Field Crops Research, 7 (1983) 141—160
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

RADIATION INTERCEPTION AND GROWTH IN AN INTERCROP OF PEARL MILLET/GROUNDNUT

B. MARSHALL[1]* and R.W. WILLEY[2]

[1] *O.D.A. Microclimatology Group, University of Nottingham School of Agriculture, Sutton Bonington, Loughborough, Leics. (Great Britain)*

[2] *International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru P.O. 502324, Andhra Pradesh (India)*

*Present address: Scottish Crop Research Institute, Invergowrie, Dundee, Angus
DD2 5DA (Great Britain)

(Accepted 25 January 1983)

ABSTRACT

Marshall, B. and Willey, R.W., 1983. Radiation interception and growth in an intercrop of pearl millet/groundnut. *Field Crops Res.*, 7: 141—160.

Quantum flux measurements of the transmission of photosynthetically active radiation (PAR) are presented for the monocrops and an intercrop of an 82-day millet and 105-day groundnut. The intercrop row arrangement was 1 millet : 3 groundnut and intra-row spacing of each species was the same in monocrop and intercrop. The results for PAR were compared with similar measurements of total solar radiation. A linear relation was found between the logarithms of the transmission coefficients in the two wavebands. The relation was independent of both age and structure of the canopies and was used to convert measurements of total solar radiation into quantities of PAR intercepted by the crops.

Dry weight of monocropped millet increased linearly with intercepted PAR during the vegetative and much of the reproductive phases. In contrast, dry weight of monocropped groundnut only increased linearly in the vegetative phase. During the first half of pod filling, there was no increase in dry weight despite a substantial quantity of PAR interception. In the second half, dry weight of the groundnut increased by a further 30%. Similar relations were observed for the two components of the intercrop.

On the basis of a Land Equivalent Ratio (LER) intercropping gave 28% more total dry matter (LER = 1.28) than growing the two crops separately. The processes producing the intercropping advantage are separated by defining two ratios; the Resource Capture Ratio (RCR) and the Conversion Efficiency Ratio (CER). These ratios compare, on a per plant basis, the performance of the component species in the intercrop relative to their respective monocrops in terms of the interception of radiation and the production of dry matter/unit of radiation intercepted, respectively. Per row, the millet intercepted 2.1 (RCR = 2.1) times more PAR in the intercrop than in the monocrop and used it with a similar efficiency (CER = 0.97) to produce twice as much dry matter. Per row in the intercrop, the groundnut intercepted 27% less PAR than in the monocrop (RCR = 0.73) but used it with 46% (CER = 1.46) greater efficiency to yield the same.

INTRODUCTION

Intercropping is a farming system commonly practised in the tropics. Besides providing a safeguard against failure of a single crop, greater yields per unit land area can be achieved by intercropping rather than monocropping (Baker, 1978; Reddy and Willey, 1981). Willey (1979) discussed various methods of assessing yield advantage of an intercrop and concluded that the Land Equivalent Ratio (LER) provided a practical yardstick. For a cereal/legume intercrop, such as the pearl millet/groundnut reported here, yield advantages of 25% (LER = 1.25) or more have been recorded (Reddy and Willey, 1981). However, parameters such as LER, competition ratio (Willey and Rao, 1980) or aggressivity (McGilchrist, 1965) do not identify the processes producing the advantage. To quantify these processes it is necessary to measure the amounts of resources captured and the efficiencies with which the resources are used.

For many crops, the rate of growth during the vegetative phase is directly proportional to the quantity of radiation intercepted (Williams et al., 1965; Biscoe and Gallagher, 1977). Moreover, the final dry weight and yield of a crop is often strongly related to radiation intercepted during growth (Bierhuizen et al., 1973; Scott et al., 1973). P.J. Gregory and G.R. Squire (University of Nottingham School of Agriculture, personal communication, 1982) showed that milled dry weight increased linearly with the amount of radiation intercepted during the vegetative phase provided that water was plentiful.

The varieties of millet grown in India reach a height of 1.4—1.8 m and are mature 80—100 days after sowing (DAS). In contrast, groundnuts are often low lying, rarely exceeding 0.3 m in height. Groundnuts have a slightly longer growing season of 100—110 days. Thus, when grown as an intercrop, groundnut is overshadowed by the millet for much of the time. Because the spectral composition of light is changed in passing through leaf canopies, it is necessary to measure not only the quantity but the quality of radiation incident on the groundnut in the intercrop.

Few, if any, observations of crop growth as a function of radiation intercepted are reported in the literature for legumes. Groundnut has a photosynthetic pathway which is less efficient than that of millet, and the radiative energy absorbed is used for the fixation of nitrogen as well as the synthesis of carbohydrates. The partition of this energy between the two processes is strongly dependent on the quantity of current photosynthate, so that a reduction in light intensity, or defoliation, causes drastic and immediate reductions in the rate of fixation (Hardy and Havelka, 1973; Pate, 1973; Herridge and Pate, 1977).

Since the rate of photosynthesis depends upon the quantum content of radiation in the photosynthetically active waveband (0.4—0.7 μm, usually referred to as PAR) it is appropriate to measure the fraction of the incident quantum flux intercepted by the canopies. This paper describes: the transmission characteristics of monocrop and intercrop canopies; the correlation between the quantum and total solar radiation fluxes transmitted by the canopies; and the cumulation of dry matter as a function of intercepted PAR. The radiation intercepted by the intercrop is separated between the two species and their performance compared to the monocrops in terms of the quantity of radiation intercepted and the efficiency with which the radiation is used to produce dry matter.

The present study was part of a larger project undertaken by the Cropping Systems Section at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) to determine whether intercropping pearl millet (*Pennisetum typhoides* S. & H.) and groundnut (*Arachis hypogaea* L.) led to yield advantages and to measure the utilisation of resources by the crops. The agronomic results of the experiment and an analysis of resource use have been published by Reddy and Willey (1981).

MATERIALS AND METHODS

Site and season

The experimental site was a 0.4 ha area of the field RA 10 at ICRISAT on a medium-deep alfisol. Measurements were made during the rainy season in 1978 which was characterised by rainfall of 932 mm (average 760 mm) distributed throughout growth; details of temperature, solar radiation and rainfall are given by Reddy and Willey (1981).

