Plant growth and development in relation to the microclimate of a sorghum/groundnut intercrop

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ABSTRACT

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An intercrop of one row of sorghum (Sorghum bicolor (L.) Moench) and three rows of groundnut (Arachis hypogaea (L.)) and sole crops of the two species were grown with limited water supply on an alfisol in central India. The faster growth rate of intercropped sorghum was the result of a greater fraction of light being intercepted rather than a higher efficiency (e) of conversion of light into dry matter. In intercropped groundnut, there was a strong correlation between the growth rate of each row and the fraction of light it intercepted, and although shading by the sorghum reduced the latter in comparison with the sole crop, e was higher.

Two patterns of response were evident in the intercropped groundnut. Those involving resource use (light and water) and dry matter production were lowest in the outer two rows and highest in the centre row, while those involving development (e.g. pod numbers) increased from the least shaded row to the most shaded. Competition for water by the more aggressive sorghum was thought to be responsible for the first response, and temperature and water potential gradients caused by differing degrees of shading for the second. The effect of the interaction of these two responses on the harvest index is discussed.

INTRODUCTION

Intercropping is practised widely by subsistence farmers in tropical regions. Not only can such systems produce higher yields than monocropping (Reddy

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and Willey, 1981), but yields are often more stable (Rao and Willey, 1980) than the sole crops. It has been generally accepted that higher yields are due to spatial and temporal "complementarity" (Willey, 1979); i.e. that each component of the mixture is able to make use, either in time or space, of resources such as water, light and nutrients, that the other component is unable to utilise.

However, while there is little doubt that complementarity is a major factor, the possibility of modification of the microclimate within the intercrop, and the effect this might have on the growth of the component species, has received scant attention. This factor may be of special importance when shading occurs, for example, when a short legume is grown with a tall cereal. Protection of the shorter crop from extremes of solar radiation and temperature may also contribute to greater yield stability.

Passing references to the importance of microclimate modification in relation to species mixtures have been made (e.g. Huxley, 1983; Brunig and Sander, 1983), and Stigter (1984) has discussed the role of shading in the manipulation of microclimate in traditional farming systems. As part of an on-going investigation into intercropping at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Harris and Natarajan (1987) described the microclimate in an intercrop of sorghum and groundnut, and identified lower temperatures resulting from shading as a possible cause of intercrop advantage. This paper describes subsequent work examining the effect of microclimate on the growth and development of individual rows within a similar intercrop of sorghum and groundnut. The capture of water and light and the efficiencies of their use in the production of dry matter on an area basis in relation to this work are discussed in more detail elsewhere (Azam-Ali et al., 1990).

MATERIALS AND METHODS

Experimental design and management

Before sowing, a basal dressing of 28:28:0 N:P:K was applied at a rate of 200 kg ha⁻¹ to the whole experimental site, located on a medium-depth alfisol at ICRISAT, India (17°30'N, 78°16'E). The crops were sown on November 21, 1984. Three treatments were compared; a sole sorghum (Sorghum bicolor (L.) Moench., cv. CSH-8) crop, a sole groundnut (Arachis hypogaea (L.), cv. Kadiri 3) crop, and an intercrop consisting of one row of sorghum and three rows of groundnut. Three replicates of each treatment were arranged in a Latin square design; each plot was 30×24 m. Plots were sown east-west with 30 cm spacing between rows. Sorghum plants were thinned to 20 cm and groundnut plants to 10 cm within the row. To promote establishment, the plots were sprinkler irrigated lightly three times until 20 days after sowing

(DAS). Subsequently there were only two irrigations; at 80 DAS, and again at 109 DAS after the removal of the sorghum, both to near field capacity as determined by neutron probe measurements. No rain fell throughout the duration of the experiment. Routine pest and disease control was maintained weekly by hand spraying. All plots were hand-weeded periodically during the season.

Intensive measurements of the microclimate and associated physiological variables within each treatment were made between the irrigation at 80 DAS and the removal of the sorghum at 107 DAS, coinciding with the reproductive phase for both species.

