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Physiological Basis for Yield Advantage in a Sorghum/Groundnut Intercrop Exposed to Drought.
1. Dry-Matter Production, Yield, and Light Interception

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ABSTRACT

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An intercrop consisting of one row of sorghum between two rows of groundnut was grown, together with sole crops of the components at the same intra-row spacing as in the intercrop. Two irrigation treatments were applied: a 'wet' treatment in which water stress was kept to a minimum by frequent irrigation; and a 'dry' treatment which received less water.

On the basis of a Total Crop Performance Ratio (TCPR) the wet intercrop gave only 3% more total dry matter (TDM) than the two crops separately, whereas in the dry treatment the advantage was 21%. However, reproductive yield advantages were 14% and 88% in the wet and dry treatments, respectively, and resulted from larger harvest indices in the intercrops.

Intercropped sorghum produced more TDM than would be expected if intercropping had no effect, while intercropped groundnut produced less. Leaf area indices were smaller than expected in all intercrop components. However, sorghum intercepted more radiation per unit row in the intercrop than in the sole crop, but used it to produce dry matter less efficiently when water was plentiful. Groundnut intercepted less radiation than expected, but used it with greater efficiency in both wet and dry treatments. As well as intercepting more radiation, intercropped sorghum also

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used it more efficiently when water was limited, suggesting that sorghum was able to compete more successfully for soil water with groundnut in the intercrop than with itself in the sole crop.

INTRODUCTION

Intercropping is a very common farming practice in the semi-arid tropics, and higher yields can often be achieved by growing two or more crops together than by growing the component crops separately (Willey, 1979). As yet, the physiological mechanisms responsible for these yield advantages have not been reliably identified, although it has been shown that intercrops use available resources more efficiently than do sole crops (Natarajan and Willey, 1980; Reddy and Willey, 1981; Marshall and Willey, 1983).

Yield advantages from intercrops can arise in two ways. Component crops may have different durations or different growth patterns, and thus make major demands on resources at different times. This leads to better temporal use of resources, of which there are many examples (Willey, 1979; Natarajan and Willey, 1980). There is less evidence to show that intercropping can result in better spatial use of water, nutrients, light, etc., although Reddy and Willey (1981) have shown increased efficiency in the spatial use of light in a millet (*Pennisetum typhoides* S. & H.) and groundnut (*Arachis hypogaea* L.) combination.

Surveys by Jodha (1976) in India and by Ogunforwora and Norman (1973) in Nigeria have shown that, in areas where inputs are few, intercropping is more common. Natarajan and Willey (1980) suggest that greater yield stability between seasons is probably the main reason for this choice, rather than higher yields per se. Since water is a major limiting resource in the semi-arid tropics, Baker and Norman (1975) have suggested that better use of water by intercrops is the reason for their popularity with farmers in this region.

In India, Natarajan and Willey (1986) showed that intercrops of sorghum (*Sorghum bicolor* L.) and groundnut produced larger relative yield advantages when grown under drought than they did when kept well-watered. The combination of sorghum with groundnut may combine both temporal and spatial 'complementarity', and give large yield advantages (Rao and Willey, 1980; Tarhalkar and Rao, 1981).

To clarify the relation between relative yield advantage and drought, a sorghum/groundnut intercrop and sorghum and groundnut sole crops were grown under two irrigation regimes: well-watered and drought-stressed. A series of detailed physiological and environmental measurements was made on the crops in an attempt to identify the mechanisms responsible for yield advantages.

Results are presented in a series of three papers. This paper (part 1) reports and attempts to explain changes in total dry-matter production, yield, and light interception patterns throughout the experiment. Part 2 (Harris and Natarajan, 1987, this volume) shows how the interaction between water application and intercropping affects plant water potential, temperature, and allocation of dry matter to various plant structures. In a third (future) paper, net rates of leaf photosynthesis and water use will be compared in the sole and intercrops, and the relation between intercrop advantages and shading of groundnut explored.