Crops and management

Pearl millet (cv. 'BK 560') and groundnut (cv. 'Robut 33-1') were sown on 25 June 1978 in rows 30 cm apart and running almost north/south. The intercrop consisted of one row millet and three rows groundnut with the same inter-row spacing as the monocrops while the intra-row spacing was the estimated optimum for each of the monocrops.

Details of plant density and fertiliser applications are given by Gregory and Reddy (1982).

Experimental design

The treatments were laid out in four randomised blocks. Fig. 1 shows the experimental design and sizes of the plots. The gentle slope to the south and the heavy rainfall caused problems during the early growth of the crops (particularly the groundnuts) at the southern end of blocks 3 and 4.

The blocks were divided into two portions: one portion was used for instrumentation (neutron probe, tensiometers, periscope, observation tubes and tube solarimeters) and no plants were removed from this area until the final harvest; the second portion was used for destructive har-

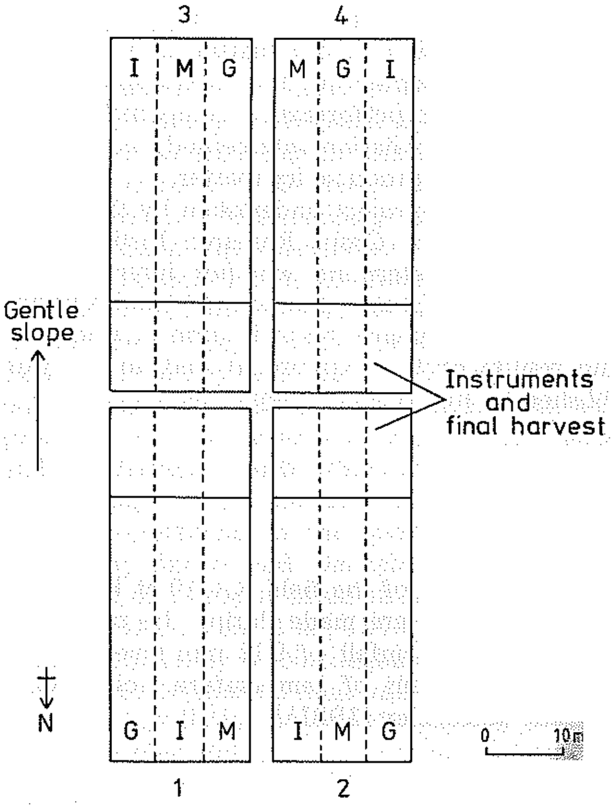

Fig. 1. Plan of the field site showing the area set aside for instrumentation; the remainder of the site was used for growth measurements. Groundnut (G), millet (M) and intercrop (I) plots are indicated.

vesting of plant material. Growth was measured every week, starting 20 Days After Sowing (DAS). A sample of monocrop comprised all the plants in 1 m of row in six adjacent rows (i.e. 1.8 m^2) and an intercrop sample was all the plants in 1 m of row in eight adjacent rows (2.4 m^2; six groundnut and two millet rows). Harvesting positions were obtained by systematically moving down the plots towards the instrumentation areas leaving 2 m between harvested areas. With this method of sampling, large differences between blocks 1 and 2, and blocks 3 and 4 were apparent in the early harvests because of the waterlogging. However, these systematic differences disappeared as the season progressed and samples in blocks 3 and 4 were taken further up the slope.

The results of the shoot growth measurements, from 33 DAS until the final harvests, are in the Appendix. Blocks 3 and 4 have not been included in the "Corrected Means" for the first five harvests. Thereafter there were no significant differences between replicates and all the blocks were included in the average. All values of dry matter in this paper refer to the corrected means.

Transmission measurements

To measure the fraction (τ_Q) of the incident quantum flux transmitted by a canopy, one Lambda quantum sensor was placed horizontally above the crop to record the incident flux density. A second instrument was placed below the foliage within an aluminium track lying on the soil surface. A figure for the mean transmission of the canopy ($\overline{\tau}_Q$) was obtained by pulling the sensor along the track and averaging a set of readings at 5 cm intervals. These measurements also gave a record of gap distribution and structure of the canopy.

The measurements were made twice weekly between 29 and 71 DAS, on the monocropped millet in block 1 and on the monocropped groundnut and intercrop of block 2. A second set of measurements was made above the groundnut in the intercrop when the millet had separated from the groundnut in the vertical plane (43—71 DAS). The aluminium track was supported on a small wooden trestle just above the groundnut so that the quantity of PAR transmitted through the millet could be calculated. The mean transmission of total solar radiation ($\overline{\tau}_T$) was measured with tube solarimeters and integrators (24 h continuous integration). The instruments were not affected by waterlogging and results from all four blocks were used throughout. Details of these measurements are given by Reddy and Willey (1981).

A series of measurements were made above the intercropped groundnut on the 18 August (54 DAS) to study the temporal variation in the transmission of PAR and total solar radiation. The values of τ_T and τ_Q changed with solar angle as expected for a stand with a marked row structure. However mean transmission coefficients, $\overline{\tau}_T$ and $\overline{\tau}_Q$ were found to be within ± 10% of the true daily mean provided the measurement is made between 08.00 and 16.00 h local time, excluding the period from 11.00 to 13.00 h when the transmission can be 15% greater than the daily average (for further details see Gregory and Marshall, 1980).

Theory

The attenuation of radiation in a crop is often assumed to obey Beer's Law of exponential decay as it passes through successive layers of leaves (Kasanga and Monsi, 1954). The transmission coefficients below a leaf area index L will be:

$$\overline{\tau}_T = \exp\left(-K^*_T L\right) \qquad (1)$$

for total solar radiation, and;

$$\overline{\tau}_P = \exp\left(-K^*_P L\right) \qquad (2)$$

for PAR, where K^*_T and K^*_P are the extinction coefficients for total solar radiation and PAR, respectively. Taking natural logarithms of equations 1 and 2 and eliminating L gives:

$$\ln(\overline{\tau}_P) = (K^*_P/K^*_T)\ln(\overline{\tau}_T) \tag{3}$$

Thus, if the assumption of an exponential decay is correct, there should be a linear relation between the logarithms of $\overline{\tau}_P$ and $\overline{\tau}_T$ with a slope equal to the inverse ratio of their extinction coefficients.