Growth analysis

From 21 DAS, two samples per plot were selected randomly at weekly intervals for routine growth analysis. In the sole crops, each sample consisted of two adjacent 1-m rows in the sorghum, and a 1-m row in the groundnut, giving a maximum of ten plants. Sole sorghum rows were referred to as S, and sole groundnut as G. In the intercrop, each sample consisted of two 1-m rows of sorghum and the three 1-m groundnut rows between them. Thus, at each harvest, 20 plants of each row were removed for analysis. Values of each measurement in the two-plot samples were pooled to give plot means. Intercrop groundnut rows were harvested separately; the northernmost row (least shaded) was referred to as G1, the middle row as G2, and the southernmost (most shaded) as G3. Intercropped sorghum rows were referred to as SI. Leaf number was recorded for both species, and peg and pod numbers for groundnut. Leaf area was measured with a leaf area meter (LiCor 3100*). Each plant component was then oven-dried at 80°C for 48 h, and its dry weight recorded. Pod production in groundnut and grain production in sorghum were first recorded at 82 DAS. Final harvest of the sorghum was at 103 DAS, maturity being determined by the presence of the black-layer stage, although complete removal of the sorghum was not achieved until 107 DAS, allowing some further physiological measurements. Final harvest of the groundnut was at 152 DAS.

Transpiration

The method described by Azam-Ali (1983) was used to estimate rates of transpiration from leaf surfaces, using the equation

$$E = \frac{\chi_1 - \chi_a}{r_a + r_s} \tag{1}$$

*Use of trade names does not imply endorsement or recommendation by ICRISAT in preference to other similar products.

where: E is the transpiration rate per unit of leaf area $(g m^{-2} s^{-1})$; χ_1 is the saturated water concentration $(g m^{-3})$ at leaf temperature (T_1) ; χ_a is the atmospheric water concentration $(g m^{-3})$; r_a is leaf boundary layer resistance $(s m^{-1})$; r_s is the leaf stomatal resistance $(s m^{-1})$. T_1 and r_s were measured with a porometer (LiCor 1600), and χ_a calculated from aspirated psychrometer measurements of dry (T_d) and wet bulb (T_w) temperatures using the equation given by Campbell (1977). A relation between r_a and windspeed was determined by measuring the rate of evaporation from wet blotting paper leaves (Azam-Ali, 1983) for a range of windspeeds in both sole crops and the intercrop. Values of r_a , thereafter, were estimated from concomitant measurements of windspeed using a pulse anemometer (Vector Instruments) connected to a data logger (CR7, Campbell Scientific Inc., UT).

Measurements of T_1 , T_d , T_w and r_s were taken at five times during the day, at 08:00, 10:00, 12:00, 14:00 and 16:00 h Indian Standard Time (IST). In plots containing sorghum, two plants were selected at random, and for each plant, resistances were measured on a leaf at the top and on a leaf midway down the canopy. Measurements were made at the mid-portion of a leaf parallel with the midrib. In plots containing groundnut, resistances were measured on a single leaflet of two randomly selected plants. In the intercrop, each groundnut row was measured independently. Thus, r_s was measured on twelve leaves per treatment in the sole sorghum and the sorghum component of the intercrop and on six leaves per treatment in the sole groundnut and each component groundnut row of the intercrop. On all selected leaves, both abaxial and adaxial surface resistances were measured; overall leaf resistance was calculated as the inverse of the sum of inverses of the abaxial and adaxial surface resistances. Both shaded and sunlit leaves were measured at random in both crops to give an estimate of overall crop resistance.

Daily transpiration was calculated by integrating the area under the diurnal curve of hourly transpiration calculated using eqn. (1), assuming that transpiration was zero during the hours of darkness from 18:00 to 06:00 h IST.

Radiation interception

The horizontal distribution of light in each canopy was measured using an instrument which recorded the light intensity at 2-cm intervals across a transect normal to the direction of the crop rows. From these measurements, the fraction of solar radiation (g) intercepted by the vegetation was calculated. The instrument, termed a "mouse", and the method of calculating g are described by Matthews et al. (1987).