MATERIALS AND METHODS

The work on a sorghum/groundnut intercrop described here was part of a larger experiment carried out at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India (17°38′N, 78°21′E), in a programme investigating the interaction between drought and other agronomic factors in a range of intercropping systems. Sorghum (hybrid CSH-8) and groundnut (cv. Kadiri 3, formerly Robut 33-1) were sown on 23 December 1983, in rows 30 cm apart, on a flat medium-deep Alfisol (Russell, 1980) and thinned 3 weeks later to leave plants 20 cm apart within rows for sorghum (16.6 plants m^{-2} for the sole crop) and 10 cm within rows for groundnut (33.3 plants m^{-2} for the sole crop). The intercrop consisted of one row of sorghum alternating with two rows of groundnut, with each crop at the same within-row spacing as its sole crop. All sorghum plants were topdressed with ammonium sulphate applied evenly along each sorghum row to supply 80 kg ha^{-1} nitrogen to the sole crop and one-third the rate (26.7 kg ha^{-1}) to the intercrop. Groundnut plants received no added N. Phosphorus as P_2O_5 was applied as a basal dressing over the whole experimental area at a rate of 20 kg ha^{-1}. Hand-weeding was carried out in all crops at 18 and 52 days after sowing (DAS).

Between sowing and 35 DAS, 120 mm of water was applied uniformly to all stands. Thereafter, differential irrigation was applied. To conform with the design of the main experiment, one replicate each of the intercrop and sole crops was arranged on either side of two lines of sprinklers with rows at right angles to the 'line-source', giving four replicates. During an irrigation, the amount of water received at any point is inversely proportional to the distance away from the sprinkler line (Hanks et al., 1976). For the more specific objective of the work described here, two zones were designated: from 1 to 5 m from the line source, 'wet'; and 8 to 12 m from the sprinklers, 'dry'. Symmetrical distribution of water about the line-source requires absolutely calm conditions, which were rare. Actual water application was measured using buckets placed at the median distance from the line within each zone.

Line-source irrigations took place at 48, 60, 71, 90, 98 and 111 DAS, and a further uniform irrigation was applied at 78 DAS, when 26 mm rain also fell. The total amounts of water applied were 460 mm (wet) and 263 mm (dry).

Radiation interception

Radiation interception by all three treatments was calculated from measurements of the radiation received by 90-cm tube solarimeters (Delta-T Devices*) mounted above and below the canopy. In addition, the radiation intercepted by each component of the intercrop was measured by installing tube solarimeters beneath the sorghum canopy but immediately above the two groundnut rows. These solarimeters spanned only the middle 60 cm of inter-sorghum space occupied by the groundnut. Interception by the two components was calculated in the manner described by Marshall and Willey (1983). Interception by groundnut was calculated first, assuming that lateral spread of the groundnut canopy did not extend beyond the area covered by the 60-cm solarimeters. Sequential photographs taken up to the final harvest of sorghum confirmed that this assumption was valid. The amount of light intercepted by sorghum was calculated as the difference between total intercrop interception and that attributed to groundnut. Solarimeter records were collected from two of the four replicates on alternate days (i.e. each plot was measured every other day). Data are presented as the means of 4 days, representing 2 days from each of 2 pairs of replicates.

Growth analysis

Plants were harvested for growth analysis at 25, 48, 60, 73, 81 and 90 DAS (groundnut) and 31, 48, 60, 73, 81 and 90 DAS (sorghum). Final harvest was at 108 DAS for sorghum and 126 DAS for groundnut. At each harvest, all above-ground material (including pegs and pods in groundnut) was collected from a 4-m row section of unit crop within each treatment zone, i.e. 4 m of one row in the sole crops, but 4 m of one sorghum row plus two 4-m rows of groundnut in the intercrop. All material was separated into leaves, stems, pegs, pods and panicles. Leaf area was measured using a LICOR LI 3100 leaf-area meter, then all material was dried at 80°C to constant weight. Data from one of the replicates was discarded because of unrepresentative growth in a plot with non-uniform soil and infestation of the sorghum by *Striga*.