The extinction coefficient for a particular waveband is a function of both the canopy structure and the optical properties of the leaf (Goudriaan, 1977) and can be written:

$$K^*_{\Delta\lambda} = K_b(1 - \sigma_{\Delta\lambda})\,0.5 \tag{4}$$

where K_b is the extinction coefficient for black leaves that have the same leaf angle distribution as the canopy and the scattering coefficient, $\sigma_{\Delta\lambda}$, is the sum of the reflection and transmission coefficients of the leaf tissue in the waveband $\Delta\lambda$. Thus the ratio:

$$K^*_P/K^*_T = \left[\frac{1 - \sigma_P}{1 - \sigma_T}\right]^{0.5} \tag{5}$$

where σ_P and σ_T are the scattering coefficients for PAR and total solar radiation, respectively. The ratio is dependent on the optical properties of the leaves and independent of canopy structure. Taking appropriate values for σ_P and σ_T of 0.1 and 0.5, respectively, gives a value of 1.34 for the ratio of the extinction coefficients.

McCartney (1978) showed that the quantum content of PAR remained unchanged on passage through a canopy. Therefore the transmission coefficients for the quantum flux, $\overline{\tau}_Q$, and the energy flux, $\overline{\tau}_P$, of PAR will be identical. The measurements of $\overline{\tau}_Q$ made with the quantum sensors can be used to establish the ratio K^*_Q/K^*_T which will be equal to K^*_P/K^*_T in equation (3), since $\overline{\tau}_Q$ and $\overline{\tau}_P$ are interchangeable.

The continuous measurements of $\overline{\tau}_T$ made with the tube solarimeters can now be converted into values for $\overline{\tau}_P$, given an empirical value K^*_P/K^*_T. The fraction of PAR intercepted for a crop is then:

$$F'_P = 1 - \overline{\tau}_P \tag{6}$$

The prime denotes that F_P is the fraction of radiation intercepted, i.e. the sum of the reflected and absorbed components. The quantity of PAR intercepted by the crop was then given by the product of the PAR incident above the crop, S_P, during that period and the appropriate value of

F_P'. Incident PAR was not measured directly and it was assumed to equal one half of the total solar radiation incident on the crop (Szeicz, 1974a).

Fig. 2 shows the method used for partitioning the intercepted PAR between the two components of the intercrop, once there was significant interception by the millet above the groundnut. This occurred approximately 40—82 DAS (final harvest for millet).

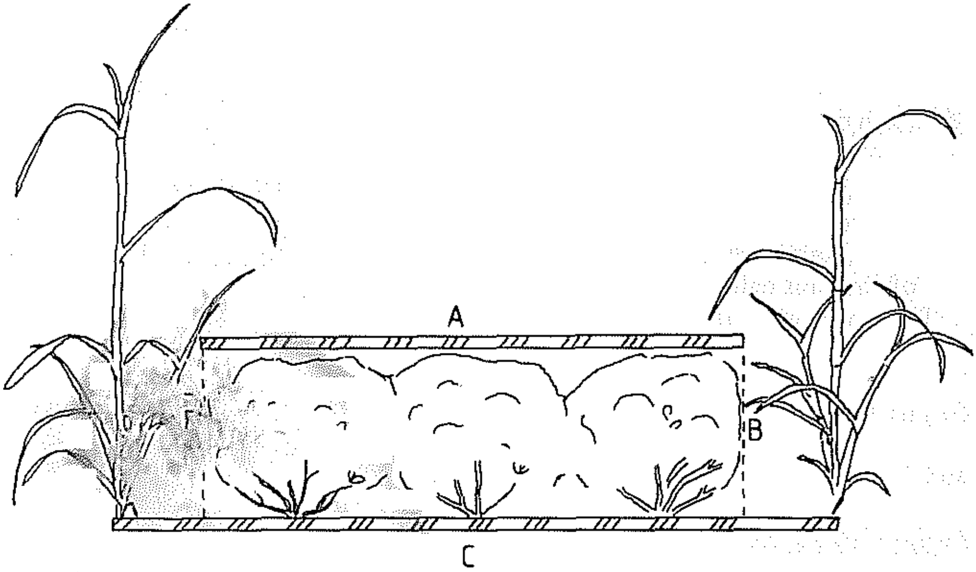

Fig. 2. Partitioning of radiation between the two components of the intercrop. The positions of the radiation measurements are indicated by the hatched bars. The quantity of PAR intercepted by the groundnut is equal to the difference between the radiation entering side A and leaving at side C, the soil surface. Net exchange of radiation at sides B and D is assumed to be negligible.

It is assumed that the groundnut canopy can be enclosed by an imaginary box, within which there are no millet leaves, of sides A and C (0.9 m in extent (and sides B and D (equal to the height of the groundnut). This assumption is supported by photographs taken against a grid, at regular intervals in time, across one unit cell of the intercrop. Second, it is assumed that there is no net exchange of radiative energy across boundaries B and D. This will overestimate the quantity of radiation intercepted by the groundnut because radiative fluxes downward are lower within the millet rows than within the groundnut. Therefore there will be tend to be a small net transfer of radiative energy out of the box across boundaries B and D. Third, it is assumed that the mean transmission coefficient beneath the intercropped groundnut, $\tau_{P,BIG}$ is equal to the mean transmission beneath the entire unit cell of intercrop, $\tau_{P,I}$. Because the transmission is lower beneath the millet rows. $\tau_{P,I}$ will be less than $F_{P,BIG}$. Thus in substituting $\tau_{P,I}$ for $\tau_{P,BIG}$, the quantity of radiation leaving the box at the soil surface will be underestimated, and the radiation intercepted by the groundnut, overestimated. However, this effect is small: the greatest difference was observed 39 DAS when $\overline{\tau}_{Q,I}$ and $\overline{\tau}_{Q,BIG}$ were 0.44 ± 0.05 (s.e.) and 0.41 ± 0.06 (s.e.), respectively. There was no difference by 50 DAS.

