The relay nature of the wheat–cotton intercrop system makes that both crops can be considered dominant for most of the time; i.e. the wheat crop does not receive any shading at all from the cotton, and although the cotton is strongly shaded during its seedling stage, the majority of light capture and dry matter production occurs in the period after harvest of the wheat, when cotton is the only and therefore dominant crop in the system.

The LUE of wheat in intercrop systems and monoculture during the reproductive period ranged from 1.94 to 2.29 g DM MJ (PAR)$^{-1}$ and ranged from 2.71 to 3.43 g DM MJ (PAR)$^{-1}$ from stem elongation to harvest in 2002. This value is close to the value of 2.6–3.1 g DM MJ (PAR)$^{-1}$ reported by Kiniry et al. (1989) and within the range from 1.8 to 4.2 g DM MJ (PAR)$^{-1}$ reported by Olesen et al. (2002) and O'Connell et al. (2004). A lower LUE in the grain-filling phase was also found for oilseed rape (Justes et al., 2000). The lower value of LUE at the end of the growing period could partly be explained by a lower photosynthetic capacity of reproductive organs compared to the leaves, while the photosynthetic rates of the leaves decline due to N-reallocation and senescence (Justes et al., 2000). Moreover, light use efficiencies during the reproductive phase of the wheat may also have been affected by supra-optimal high summer temperatures and drought stress, due to high evaporative demand, even with proper irrigation.

The LUE of cotton in intercropping systems and monoculture ranged from 1.26 to 1.39 g DM MJ (PAR)$^{-1}$, with no significant difference between intercropping and monoculture. The measured range of LUE is consistent with the range of LUE values (1.2–1.7 g MJ^{-1}) reported for various genotypes of upland cotton (Rosenthal and Gerik, 1991; Pinter et al., 1994; Sadras and Wilson, 1997).

4.2. Light interception and crop geometry

Increased light capture was shown to be the sole factor responsible for the high productivity of the wheat–cotton intercropping systems, reflected in the earlier reported high LER-values (1.28–1.39; Zhang et al., 2007) of these systems. The widths of wheat and cotton strips were found to affect total light interception as well as the distribution of captured light over both component crops. To some extent this might come as a surprise, as throughout the entire growing season of nearly 12 months, both crops are present simultaneously for only 7 weeks. In this period competition is asymmetric, with wheat affecting cotton through shading, but not reciprocally. More importantly, however, both crops influence one another indirectly by affecting each other's planting pattern. The width of the wheat strips and the distances between them determine the potential configurations of the cotton crop, after the harvest of the wheat, and vice versa: desired configurations of the cotton determine possible arrangements for the wheat. Differences in light capture and distribution of light over the two crops thus mainly result from the fraction of land area planted by each crop (reflected in the row length density), the width of individual strips and the number of rows planted per strip.

In this study, width of wheat and cotton strips were closely related, resulting in systems in which the fraction area planted with wheat was always between 50 and 60% of that in monoculture. Patterns of LAI relative to the LAI of the wheat monoculture closely resembled these values. Estimated LI of wheat in the intercropping systems was however much closer to that of the monoculture and varied between 71 and 83%. Not surprisingly, systems with a higher fraction area planted with wheat were also found to have a higher proportion of incoming radiation intercepted by wheat. The high values of LI (71–83%), compared to the relative row length density of 50–60%, mainly result from additional light interception by border rows. Indeed, the yield is higher in border rows than in middle rows (Zhang et al., 2007). Comparison of the LI of the 3:1 and 6:2 system, both with a relative row length density of the wheat of 60%, compared to monoculture, showed that a distribution of wheat in narrower strips increased light interception. This observation confirms the important role of border rows as a compensatory mechanism for LI.

The presence of wheat at the sowing of cotton, and in the seven weeks following from that, had a clear influence on the cotton seedlings. Detailed observations on light distribution in the intercrop showed that the shading effect on cotton seedlings was most severe in systems with a narrow cotton strip (3:1 system; light interception 68%), but even in the system with the widest cotton strip (6:2 system) half of the light was lost. Shading was found to have a significant effect on leaf area development of the cotton seedlings. At the time of wheat harvest this resulted in a delay of LAI growth of (Fig. 7), with modest differences between intercropping systems. Widening of the gap between wheat strips from 60 cm (3:1) to 100 cm (6:2) did not offer much relief from this delaying effect of wheat on cotton. However, an increase in density of the cotton in the

3:2 and 4:2 systems, compared to monoculture, was an effective way to enhance the LAI growth of cotton in an intercrop.