To assess the advantage of the intercrop in terms of the dry weight of harvested material, the yield per unit area of a component of the intercrop, I, was divided by the proportion, p, of that component in the intercrop to give the yield per unit area sown to that component, I/p. This quantity was then expressed as a fraction of the same component in a sole plot, S, to give Crop Performance Ratios (CPR) of $I_g/(p_g \cdot S_g)$ for groundnut and $I_s/(p_s \cdot S_s)$ for

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sorghum. The corresponding ratio for the whole intercrop, a Total Crop Performance Ratio, is given by

$$\text{TCPR} = (I_g + I_s)/(p_g \cdot S_g + p_s \cdot S_s)$$

The 'expected' performance of a component of an intercrop is often discussed in this paper, and is based upon its actual performance in the sole stand. This expected performance is calculated as the value per unit area in the sole stand multiplied by the sown proportion of that component in the intercrop. Values of CPR exceeding 1 imply that a component yielded more dry matter per unit sown area in the intercrop plot than in the sole plot, and thus performed better than 'expected' based on sole-crop yields. Values of TCPR exceeding 1 imply that the intercrop plot yielded more than sole plots, with the area for each component identical to the corresponding area in the intercrop plot. Crop performance ratios for radiation interception can be calculated in the same way, although CPR for harvest index and radiation conversion efficiency must be calculated simply as I/S because neither quantity is expressed per unit area.

For our analysis, CPR and TCPR are more appropriate bases for calculating the biological advantage of an intercrop than the more conventional Land Equivalent Ratio (LER), because we have attempted to compare the 'efficiency' with which sole crops and intercrops use intercepted radiation to produce dry matter. We do not wish to imply that LER is 'better' than TCPR, or vice versa, although the two indices are not numerically identical (R.B. Matthews, personal communication, 1987). Further work is in progress in an attempt to clarify the expression of intercrop advantages.

RESULTS

Table 1 shows biomass and filled-pod or grain yields at final harvest for all crop and treatment combinations. Values for intercropped groundnut include growth made over 18 days following the removal of intercropped sorghum. Sole sorghum produced more biomass and a higher yield than did sole groundnut in all irrigation treatments, although both measures of growth decreased as water application decreased. In the wet treatment of the intercrop, sorghum produced more TDM than expected from its 33%-sown proportion, while groundnut produced less than its expected 67%, and the TCPR was only 1.03. In contrast, both components produced relative advantages in the dry treatment (TCPR = 1.21).

The same trends are even more apparent when pod or grain yield is considered. Although actual yields fell as water was restricted, relative yields increased in both component crops. Only groundnut in the wet treatment failed to produce more pod weight than expected, and total yield advantages were 14% in the wet and 88% in the dry treatment. Thus while actual values of TDM and yield decreased as drought stress increased, relative gains due to inter-

TABLE 1

Mean dry matter and yield (t ha^{-1}, 3 replicates) for all crops, and CPR, TCPR and TLER for the intercrops

		Total dry matter	CPR	Filled-pod or grain weight	CPR
a. Sorghum					
Sole sorghum	wet	9.77		5.02	
	dry	5.32		2.06	
Intercrop sorghum	wet	4.15	1.29	2.28	1.38
	dry	2.52	1.44	1.31	1.93
Standard error of treatment mean		±0.20		±0.13	
b. Groundnut					
Sole groundnut	wet	7.39		3.17	
	dry	3.99		0.56	
Intercrop groundnut	wet	4.31	0.87	2.05	0.97
	dry	2.83	1.06	0.67	1.79
Standard error of treatment mean		±0.27		±0.13	
c. Total CPR and LER					
Total CPR	wet	1.03		1.14	
	dry	1.21		1.88	
Total LER	wet	1.01		1.10	
	dry	1.18		1.83	

cropping increased. Partitioning of dry matter to reproductive structures was clearly increased by intercropping, and this increase was greater under drought. The yield data from the dry treatments were very variable and the true difference between sole and intercrops may not have been as large as that represented by the means in Table 1. However, patterns with time of pod production were consistent with the differences reported here, and are discussed together with other factors affecting partitioning in the accompanying paper of this series (Harris and Natarajan, 1987, this volume).