By definition, the fraction of PAR intercepted by the groundnut component, $F_{P,IG}$ is the ratio of the quantity of PAR intercepted by the groundnut to the total quantity of PAR incident across the unit cell of intercrop. Formally we can say:

$$F'_{P,IG} = 0.75(S_{P,AIG} - S_{P,BIG})/S_P \tag{7}$$

where S_P, $S_{P,AIG}$ and $S_{P,BIG}$ are the intensities of PAR above the canopy, and above and below the intercropped groundnut, respectively. The factor, 0.75, takes account of the fact that the box only covers three quarters of the unit cell.

The intensity of PAR above and below the intercropped groundnut are:

$$S_{P,AIG} = \overline{\tau}_{P,AIG}\, S_P \tag{8}$$

and

$$S_{P,BIG} = \overline{\tau}_{P,BIG}\, S_P \tag{9}$$

where $\overline{\tau}_{P,AIG}$ and $\overline{\tau}_{P,BIG}$ are the appropriate transmission coefficients for PAR above and below the intercropped groundnut. Substituting equations 8 and 9 into equation 7, then:

$$F'_{P,IG} = 0.75\,(\overline{\tau}_{P,AIG} - \overline{\tau}_{P,BIG}) \tag{10}$$

Because the tube solarimeters at the soil surface covered one unit cell of the intercrop the value for $\overline{\tau}_{P,I}$, which derives directly from these measurements, was used in equation 10 rather than $\overline{\tau}_{P,BIG}$. As stated in the assumptions, there is little difference between these two values.

The interception coefficient for the millet component is then

$$F'_{P,IM} = F'_{P,I} - F'_{P,IG} \tag{11}$$

i.e. the difference between the interception coefficients for the whole intercrop and the groundnut component.

RESULTS

Transmission

Fig. 3 shows the transmission of PAR, measured with the quantum sensors, on three representative days beneath three rows of millet, three

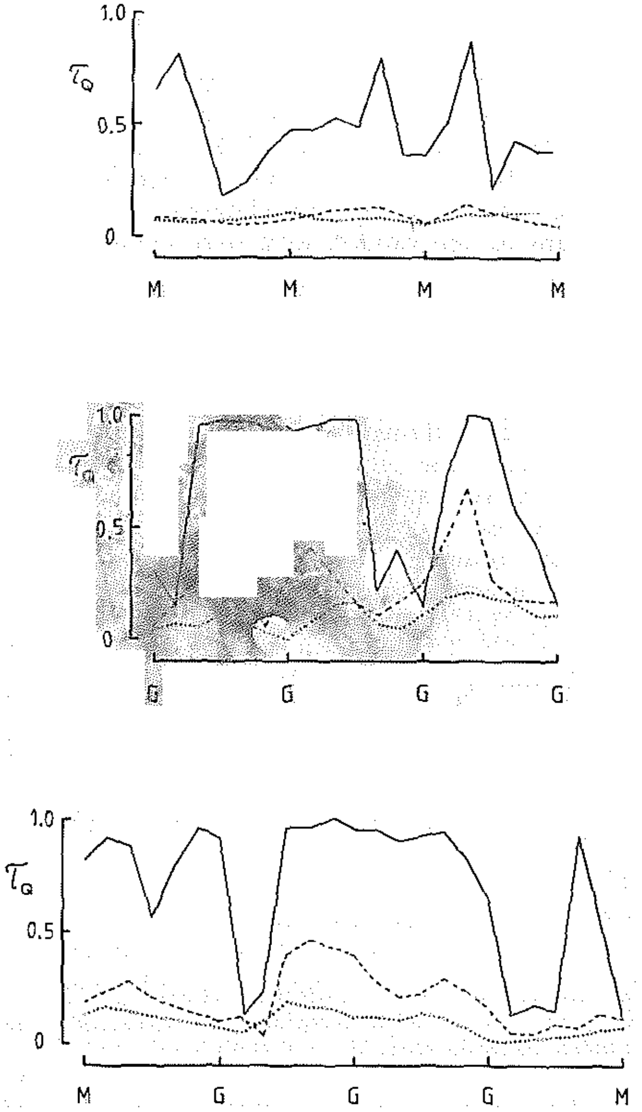

Fig. 3. Measurements of the transmission coefficients of PAR made 32 (——), 46 (- - - -) and 57 (.....) DAS, at the soil surface across three unit cells of millet and of groundnut and one unit cell of intercrop. The positions of the millet and groundnut plants are indicated by the letters M and G, respectively. The inter-row spacing is 30 cm.

rows of groundnut and four rows of intercrop. The rapid development of the millet canopy contrasts with that of the groundnut. The only evidence of row structure in the millet was at 32 DAS. Five days later (not shown) the row structure had disappeared and $\overline{\tau_Q}$ was 0.16. $\overline{\tau_Q}$ fell to a minimum of 0.07 at 46 DAS concomittant with maximum Green Leaf Area Index (GLAI) of 2.8 and remained unchanged until 57 DAS. As the crop matured there was evidence of an increase in transmission, consistent with the measurements of total solar radiation reported by Reddy and Willey (1981).

In contrast, in the groundnut stand, there was still evidence of row structure at 57 DAS. The high transmission values due to a single late developing plant (30 cm along the track) can be seen at 32 DAS. However, by 46 DAS this region was giving the lowest transmission. Missing or late emerging plants occurred at a frequency of approximately one in ten. Because of the spreading nature of the variety, gaps were closed by the time of maximum GLAI (3.2 at 60 DAS) when $\overline{\tau_Q}$ was at a minimum of 0.10.

Fig. 4 shows the variation in transmission of PAR across one unit cell above the intercropped groundnut. During the three days shown, when the intercropped millet was close to maximum GLAI of 1.8 (43 DAS), there is no significant change in the pattern of transmission. The greatest values of transmission occurred over the central row of groundnut, with significantly lower values over the groundnut rows on either side and even lower transmission values within the millet rows. This variation in transmission above the intercropped groundnut implies that each groundnut row had a unique radiation environment and possibly a unique growth rate in consequence.