Measurements were made on cloudless days (92, 100, 105 and 107 DAS) around midday; two measurements were after the final harvest of the sorghum (103 DAS) but before complete removal from the plots (107 DAS). Before

and after each set of measurements, readings of the incident radiation were taken with the mouse. In the sole crops of sorghum and groundnut, readings were then taken with the mouse positioned at ground level, spanning five adjacent rows. In the intercrop, a reading was taken with the mouse positioned just above the groundnut rows, spanning one complete unit (one sorghum and three groundnut rows), and then again directly underneath at ground level. The difference between the two readings at each point was taken to represent the quantity of light intercepted by the groundnut rows. Two measurements were taken in each plot.

The value of g for each row was calculated as the mean of the readings within half the inter-row spacing (i.e. 15 cm) either side of the row. Thus each row value is the mean of 15 individual values. Values of g for the whole plot were calculated as the mean of each row value in the case of the sole crops, and the sum of the sorghum, G1, G2 and G3 row values in the intercrop. The data presented are the means of all sets of measurements between 92 and 107 DAS inclusive.

Macroclimate

Copper-constantan thermocouples housed in a Stevenson screen were used to measure dry- and wet-bulb temperatures (T_d, T_w) . The wet-bulb thermocouple was enclosed in a cotton wick attached to a reservoir of distilled water which was replenished daily. Irradiance was measured with a Kipp-Zonen solarimeter, and ambient windspeed (U_s) with a pulse anemometer (Vector Instruments). All instruments were mounted 2.25 m above the ground, and were connected to a data logger housed adjacent to the field, which measured sensor output at 1-min intervals and recorded hourly averages.

Microclimate

For each stand, profiles of U_s , T_d and T_w were obtained using instruments mounted on two vertical metal masts located near the plot centre. In the sole crops the masts were located midway between two adjacent rows and in the intercrop on the middle groundnut row. Windspeed was measured using pulse anemometers, and T_d and T_w with aspirated psychrometers. All were connected to the data logger. Readings of each variable were taken at five positions at 25-cm intervals starting from ground level. Each day, both masts were shifted together from plot to plot, enabling measurements to be made in any one plot every 9 days.

Leaf temperatures, T_1 , were measured with 38-s.w.g. copper-constantan thermocouples located on the undersides of the leaves to avoid direct radiation, and held in place with plastic clips. The thermocouples were placed at a range of heights within each stand, corresponding to the positions at which

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anemometers and psychrometers were installed, and were checked daily and repositioned if necessary. In each plot three thermocouples were connected in parallel to give a single average reading.

Soil temperatures in each plot were measured using 20-s.w.g. thermocouples buried at a depth of 5 cm beneath the crop rows. The soldered junctions of the thermocouples were waterproofed to prevent shorting. As with the leaf thermocouples, three were joined in parallel to give an average reading per plot. All soil and leaf thermocouples were connected to the data logger.

Leaf water potentials

Mid-day leaf water potentials (ψ_1) were measured in all plots at 82, 84, 86, 93, 100 and 105 DAS using a pressure chamber (PMS Instruments Inc., OR). Within each plot, four plants were selected at random, and two leaves, one from the top and the other from the middle of the plant, were excised at a point midway along the leaf, and enclosed in a moist cloth to minimise water loss during transfer to the pressure chamber.

RESULTS

Macroclimate

Environmental conditions during the experiment are summarised in Fig. 1. Mean air temperature varied from 20 to 30°C, and maximum air temperature from 28 to 39°C; the corresponding range of maximum saturation def-



Fig. 1. Environmental conditions for the duration of the growing period.

cit (SD) was from 2.5 to 5.5 kPa. Class A pan evaporation, obtained from he ICRISAT meteorological station 200 m from the field site, ranged from 4 o 10 mm day⁻¹. Daily incoming solar radiation varied from 14 to 25 MJ m⁻² day⁻¹

Dry matter production

For sorghum, there was a significantly higher total dry weight and grain weight per plant in the intercrop compared with the sole crop (Table 1). This, however, was not the result of increased leaf area; leaf numbers, weight and area were higher in the sole crop, although differences were not significant. There was also a higher harvest index (the ratio of grain weight to total dry weight at final harvest) in the intercrop.