The temporal pattern of dry matter production is shown in Fig. 1. In both wet and dry treatments, intercropped sorghum grew better than expected from 50 to 60 DAS whereas intercropped groundnut grew worse than expected throughout the experiment, although there was less difference between actual and expected total dry matter in the dry treatment. The intrinsic difference between C3 and C4 species was obvious: sole sorghum production rates were much faster under both irrigation regimes (ca. 15 and 7 g m^{-2} day^{-1}) than those of sole groundnut (ca. 9 and 4 g m^{-2} day^{-1}) in the wet and dry, respectively. However, in sole groundnut and the groundnut component of intercrops, growth was maintained longer than in sorghum.

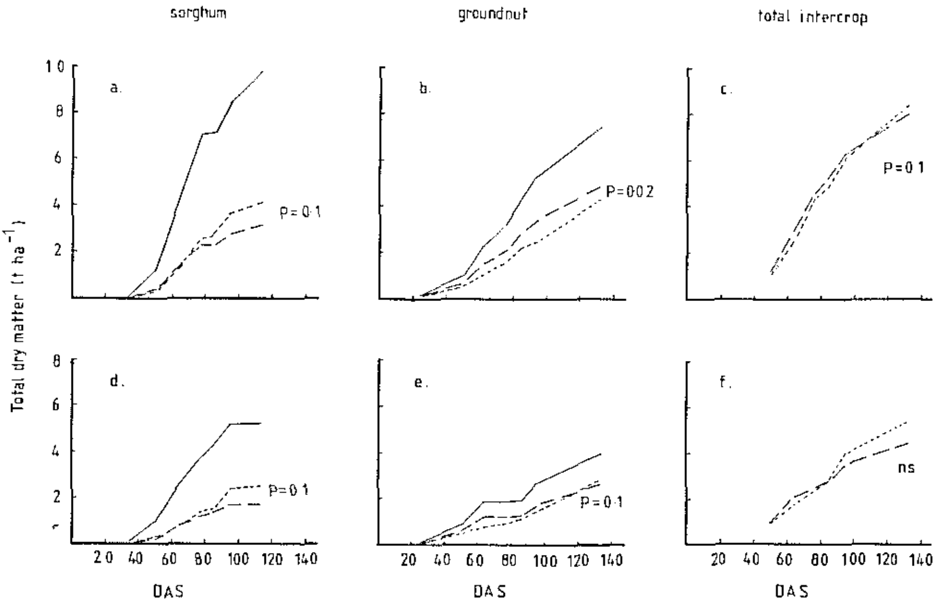

Fig. 1. Total dry matter production with time. a–c, wet treatment; d–f, dry treatment. ——, sole crop; – – –, expected values calculated on the basis of sole crop data; ----, actual intercrop results. Values of P are the levels of significance attained in a paired t-test comparison of the differences between actual and expected intercrop results over the whole experiment; ns = not significant.