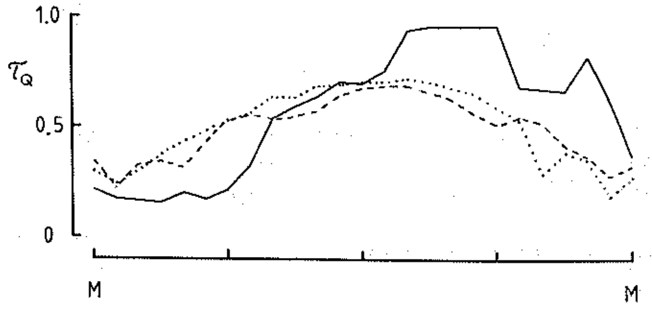

Fig. 4. Measurements of the transmission coefficients of PAR made 43 (——), 52 (- - - -) and 57 (.....) DAS, across one unit cell (120 cm) of intercrop above the groundnut. The positions of the millet plants are indicated by the letter M.

To test the hypothesis embodied in equation 3, the measurements of PAR transmission were plotted against the daily integrated values of transmission for total solar radiation on logarithmic scales (see Fig. 5). The correlation is good ($r^2 = 0.92$) and the slope of the line is 1.4 ± 0.1 with

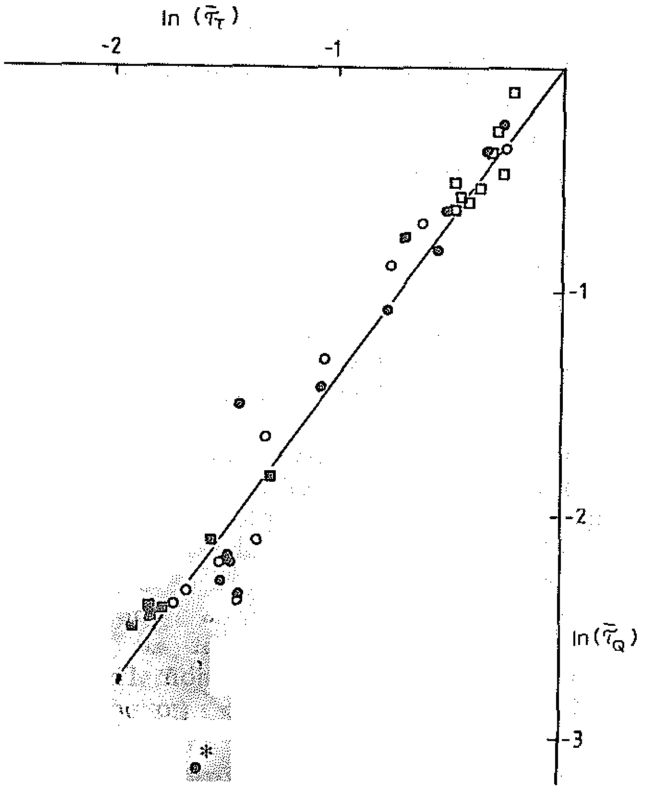

Fig. 5. Logarithmic plot of the transmission coefficients of PAR and total solar radiation throughout the season for millet (▨), groundnut (●), intercrop (○) and above intercropped groundnut (□). The regression line fitted through the origin is also shown. The value of the slope is 1.4 ± 0.1.

a zero intercept. Thus the transmission for PAR can be estimated from that for total solar radiation:

$$\overline{\tau}_P = \overline{\tau}_Q = \overline{\tau}_T^{1.4} \tag{12}$$

Despite large differences in canopy structure between the intercrop and the two sole crops the relation is independent of the canopies considered. The scarcity of points for monocropped millet (▨) at high values of transmission reflects the rapid development of this canopy early in the growing season. The millet canopy also developed rapidly in the intercrop, however, the transmission of PAR to the groundnut never fell below 40% of incident.

The error in the logarithm of a transmission coefficient, $\overline{\tau}$, due to an error in the estimate of $\overline{\tau}$, e_τ, is:

$$e_{\ln(\tau)} = (1/\overline{\tau})e_\tau \tag{13}$$

Thus for the minimum value of $\overline{\tau}_Q$ recorded (0.05, Fig. 5) any error in this estimate would be amplified in the natural logarithm by a factor twenty. The large deviation in the point for monocropped groundnut (◉*, Fig. 5) when the canopy was complete, and in the point for the intercrop (○*), recorded at a similar time, is due to an uncertainty in the value of $\overline{\tau}_Q$ of less than ± 0.05.

Growth and intercepted radiation

Fig. 6 shows the relation between dry matter accumulation of millet (A), groundnut (B) and intercrop (C) and the quantity of PAR intercepted from 33 DAS (origin) until final harvests (A — 82 DAS, B and C — 103 DAS).

In the monocropped millet, dry matter increased linearly with PAR intercepted beyond maximum GLAI. The slope of this line is a measure of the conversion efficiency of the energy intercepted into dry matter and is equal to 4.1 g (DM) MJ^{-1}. This efficiency, similar to the value for other C_4 species (Monteith, 1972) was maintained through the first half of grain filling, after which it decreased as expected because of senescence.

In contrast, dry matter accumulation of groundnut was linear only up to maximum GLAI, when pod filling also started (6[illegible] DAS) giving an efficiency of conversion of 2.5 g (DM) MJ^{-1}. From the commencement of pod filling until the pods reached half their final dry weight (82 DAS) the increase in dry weight was slight compared to the large amount of radiation intercepted in the same period but thereafter there was an apparent increase in efficiency of energy conversion.

In the intercrop, GLAI reached a maximum 61 DAS. The initial slope of 4.3 g (DM) MJ^{-1} is close to that for the sole millet at the same stage. There was no increase in dry matter from 68 to 82 DAS when the millet component was harvested. The groundnut then produced a further 1 t (DM) ha^{-1} before final harvest (103 DAS) — equivalent to 25% of its total dry weight. More than 50% of the total dry matter accrued in the period from 40 to 82 DAS when the groundnut experienced considerable shading by the millet canopy.