In groundnut, the situation was more complex. While the mean dry weight per plant was slightly higher in the sole crop compared with that in the intercrop (averaged over all three rows), there was considerable variation in the performance of individual rows of the intercrop (Table 2). Leaf weight, leaf area and total plant weight in G2 were all higher than in the other two ground-

TABLE 1

Growth analysis summary for sorghum at final harvest on 103 DAS. Figures are expressed per plant

	Sole	Intercrop	LSD (5%)
Leaf no.	3.6	2.2	1.9
Leaf area (cm ²)	331.17	234.50	222.23
Green leaf wt. (g)	2.16	1.72	1.70
Grain wt. (g)	15.99	24.05	4.38
Total dry wt. (g)	37.96	51.42	13.56
Partitioning	0.423	0.466	0.060

TABLE 2

Growth analysis summary for groundnut at 110 DAS after removal of sorghum. Figures are expressed per plant. Reproductive weight is the combined weight of pegs and pods

	Sole	Gl	G2	G3	LSD (5%)
Total leaf no.	62.0	52.8	65.8	67.5	14.0
Green leaf wt. (g)	5.28	4.65	6.70	4.82	2.11
Leaf area (cm ²)	626.17	543.00	831.00	619.83	259.8
Pod no.	7.5	3.0	5.3	8.7	3.8
Pod wt. (g)	0.00	0.05	0.35	0.31	0.54
Reproductive wt. (g)	1.25	0.70	1.01	1.41	0.88
Total dry wt. (g)	13.01	10.90	15.84	11.52	5.21
Partitioning	0.000	0.005	0.013	0.022	0.025

nut rows. In addition, there was a tendency for G2 to produce higher dry weights than the sole crop plants, although these differences were not significant. Characters related to the rate of development of the plant, however, showed a different pattern. Leaf number and pod number were significantly higher in G3, the row most shaded by the sorghum, than those in G1, the least shaded row. Reproductive weight (pegs and pods) followed a similar pattern, as did harvest index. Thus, growth processes and developmental processes in groundnut appear to be affected in different ways in the intercrop.

In general, differences between groundnut rows that were evident at 110 DAS were maintained until final harvest at 152 DAS (Table 3), particularly in relation to reproductive development characters. G3 produced the highest pod weight per plant, and had the highest harvest index. However, with the removal of the sorghum, the dry matter production of this row also recovered, producing a higher leaf area and total dry weight than even G2 at final harvest. G1, on the other hand, never recovered to the extent of the other rows, and remained the lowest for almost every character.

Vertical profiles

No significant differences were found between either of the sole crops or the intercrop for vertical profiles of air temperature, humidity or windspeed. Therefore, data are not presented.

Transpiration

In the intercropped sorghum, transpiration per unit leaf area was similar to that in the sole crop immediately after the irrigation at 80 DAS, but did not fall as low as the latter when water became scarcer (Fig. 2a). By 100 DAS, the

TABLE 3

Growth analysis summary for groundnut at final harvest on 152 DAS. Figures are expressed per plant. Reproductive weight is the combined weight of pegs and pods

	Sole	Gl	G2	G3	LSD (5%)
Total leaf no.	98.0	102.0	108.4	100.4	12.9
Green leaf wt. (g)	7.14	6.05	8.31	7.94	1.84
Leaf area (cm ²)	835.50	734.50	964.00	995.50	258.58
Pod no.	22.1	14.2	17.4	16.5	8.3
Pod wt. (g)	2.59	2.19	2.76	3.58	1.71
Reproductive wt. (g)	3.95	3.01	3.96	4.79	1.79
Total dry wt. (g)	18.57	15.75	20.48	21.47	4.96
Partitioning	0.141	0.134	0.133	0.176	0.087



Fig. 2. Transpiration rates per unit leaf area for the period 83-107 DAS for: (a) sorghum; (b) groundnut. S1, intercrop sorghum; S, sole sorghum; G1,G2,G3, intercrop groundnut rows (see text for details); G, sole groundnut.

difference between sole and intercrop was significant, which was maintained until the final measurements at 107 DAS before sorghum removal.