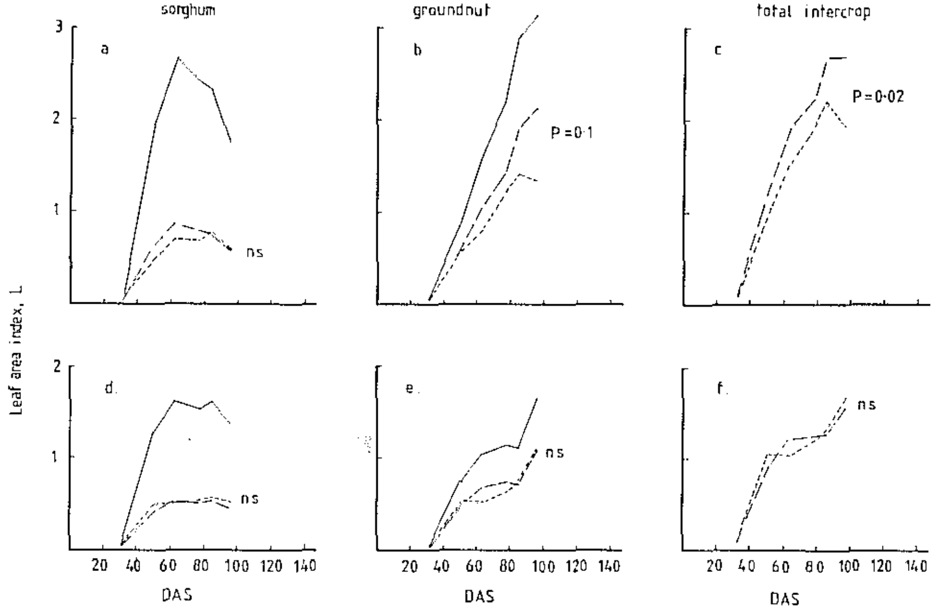

Fig. 2. Leaf area index (L). Symbols as in Fig. 1.

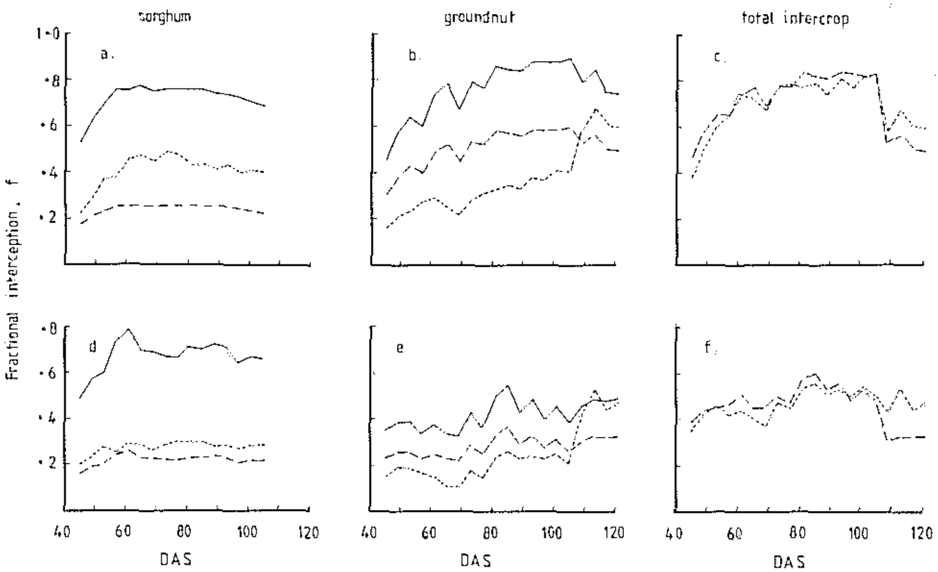

Fig. 3. Fractional interception of solar radiation (*f*) with time. Symbols as in Fig. 1.

The two species had different patterns of leaf area development (Fig. 2). In sorghum, leaf area index (*L*) increased rapidly to a maximum, followed by a decline due to senescence of leaves acropetally. Comparison of wet and dry treatments shows that while the initial increase and final decline in leaf area occurred at approximately the same time and at the same rate in both treatments, drought reduced the maximum value of *L* by approximately 40%. In contrast, *L* increased more slowly in the sole groundnut, but the indeterminate nature of the species allowed *L* to increase up to 90 DAS in both wet and dry treatments; however, drought reduced the rate of increase after 60 DAS.