Reddy and Willey (1981) showed, on the basis of LER, that intercropping gave 28% more total dry matter per unit of total solar radiation intercepted. To identify which component was responsible for this increased efficiency it was necessary to partition the intercepted radiation appropriately between the groundnut and millet canopies. Further, this allocation must be in terms of PAR since the quality of light, in terms of the ratio of PAR to total solar radiation, reaching the groundnut was reduced by the millet foliage above. To enable the radiation to be separated the following assumptions were made: from 33 to 40 DAS the intercepted PAR was divided according to the interception coefficients (estimated from the LAI's on a per row basis) of the two canopies; from 40 to 47

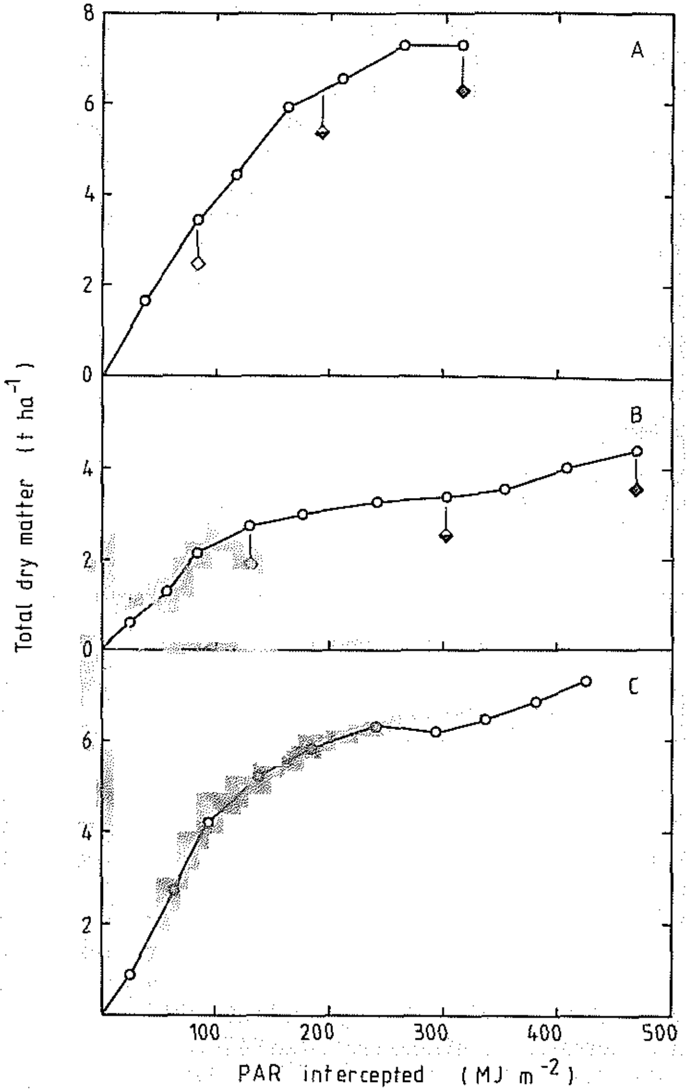

Fig. 6. Accumulated dry matter as a function of the quantity of PAR intercepted for millet (A), groundnut (B) and intercrop (C). The accumulations were started from 33 DAS (origin) until final harvest. The start (◇), midpoint in time (◈) and finish (◆) of grain or pod filling are indicated.

DAS an average value of 0.65 was used for $\overline{\tau}_{P,AIG}$, based on quantum flux measurements made at 43 and 47 DAS, and from 40 to 82 DAS the interception of PAR by the groundnut was taken to be equal to all the radiation entering the groundnut rows from above minus the radiation leaving the groundnut rows at the soil surface (see Theory section and equation 10). The remainder of the radiation intercepted by the intercrop was allocated to the millet.

Fig. 7 shows the dry matter accumulated for the two components plotted against intercepted PAR. The shape of the two curves are similar to their corresponding monocrops. The groundnut in the intercrop attained the same dry weight per row as the monocrop, but with less PAR. Therefore the groundnut used the intercepted PAR more efficiently. On the other hand, the millet produced double the dry weight per row by final harvest compared to the monocrop. However, this was achieved by intercepting more PAR and not through an overall increase in efficiency.

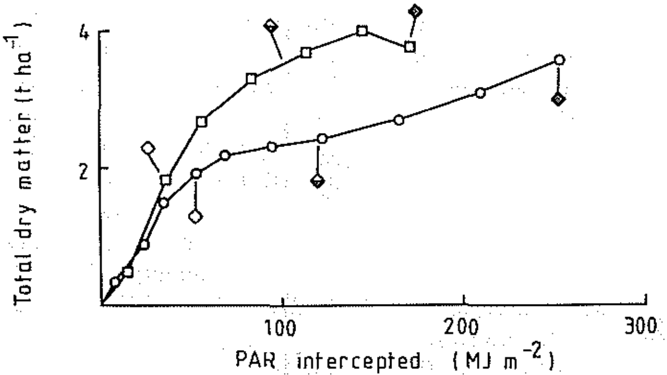

Fig. 7. Accumulated dry matter as a function of the quantity of PAR intercepted for the two components of the intercrop (□, millet; ○, groundnut). The start (◇), midpoint in time (◈) and finish (◆) of grain or pod filling are indicated.

The weekly mean values of efficiency of dry matter production are infrared radiation (IR). PAR is strongly absorbed by leaf tissue — the ciency for the millet in the intercrop increased compared to that of the monocrop, around maximum GLAI (45 DAS). If this increase was real, it is possible that the lower leaves of the millet in the intercrop senesced less rapidly than the corresponding leaves of the monocrop because they were better illuminated. However, there was no difference in the overall efficiencies of the two millet canopies. The groundnut within the intercrop showed consistent increases in efficiency from 47 DAS through to final harvest.