In groundnut, there was no difference in transpiration rates between the sole crop or any of the intercrop rows immediately after the irrigation (Fig. 2b). However, as the supply of water decreased, G2 was able to maintain a higher rate of transpiration per plant, so that by 107 DAS, rates were significantly faster than in neighbouring rows of the intercrop, and than in the sole crop.

Radiation interception

The fraction of solar radiation (g) intercepted by the whole intercrop

(0.370) was what would be expected if the sole crops were sown in the same proportions as the intercrop (Table 4). However, there were considerable differences between actual and expected values of the two species within the intercrop, with sorghum intercepting almost twice as much as expected, and groundnut only half as much.

Closer examination of the interception by individual rows is necessary to explain how intercepted radiation is partitioned between the component species differently to that expected on the basis of the sole crops. Figure 3 shows mean g between 92 and 107 DAS for the individual rows of the intercrop (calculated as the light intercepted by each row as a fraction of the light incident on the whole intercrop unit), and for the two sole crops. As the sun was not directly overhead, even at midday, the sorghum in the intercrop intercepted some radiation that would have reached the groundnut rows, shown

TABLE 4

Mean midday fractional radiation interception (g) between 100 and 107 DAS by sorghum and groundnut as sole crops and in the intercrop

	Sole	Intercrop	CPR^2	
		Actual	Expected	
Sorghum	0.556	0.266	0.139	1.91
Groundnut	0.308	0.104	0.231	0.45
Total	-	0.370	0.370	1.00

¹Expected values in the intercrop are based on sole crop values weighted by proportions of each species in the intercrop.

²Crop performance ratio (ratio of actual to expected g), as defined by Azam-Ali et al. (1990).



Fig. 3. Mean midday fractional radiation interception of individual rows. Each row value is the mean of 60 individual readings from measurements made on 92, 100, 105 and 107 DAS. Midday sun zenith angle varied from 64.6 to 67.3° over the period. Notation as in Fig. 2. Additional explanation is given in the text.

'white' for G1, G2 and G3 in Fig. 3. This represents the degree of shading, and was greater in G3 and least in G1. For groundnut, G2 intercepted a larger fraction of light than either G1 or G3, shown 'black' in Fig. 3, but all of these were substantially lower than in the sole crop.

There was a strong correlation between the fraction of light intercepted by each individual row between 92 and 107 DAS and its growth rate over the period 80–103 DAS (Fig. 4), although a test of deviation from the line fitted through the other points showed the point for G to be significantly lower (P < 0.005). The fastest growth rate within the three intercropped groundnut rows was that of G2 which also intercepted the most radiation of the three. The slope of the regression line between the growth rate dW/dt (g m⁻² day⁻¹) and fractional interception, *f*, is proportional to the radiation conversion efficiency *e* (g MJ⁻¹) according to the equation

$$e = \frac{\mathrm{d}W}{\mathrm{d}S_{i}} = \frac{\mathrm{d}W/\mathrm{d}t}{f\mathrm{d}S/\mathrm{d}t} \tag{2}$$

where S and S_i are the accumulated flux densities (MJ m⁻²) of incident and intercepted radiation, respectively, and it is assumed that the changes in f and dS/dt are small over the time period involved. Values of e can be estimated approximately if it is assumed that the mean value of dS/dt over the period is 19 MJ m⁻² day⁻¹ (see Fig. 1); using the fractional interception values and growth rate values of Fig. 4, the values 0.65, 0.35, 0.67, 0.64, 0.69, and 0.60 g MJ⁻¹ are obtained for S, G, G1, G2, G3, and SI, respectively.