In the wet intercrop, sorghum produced less leaf area than expected on the basis of sole-crop results, whereas there was virtually no difference in the dry. Groundnut *L* was smaller than expected in both treatments, although again differences in the dry treatment were small (and occurred only between 50 and 80 DAS). The *L* of the total intercrop was consistently less than expected in the wet treatment, and generally as expected in the dry.

Fractional interception of solar radiation (*f*) from 45 DAS onwards is shown in Fig. 3. Short-term fluctuations in *f* were pronounced in all stands with a groundnut component, and were possibly due to leaf-folding in response to water deficit. This was most apparent in the dry treatment, but leaf-folding was observed also in the wet crops towards the end of the interval between irrigations. Inward rolling of leaf margins in sorghum was observed in response to stress only in the dry treatments. Values of *f* for sorghum in the wet intercrop were very much larger than expected throughout the period 40–108 DAS, and were also consistently larger in the dry treatment. Thus it seems that isolated rows of sorghum intercepted more light per row than did sole-cropped sorghum, despite having less leaf area per plant.

In contrast, groundnut *f* was much smaller than expected in both treatments, although the removal of sorghum at 108 DAS was followed by a large increase in *f* to values greater than expected for the last 18 days. Removal of sorghum presumably allowed groundnut to exploit residual soil moisture free from competition. Fractional interception by the total intercrop was also less than expected in both treatments for most of the season except for the period after sorghum was removed.

Groundnut intercepted a smaller proportion than expected of the total light intercepted by the intercrops throughout the period 45–108 DAS (Fig. 4). The influence of a rapid expansion of sorghum leaves can be seen between 45 and 70 DAS, as can the increasing proportion of total *f* due to groundnut as sorghum leaves senesced from 70 DAS onwards.

This decline in *f* of sorghum would have been greater but for the persistence of senescent leaves on the stem. These non-productive leaves continued to intercept radiation without contributing assimilate, and formed an increasing proportion of sorghum leaf area as maturity approached. However, in all treatments, accumulated dry matter increased approximately linearly with intercepted radiation (Fig. 5). The linear regression of dry weight on intercepted radiation was calculated for all combinations to give a coefficient which is the average efficiency for solar energy conversion (*e*) over the period (Table 2).

Conversion efficiencies (*e*) for sorghum were larger than for groundnut in all treatments, again reflecting a well-documented difference between C3 and C4 species and are in agreement with other published values (Tinus, 1974).

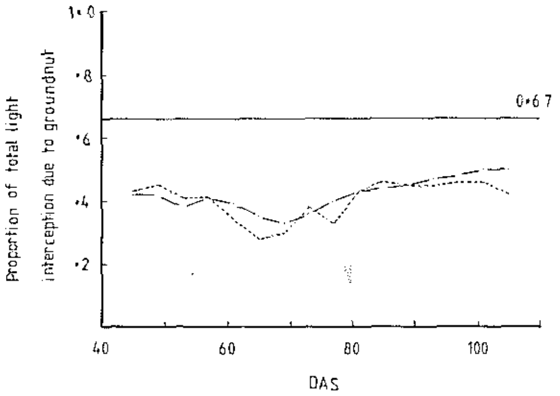

Fig. 4. Proportion of the total light interception of the intercrop due to groundnut. -·-·-, wet treatment; -----, dry treatment. Horizontal line represents the expected proportion calculated using the sown proportions of the two components.