After harvest of the wheat crop, the cotton leaf area grows rapidly. Observations on LAI (Fig. 7) indicate that in this phase row length density was the most important determinant of leaf area development. In the 3:2 and 4:2 system, being systems with a plant density exceeding that of the monoculture, the increased leaf area development resulted in maximum LAIs identical to or even higher than in the monoculture cotton. Cumulative modeled light interception reached values as high as 93% (3:2 system) and 86% (4:2 system) of that of the monoculture. However, in systems with a lower row length density than the monoculture, leaf area development stayed markedly behind and cumulative LI reached values of only 73% (3:1 system) and 67% (6:2 system) of that of the monoculture. The significant difference in LI between the two last intercropping systems, which were both characterized by a row length density of 1 m/m^2, demonstrates that a more even distribution of cotton rows improves LI, though to a much smaller extent than an increase in row length density. Light capture of cotton in intercropping systems is thus markedly favoured by systems that allow for the creation of a high row length density and an even stand and a higher proportion of border rows. This asks for systems with relatively narrow wheat strips.

The light interception model used in this study provides a tool to evaluate systems as to their capture of PAR. A sensitivity analysis was conducted to investigate the effect of parameter choices on calculated light interception of intercropped cotton, by using a homogeneous canopy model and a model for light interception in a row structured canopy, using parameters presented in Table 2. It was found that the LI of intercropped cotton according to a row crop model was very close to that calculated with a homogeneous canopy model, except in the 6:2 system (Fig. 1), which is the most heterogeneous canopy of all systems, with wide gaps during the monoculture phases i and iii before and after the seven weeks of intercropping. This suggests that in systems with narrow strips and narrow paths between those strips, light interception and production are not so much limited by the heterogeneity of the leaf canopy as by the sheer magnitude of the LAI, expressed per unit intercrop area. It is concluded that increased planting density may further increase light capture in intercrops.

This study focused on the effects of strip and path width and the number of crop rows per strip on light interception and productivity. Light penetration can also be affected by the azimuth orientation of rows and strips. For instance, the growth of intercropped mungbean, that was shaded by a dominant tall maize intercrop, was favoured when rows were planted in the north-south direction (Dhingra et al., 1991). A narrower path between strips (or rows) of a taller crop might reduce the row orientation effect (Midmore, 1993). In our study, we found a PAR density difference between west and east rows in a near north-south oriented intercropping. In Northern China, farmers generally plant the rows in a North-South orientation. One advantage of this orientation is that with prevailing northerly winds, this row orientation allows greater wind speed and cooling capacity in the cotton crop during the height of summer. The cooling of the fruits is thought to minimize fruit respiration and maximize fruit retention, but this has not been firmly established. The ecophysiological consequences of row orientation deserve further attention in research.

The synthesis of results leads to the following conclusions with respect to optimal wheat and cotton intercropping systems: (i) wheat–cotton intercropping systems enjoy increased light interception in comparison to monocrops, partially by utilizing PAR during winter and spring by the wheat crop which would otherwise be 'wasted' when growing only a monoculture of cotton, and also by a comparatively high light interception by wheat when grown in strips with bare soil interspersed; (ii) total light interception is determined by the width of the strips of the component crops in relay intercropping systems; narrowing the path between the wheat strips increases light interception and yield of wheat, but it also aggravates the shading of cotton seedlings during the intercropping period; (iii) the intercropping designs 3:1, 3:2 and 4:2 are equivalent in their light capture and yield, but they allocate light acquisition and yield differently over the component crops; there is probably only limited space for improvement, and especially by techniques that would increase early development and harvest index of the cotton crop; (iv) there may be promise in systems that allow for higher radiation interception and a warmer environment for the cotton, by using cultural techniques (raised beds, plastic film). Above-mentioned options for system improvement will be investigated in future work.

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