The processes producing the intercropping advantage can be separated by defining two ratios. First, the Resource Capture Ratio (RCR) which is the quantity of radiation intercepted per row by a component of the intercrop relative to that in the corresponding monocrop; and second, the Conversion Efficiency Ratio (CER) which is the efficiency with which the intercepted radiation is converted into dry matter in the intercrop relative to that in the monocrop. The product of the proportion of intercrop originally allocated to a component and the two ratios, RCR and CER, gives the LER of that component. The overall LER for the intercrop is then given by the sum of the component LER's. Table II summarises the performance of the millet and groundnut components in the in-

TABLE I

Weekly mean values of dry matter production per unit of PAR intercepted for monocrops and components of the intercrop (g/MJ)

Days after sowing	Millet		Groundnut		Intercrop combined
	Monocrop	Intercrop	Monocrop	Intercrop	
33—40	4.2	3.4	2.5	3.9	3.6
40—47	4.0	6.0	2.4	3.2	4.8
47—54	2.9	4.4	2.5	5.0	4.7
54—61	3.3	2.1	1.4	2.5	2.3
61—68	1.3	1.5	0.5	1.2	1.4
68—75	1.4	1.1	0.5	0.6	0.9
75—82	0.1	-1.0	0.2	0.2	-0.4
82—89			0.4	0.8	0.8
89—96			0.8	0.9	0.9
96—103			0.7	1.0	1.0
33—103	2.30	2.23	0.95	1.38	1.72

TABLE II

Summary of the performance of the intercrop components relative to the monocrops for the period 33 to 103 days after sowing; LER is the Land Equivalent Ratio

	Millet	Groundnut
Component Proportion	0.25	0.75
Resource Capture Ratio	2.12	0.73
Conversion Efficiency Ratio	0.97	1.46
Component LER	0.51	0.80
Intercrop LER	1.31	

tercrop. The two major mechanisms producing the *intercropping* advantage are the high RCR of 2.12 for millet and the high CER of 1.46 for groundnut. If either of these mechanisms had not operated there would have been no intercropping advantage. The value of 1.31 for the intercrop LER refers to the period 33—103 DAS. The LER for the whole season, 0—103 DAS, is slightly lower at 1.28.

DISCUSSION AND CONCLUSIONS

Transmission

Referring to equation 5, the ratio K_P^*/K_T^* is relatively insensitive to the value of σ_P. In going from a high value of 0.2 for σ_P to the other extreme of zero (i.e. complete absorption of PAR) the ratio changes only from 1.26 to 1.41, when $\sigma_T = 0.5$. The ratio is more sensitive to the value of σ_T. However, σ_T is a conservative quantity. The energy content of total solar radiation is equally divided between the two wavebands of PAR and infrared radiation (IR). PAR is strongly absorbed by leaf tissue — the value of σ_P tends to zero. In contrast, IR is only weakly absorbed — the value of σ_{IR} tending to unity. Thus the scattering coefficient for the whole spectrum (σ_T) is 0.5, the average of the two wavebands and independent of the age of the leaf tissue.

The conservative nature of the ratio K_P^*/K_T^* is also demonstrated by Sceicz's (1974b) measurements: The ratio can be calculated for LAI's ranging from 1 to 8 and for several crops (sugar beet, field beans, kale and spring wheat). The ratio was found to be invariant and equal to 1.4 ± 0.04, except for sugar beet where there were only three observations and the ratio was 1.5. These values agree with our results where the ratio was 1.4 ± 0.1. Thus for many crops over a wide range of LAI and canopy structure the relation in equation 12 can be used.

Radiation interception and growth

The accumulation of dry matter in the two millet stands was proportional to the quantity of radiation intercepted during the vegetative and early reproductive phases. The millet intercepted 2.1 times more PAR per row in the intercrop than in the sole crop and used the intercepted radiation with almost the same efficiency. The distribution of dry matter in the millet plant was considerably affected by the greater quantity of radiation available per plant in the intercrop. There was 50% more dry weight in the main stem and three times as much in the tillers. Overall, the total dry weight per plant was doubled. A greater number of grain-bearing tillers (2.2 and 1.3 per plant in the intercrop and monocrop plants respectively) as well as a greater number of grains per head accounted for the doubling in yield per plant. The low harvest index of 0.26 was not changed (for further details see Reddy and Willey, 1981).

For groundnut, a legume, the relation between dry matter production and intercepted radiation was not linear. The apparent fall in efficiency of energy conversion at the start of pod filling could not be attributed to senescence of leaf tissue because leaves were green well into pod filling and because the quantity of dry matter produced per unit of PAR intercepted increased after the pods reached half their final dry weight. The groundnut in the intercrop intercepted 27% less PAR over the season and was growing in weaker light. The combined effect of these two processes should be to produce less dry matter per row but with greater efficiency. Precisely how much less depends upon the shape of the photosynthesis-light response of the canopy. In fact, the groundnut gave the same yield per row in the intercrop and monocrops and went on to produce dry matter with greater efficiency after the millet was harvested. Overall the groundnut was 47% more efficient in the intercrop — an increase greater than expected for a C_3 canopy growing in 50% shade (Biscoe and Gallagher, 1977).

When the groundnut was in partial shade the developmental time was not affected but the quantity of energy absorbed by the foliage was considerably reduced. A decrease of intercepted radiation can affect the partitioning of photochemical energy between the processes of dry matter accumulation and nitrogen fixation (Hardy and Havelka, 1973; Sprent, 1973). This balance is especially critical during pod filling when there is a large sink for carbohydrate as well as nitrogen (Pate, 1973; Herridge and Pate, 1977). It is of interest that Dart (1981) showed that in the intercrop the groundnut had a much slower rate of nitrogen fixation per plant than in the monocrop. Therefore there must have been a greater uptake of nitrogen from the soil because total nitrogen per plant was similar in both mono- and intercropped groundnut (Reddy and Willey, 1981). To understand the processes responsible for the increased efficiency of groundnuts in an intercrop, it will be necessary to measure, in the field, both the carbon economy of the plants, with particular reference to the response of leaf photosynthesis to light, and the nitrogen economy in terms of uptake and fixation.

In conclusion, the increased interception by the millet (RCR > 1) and the greater efficiency of the groundnut (CER > 1) were equally responsible for the intercropping advantage.

ACKNOWLEDGEMENTS

We thank the Overseas Development Administration and ICRISAT for financing the visit of B. Marshall and are grateful to Professor J.L. Monteith for his encouragement in this project and preparation of this paper. The help of M.S. Reddy in supervising the experiment and carrying out the growth analysis is gratefully acknowledged.

REFERENCES

Baker, E.F.I., 1978. Mixed cropping in Northern Nigeria. I. Cereals and groundnuts. Exp. Agric., 14: 293—298.

Bierhuizen, J.F., Ebbens, J.L. and Koomen, N.C.A., 1973. Effects of temperature and radiation on lettuce growing. Neth. J. Agric. Sci., 21: 110—116.

Biscoe, P.V. and Gallagher, J.N., 1977. Weather, dry matter production and yield. In: J.J. Landsberg and C.V. Cutting (Editors), Environmental Effects on Crop Physiology. Academic Press, New York, NY, pp. 75—100.