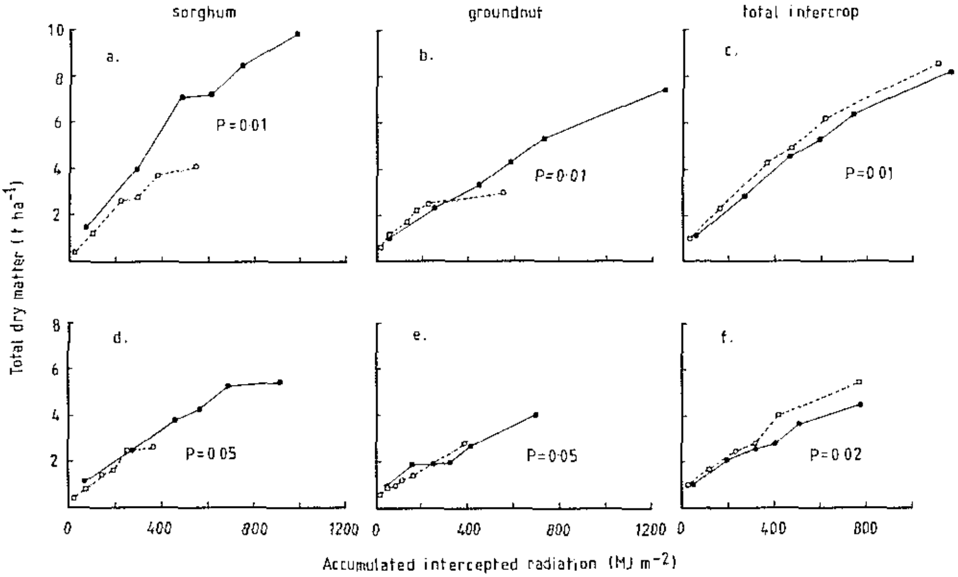

Fig. 5. Total dry matter as a function of accumulated intercepted solar radiation after 39 DAS. a–c, wet treatment; d–f, dry treatment. ——, sole crop; -----, intercrop. Values of P are the levels of significance attained in a paired-t test comparison of the differences between actual and expected intercrop results over the whole experiment; ns = not significant.

TABLE 2

Interception of solar radiation (IR), conversion efficiency (e), and harvest indices (HI) for sole and intercrops, together with their associated Crop Performance Ratios and CPR for dry matter (DM) and yield (Y)

	IR (MJ m^{-2})	e (g MJ^{-1})	HI	Crop performance ratios				
				IR	e	HI	DM	Y
Sole sorghum								
wet	1000	0.92	0.51					
dry	927	0.54	0.39					
Sole groundnut								
wet	627	0.54	0.45					
dry	349	0.44	0.19					
Intercrop sorghum								
wet	549	0.74	0.55	1.66	0.80	1.08	1.29	1.38
dry	369	0.68	0.52	1.20	1.26	1.33	1.43	1.93
Intercrop groundnut								
wet	279	0.66	0.48	0.66	1.22	1.12	0.88	0.97
dry	198	0.57	0.24	0.85	1.29	1.68	1.08	1.79

CPRs for e and Y are calculated as I/S (see text).

In three out of four cases, intercropped species used light more efficiently than did their respective sole crops. The one exception was intercropped sorghum in the wet treatment. The value of *e* was larger in the wet than in the dry in all crops.

Intercropped groundnut intercepted less radiation than expected, but used it more efficiently relative to the sole crop. In contrast, wet intercropped sorghum intercepted more radiation than expected, but used it less efficiently than the sole crop, to give a CPR for dry matter of 1.29. Intercropped sorghum behaved differently in the dry treatment, intercepting more radiation than expected and using it more efficiently, leading to a dry-matter increase of 43%.

Reproductive advantages can also be examined in terms of Crop Performance Ratio. Table 2 also shows that CPR for harvest index was greater than 1 for all intercrop components, and increased with drought.