Fig. 4. Relation between mean growth rate during the period 80-103 DAS and mean midday fractional radiation interception during 92-107 DAS of each row. The SI value, representing the total interception by the intercrop sorghum, is the sum of the Fig. 3 SI value and the shaded components of G1, G2 and G3, shown 'white' in Fig. 3. Similarly, the values of G1, G2, and G3 are the 'black' portions only of the Fig. 3 values. The equation for the line is y=0.01+12.2x (r=0.999, P<0.01). P<0.005 that sole groundnut differs from the line. Notation as in Fig. 2.

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Leaf and soil temperatures

Table 5 shows maximum leaf and soil temperatures measured within each row on 94 DAS. Presumably because of its proximity to the hot soil surface, leaf temperatures of groundnut were always higher than those of sorghum, both for sole and intercrops. Leaf temperature in the sole groundnut crop was similar to the middle row, G2, in the intercrop, although soil temperature was lower. Within the intercrop, G3, the most shaded row had significantly lower leaf and soil temperatures than either G1 or G2. Ranking of soil and leaf temperatures of these three rows corresponded to the degree of shading (Fig. 3). There was a strong negative correlation (r=-0.838, P<0.05) between soil temperature under each row and the intercepted fraction of radiation incident on that row (Fig. 5).

TABLE 5

Maximum leaf and soil temperatures ($^\circ$ C) measured on 94 DAS with copper-constantan thermocouples. Maximum air temperature was 35.6 $^\circ$ C

	Intercrop			Sole		LSD	
	SI	Gl	G2	G3	S	G	(3%)
Leaf	39.8	45.1	44.3	42.8	41.8	44.3	2.1
Soil	42.1	43.9	43.0	37.4	40.1	40.7	5.8

50 r



Fig. 5. Relation between mean midday fractional radiation interception and soil temperature under individual rows. Equation of the line is y=46.5-13.0x (r=-0.838, P<0.05). Values of g in G1, G2 and G3 are for the whole row, including the component of shading by the sorghum. Intercrop values are expressed as the fraction intercepted of the light incident on the row, rather than on the whole intercrop unit. Notation as in Fig. 2.



Fig. 6. Changes in midday leaf water potential (ψ_1) of groundnut in the sole and intercrop over the period 82–105 DAS. Notation as in Fig. 2.

Leaf water potential

Changes in midday leaf water potential (ψ_1) of groundnut during the study period are shown in Fig. 6. From about 86 DAS, ψ_1 in the rows G1 and G2 fell significantly below that of G3, differences which lasted throughout the period. G1 appeared to be the most severely water stressed of the three. Leaf water potentials in the sole groundnut were between those for G2 and G3 throughout most of the period. Corresponding leaf water potentials for sorghum over the same time period showed no significant differences between sole and intercrop; therefore data are not presented.

DISCUSSION

There appeared to be two patterns of response by the groundnut in the intercrop. Firstly, factors related to resource use and growth, such as water use, light interception and dry matter production, were lowest when the groundnut row was closest to the sorghum; the highest growth, quantity of light intercepted, and transpiration rates were observed in the middle row, G2. On the other hand, factors related to development, such as leaf number and pod number steadily increased from G1 to G3, as did leaf and soil temperatures, quantity of incident radiation, and leaf water potentials. Intercropping of the kind studied here therefore appears to act on at least two different levels: (1)that of resource allocation between the component species and the resulting effect on dry matter production; (2) by microclimate amelioration through shading, which helps to reduce tissue and soil temperatures and to maintain more favourable water relations, thereby influencing plant development.

As with other intercrop studies (e.g. Natarajan and Willey, 1986), the sorghum competed more aggressively for resources than the groundnut. Water

would appear to be the determining resource in this case rather than light, as growth of the groundnut rows nearest the sorghum was affected about equally (Tables 1-3); G1, despite having the most solar radiation available to it, produced the least dry matter. The amount of leaf area produced was limited by the availability of water to each groundnut row, which in turn limited the quantity of radiation that could be intercepted. G2 was transpiring at a significantly faster rate than even the sole crop at 107 DAS, suggesting that it was competing more successfully for water than the groundnut rows either side of it, which were suppressed by the presence of sorghum rows.