Dart, P.J., 1981. Nitrogen fixation in intercropping. International Intercropping Workshop, ICRISAT, 10—14 January 1981, Hyderabad, India.

Goudriaan, J., 1977. Crop Micrometeorology. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands, 249 pp.

Gregory, P.J. and Marshall, B., 1980. A study of an intercrop of pearl millet and groundnut with special reference to the interception of radiation and the growth of root systems. Rep. 3, O.D.A. Microclimatology Unit, University of Nottingham School of Agriculture, 48 pp.

Gregory, P.J. and Reddy, M.S., 1982. Root growth in an intercrop of pearl millet/groundnut. Field Crops Res., 5: 241—252.

Hardy, R.W.F. and Havelka, U.D., 1973. Photosynthate as a major factor limiting nitrogen fixation by field-grown legumes with emphasis on soybeans. In: P.S. Nutman (Editor), Symbiotic Nitrogen Fixation in Plants. IBP 7, Cambridge University Press, London, pp. 421—439.

Herridge, D.F. and Pate, J.S., 1977. Utilisation of net photosynthate for nitrogen fixation and protein production in an annual legume. Plant Physiol., 60: 759—764.

Kasanga, H. and Monsi, M., 1954. On the light transmission of leaves, and its meaning for the production of matter in plant communities. Jpn. J. Bot., 14: 304—324.

McCartney, H.A., 1978. Spectral distribution of solar radiation to global and diffuse. Q.J.R. Meterol. Soc., 104: 911—926.

McGilchrist, C.A., 1965. Analysis of competition experiments. Biometrics, 18: 975—985.

Monteith, J.L., 1972. Solar radiation and productivity in tropical ecosystems. J. Appl. Ecol., 9: 747—766.

Pate, J.S., 1973. Physiology of the reaction of nodulated legumes to environment. In: P.S. Nutman (Editor), Symbiotic Nitrogen Fixation in Plants. IBP 7, Cambridge University Press, London, pp. 335—360.

Reddy, M.S. and Willey, R.W., 1981. Growth and resource use studies in an intercrop of pearl millet/groundnut. Field Crops Res., 4: 13—24.

Scott, R.K., English, S.D., Wood, D.W. and Unsworth, M.H., 19[illegible]. The yield of sugar beet in relation to weather and length of growing season. J. Agric. Sci., Camb., 81: 339—347.

Sprent, J.I., 1973. Growth and nitrogen fixation in *Lupinus arboreus* as affected by shading and water supply. New Phytol., 72: 1005—1022.

Szeicz, G., 1974a. Solar radiation for plant growth. J. Appl. Ecol., 11: 617—636.

Szeicz, G., 1974b. Solar radiation in crop canopies. J. Appl. Ecol., 11: 1117—1156.

Willey, R.W., 1979. Intercropping — its importance and research needs. Part 1. Competition and yield advantages. Field Crop Abstr., 32: 1—10.

Willey, R.W. and Rao, M.R., 1980. A competitive ratio for quantifying competition between intercrops. Exp. Agric., 16: 117—125.

Williams, W.A., Loomis, W.G. and Lepley, C.R., 1965. Vegetative growth of corn as affected by population density. II. Components of growth, net assimilation rate and leaf area index. Crop Sci., 5: 215—219.

APPENDIX

TABLE A I

Monocropped groundnut total dry matter (kg/ha)

Days after sowing	Block				Mean	Corrected mean
	1	2	3	4		
33	372	636	183*	188*	345	504
40	950	1203	444*	375*	743	1077
47	1629	2128	1127*	1051*	1484	1879
54	2410	2874	1841*	1601*	2182	2642
61	3205	3273	2727*	2681*	2972	3239
68	3511	3862	3186	3413	3493	3493
75	3683	4344	3543	3582	3788	3788
82	3973	4345	3681	3646	3911	3911
89	4446	4599	3628	3729	4101	4101
96	4929	5208	3852	4215	4551	4551
103	5067	5776	4278	4630	4938	4938

Values marked * are rejected in the calculation of the "corrected mean". See Section Experimental design for explanation.

TABLE A II

Monocropped millet total dry matter (kg/ha)

Days after sowing	Block				Mean	Corrected mean
	1	2	3	4		
33	884	783	149*	381*	549	834
40	2413	2481	1041*	1277*	1803	2447
47	4041	4455	3641*	4455*	4148	4248
54	5240	5258	4642*	5986*	5282	5249
61	6602	6869	6218*	6445*	6534	6736
68	7386	7328	7302	7397	7353	7353
75	8363	7914	8039	8097	8103	8103
82	8371	8644	7660	7860	8134	8134

Values marked * are rejected in the calculation of the "corrected mean". See Section Experimental design for explanation.

TABLE A III

Intercrop groundnut total dry matter (kg/ha)

Days after sowing	Block				Mean	Corrected mean
	1	2	3	4		
33	326	459	156*	267*	302	393
40	662	904	405*	414*	596	783
47	1092	1475	655*	890*	1028	1284
54	1792	2011	956*	1165*	1481	1902
61	2174	2449	1686*	1866*	2044	2312
68	2577	2773	2313	2485	2532	2532
75	2780	3001	2646	2345	2693	2693
82	2489	3118	2638	2707	2738	2738
89	3121	3516	2839	2912	3097	3097
96	3463	3916	3228	3405	3503	3503
103	3767	4483	3630	3872	3938	3938

Values marked * are rejected in the calculation of the "corrected mean". See Section Experimental design for explanation.

TABLE A IV

Intercrop millet total dry matter (kg/ha)

Days after sowing	Block				Mean	Corrected mean
	1	2	3	4		
33	178	285	106*	140*	177	232
40	649	764	301*	454*	542	707
47	1934	2160	1047*	1799*	1735	2047
54	2868	2964	2293*	2350*	2619	2916
61	3282	3736	3223*	2998*	3310	3509
68	3979	4147	3853	3680	3915	3915
75	4313	4515	4365	3809	4251	4251
82	4058	4210	3963	3702	3983	3983

Values marked * are rejected in the calculation of the "corrected mean". See Section Experimental design for explanation.