DISCUSSION

In this paper we have analysed the productivity of each intercrop component relative to its own sole crop performance. However, it is also possible to compare the total intercrop with either of the sole crops. This is a valid comparison to make when the criterion for intercropping is to achieve maximum total biomass. The performance of the combined intercrop relative to each of the sole crops can be calculated (as $(I_g+I_s)/S_s$ or S_g) from data in Table 1. Intercropping produced 13% less total biomass than sole sorghum in the wet treatment, but produced about the same total biomass as sole sorghum in the dry treatment. More biomass was produced by intercropping than by growing sole groundnut in both wet (15% more) and dry (34%) treatments. However, the choice of sole sorghum as the best crop to sow takes no account of the relative values (calorific, monetary, etc.) of sorghum and groundnut. Choice of crops by farmers is a complex issue beyond the scope of this paper and is discussed further by Willey (1979, 1985). We have confined ourselves here to a study of the physiological changes associated with intercropping and their effects on yield.

This intercropping system showed a combination of *temporal* complementarity, because component crop durations differed, and *spatial* complementarity, the degree and pattern of which changed with time. Initially, sorghum dominated the intercrop, and depressed the growth of groundnut, but later senescence of the sorghum allowed compensatory growth of groundnut. Overall, the benefits obtained were predominantly due to increased biomass of the sorghum component, although groundnut was able to produce similar growth in sole and intercrops, even when shaded by sorghum.

An important result of this experiment was that the intercropping advantage increased when less water was available. In terms of dry-matter production, there was no advantage of intercropping in the wet treatment, but a 21% advantage in the dry, similar to advantages reported by Natarajan and Willey

(1986) for sorghum/groundnut intercrops under similar conditions. It must be borne in mind, however, that patterns of drought stress are rarely identical and conclusive detailed comparisons of crop performance should not be inferred.

Advantages gained in this sorghum/groundnut system were less than in the combination of millet/groundnut described by Marshall and Willey (1983), where the TCPR was 1.39 in rainy conditions, analogous to the wet treatment here, at least with respect to soil water. Marshall and Willey (1983) studied an intercrop comprising three rows of groundnut alternating with one row of millet, and concluded that advantage was obtained because the millet intercepted twice as much radiation per unit of row in the intercrop and used it with the same efficiency to produce twice as much dry matter, whereas the groundnut intercepted less radiation than expected on the basis of the sole crop, but used it more efficiently to produce the same dry matter. In the wet treatment described here, sorghum intercepted 66% more radiation per plant in the intercrop than in the sole crop, but used it 20% less efficiently, whereas the groundnut intercepted only 66% of the radiation per plant but used it 22% more efficiently. The response to intercropping by groundnut was therefore similar in both experiments, though it was somewhat less efficient in the present experiment. In contrast, the sorghum performed worse than the millet by intercepting less radiation and using it less efficiently (Marshall and Willey, 1983). The reason for the difference between sorghum and millet in terms of photosynthetic efficiency is not known, but differences in saturation deficit of the air in the wet and dry seasons are known to be responsible for differences in stomatal conductance in well-watered crops (e.g. Squire, 1979, for millet). The difference in interception was caused by differences in the ability of the cultivars to change their leaf area. Millet can increase leaf area per plant at low populations by rapid tillering (Azam-Ali et al., 1984), whereas CSH-8 sorghum rarely produces tillers. Millet doubled the amount of light it intercepted largely as a result of a doubling in the leaf area per plant (Reddy and Willey, 1981).

The consistent effect of the dry treatment on both sorghum and groundnut was to increase e relative to the sole crop. It is possible that sorghum competed for soil water more successfully with groundnut in the intercrop than with itself in the sole crop; evidence in support of this is presented by Harris and Natarajan, 1987 (this volume). In the case of groundnut, it is likely that shading by sorghum leaves (even after they senesced) increased photosynthetic efficiency both because of lower irradiance per se and because of the effect of reduced radiation on leaf temperature and water potential. These factors are considered in the second and third parts of this series.

Notwithstanding these various effects of intercropping on total dry-matter production (effects which may have far-reaching implications despite the small advantage they caused in this experiment), the main effect of intercropping in this system was on partitioning of dry matter. The increased harvest indices in the intercrop, particularly in response to drought, were largely responsible for combined yield advantages of 88%, and factors affecting partitioning will be examined in part 2.

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