From the straight line of Fig. 4, there appeared to be no difference in the efficiency (e) of conversion of radiation into dry matter for sorghum between the sole and intercrop – the faster growth rate in the intercrop was due to a higher fraction of light being intercepted. This contrasts with the findings of Harris and Natarajan (1987), who reported that both the quantity of light intercepted and e were greater in intercropped sorghum. Although care must be taken in drawing conclusions from points close to the origin, there was some evidence (Fig. 4) that e was increased in the intercrop groundnut to near that of the sorghum, a C4 plant; the sole groundnut, however, lay significantly below a straight line through the other points. The fraction of light intercepted by the groundnut, however, was less in the intercrop than the sole crop, an observation made by several workers (e.g. Marshall and Willey, 1983; Harris and Natarajan, 1987).

In sorghum, while harvest index was higher in the intercrop, the difference was not significant, the higher grain yield being mainly due to higher plant weight. Harris and Natarajan (1987), studying a similar sorghum/groundnut intercrop, found that the increased yield was due to both higher plant weight and higher harvest index. They ascribed the higher harvest index to the sorghum being able to maintain higher plant water potentials owing to decreased competition from the adjacent groundnut rows. In the present work, however, there were no significant differences in water potentials.

The effect of shading by a taller crop on the canopy temperature and related physiological characteristics of a shorter crop has been studied on occasions (e.g. Shackel and Hall, 1984; Harris and Natarajan, 1987; Olasantan, 1988). Wahua and Miller (1978) suggest that shading by sorghum increased the leaf water potential of soya beans in an intercrop of the two species. Certainly in the present work, leaf water potential followed the pattern of shading and temperature across the groundnut rows, rather than the pattern of transpiration rate that might be expected. However, ψ_1 is the result of the balance between water supply and demand, and although the competition from the sorghum would reduce the supply of water available to G3, the lower leaf temperatures experienced by this row may have helped it to maintain a higher ψ_1 despite less water being available.

There was a strong correlation between the

opment and the gradient of both temperature (leaf and soil) and water potential across the groundnut rows. Ong (1984) found in groundnut that as mean air temperature increased from 22 to 31° C, the pod to shoot weight ratio decreased. This was explained by the optimum temperatures for leaf and stem growth being around $28-30^{\circ}$ C (Bolhuis and De Groot, 1959), but those for pod growth being between 20 and 24° C (Cox, 1979). Partitioning of dry matter to pods would therefore be expected to decrease as temperature increased above 24° C. The increasing trend in soil temperatures experienced by G3, G2 and G1 (Table 5), and the corresponding decrease in harvest index (Table 2) would appear to confirm this. Superimposed on this, however, is the reduction in total dry matter of G1 and G3 by competition from the sorghum; the harvest index of G3 was high owing to a high reproductive weight combined with low total dry weight.

The effect of water potential on reproductive development is less clear. Ong (1984) found that as water stress in groundnut increased, leaf and stem growth declined dramatically, but pod growth was not much affected. Harris et al. (1988) reported an interaction between water potential and thermal time for leaves of groundnut. Further work is needed to clarify the effects of each of these variables.

A knowledge of the way in which resources and microclimatic variables interact is essential in order both to select appropriate varieties for use in intercrops (Francis, 1985), and to predict the optimum arrangement of intercrop components. Many breeders, for example, have assumed that selection for superior sole crop genotypes will also produce the genotypes best adapted for intercropping. However, this has not always been the case; Ntare (1989) found a variation in correlations between cowpea cultivar yields in sole crops and in intercrops with pearl millet. He concluded that the selection of cowpea cultivars for intercropping would only have limited success if it was based on their grain yield in sole crops. Part of this variability may have been owing to contrasting reactions to differences in microclimate. The data presented in this paper indicate that there can be a significant interaction between water availability, shading, leaf temperatures, water potentials, and the growth and development of the intercrop constituents. It should be possible to use this information to design optimum intercropping systems; in particular, to determine the optimum number of rows in relation to the height of the taller crop at a given site. Any detailed study of intercropping systems should therefore include measurements of microclimate if possible.

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