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Genotypic Differences in the Temperature Responses of Tropical Crops

III. LIGHT INTERCEPTION AND DRY MATTER PRODUCTION OF PEARL MILLET (*PENNISETUM TYPHOIDES* S. & H.)

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ABSTRACT

Mohamed, H. A., Clark, J. A. and Ong, C. K. 1988. Genotypic differences in the temperature responses of tropical crops. III. Light interception and dry matter production of pearl millet (*Pennisetum typhoides* S. & H.).—J. exp. Bot. 39: 1137–1143.

Leaf area development, light interception and dry matter production of four contrasting pearl millet cultivars were investigated at mean air temperatures of 19·5, 21, 26 and 31 °C. Growth was slowest at 19·5 °C and fastest at 31 °C. The canopies of the cultivars varied considerably with regard to their light transmission coefficients (K_t), from 0·47 for Sanio to 0·23 for Oasis and in their mean efficiency of energy conversion (e), from 1·0 to 2·7 g MJ^{-1}. The ranking of the cultivars in these respects is consistent with those for germination and early establishment reported in the preceding papers.

Key words—Light, dry matter production, millet.

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INTRODUCTION

Previous papers in this series have described the germination characteristics and seedling growth of several contrasting genotypes of groundnut (*Arachis hypogaea* L.) and millet (*Pennisetum typhoides* S. & H.) (Mohamed, Clark, and Ong, 1988*a*, *b*). Great variation in germination rate and cardinal temperatures was found in both crops, but such differences persisted only in pearl millet during growth. For example, the rates of leaf production and expansion of each genotype were closely related to the germination rate established on a thermal gradient plate. This paper describes the later growth of millet genotypes in terms of the rate of canopy formation and the interception of light by the foliage at temperatures between 19 °C and 31 °C.

Comparison of the growth of three *Pennisetum* species at four temperatures, from 15 °C to 30 °C, showed that large differences in the growth rate of the three species can be explained by variation in the rate of leaf production (Pearson, 1975). Less is known about the genetic variation in the 'efficiency' of solar energy conversion, e, which is expressed as grammes of

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dry matter produced per megajoule intercepted by the foliage. Squire, Marshall, Terry, and Monteith (1984) reported one value of 2·6 g MJ^{-1} for a standard millet cultivar between 22 °C and 28 °C, which decreased to 2·2 g MJ^{-1} at 19 °C and 31 °C. Temperature also influenced the amount of light intercepted before anthesis, but the transmission coefficient of foliage was independent of temperature.

MATERIALS AND METHODS

The seeds of pearl millet cultivars Oasis, Chadi, Kala and Sanio were obtained from the International Crop Research Institute for Semi-Arid Tropics (ICRISAT), India. Their weights, moisture content and storage conditions were detailed previously (Mohamed *et al.*, 1988*a*).

TABLE 1. *Nominal and actual air temperatures, soil temperatures and saturation vapour pressure deficit* (SVPD) *during the experiment*

	Glasshouses			
	1	2	3	4
Nominal temperatures (°C)				
Mean	32	25	25/19	19
Maximum	40	30	30/24	24
Minimum	24	20	20/14	14
SVPD (kPa)	1·0	1·0	1·0/1·0	1·0
Actual mean temperatures for 41 d (°C)				
Air	30·5	25·7	21·3	19·7
Soil (1·0 cm)	25·5	23·5	21·4	19·6
Soil (5·0 cm)	25·2	22·1	21·4	19·3

Seeds were grown in four glasshouses set at target mean air temperatures of 19, 22, 25 and 32 °C. Details of the glasshouse suite are given by Monteith, Marshall, Saffell, Clarke, Gallagher, Gregory, Ong, Squire, and Terry (1983). The desired and actual air and soil temperatures during the growth period are shown in Table 1. Seeds were sown at the beginning of April 1984 at a spacing of 10 × 35 cm and 5·0 cm deep. Two to three seeds were sown per hole and thinned to 1 seedling per hole at 7 to 15 d. Fertilizers equivalent to 10 kg N, 100 kg K and 25 kg P per hectare were applied just before sowing. Irrigation was supplied by seephoses, initially to field capacity (before sowing) and thereafter as required depending on temperature and dryness of the soil surface.

Growth analysis samples for all cultivars were taken at weekly intervals, from 24 d after sowing (DAS) onwards. Eight plants were used per sample. A leaf area meter (Lambda) was used for leaf area measurements. Leaves and stems were separated, oven-dried and weighed to an accuracy of ± 1·0 mg. Light interception was measured using integrators and tube solarimeters (Delta T): two of which were used connected in parallel for each cultivar. They were calibrated in pairs against a Kipp solarimeter. A further pair was located 2·0 m above the soil surface for measurements of incident radiation.

RESULTS

Figure 1a shows the time course of leaf area index (*L*) at the mean air temperature of 19·5 °C. Rapid expansion of leaves occurred only after about 30 DAS. Thereafter, clear differences existed between cultivars. Sanio was the slowest to develop and had the lowest *L* while Oasis was the fastest. At 46 DAS, for example, *L* of Oasis was 4 times that of Sanio. In general, Chadi and Kala had intermediate leaf area indices, but Chadi developed significantly faster over the last 10 d.

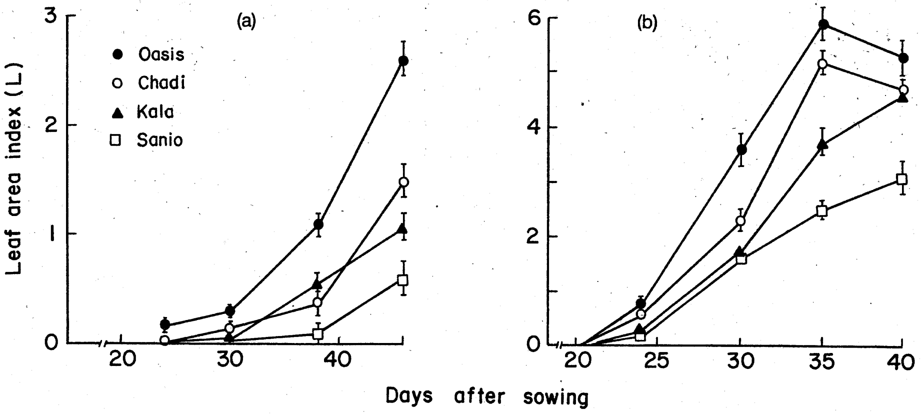

FIG. 1. (a) The time-course of leaf area development at 19·5 °C and (b) the time-course of leaf area development at 31 °C.

Figure 1b shows leaf area development at 31 °C for the same cultivars. Under this treatment Oasis achieved a maximum *L* value of 5·9 at 35 DAS compared to 3·3 and 0·7 at 26 °C and 19·5 °C, respectively. Corresponding values for Chadi were 5·2 at 31 °C, compared to 3·0 and 0·2 at 26 °C and 19·5 °C, respectively. Similarly, other cultivars developed at a faster rate at 31 °C compared to lower temperatures and major differences existed between cultivars even before 30 DAS.

Figure 2 shows the graph of *L* plotted against air temperature for all cultivars at 35–37 DAS. This particular harvest was used since Oasis and Chadi showed signs of senescence by the time of the last harvest. As shown in the figure, the leaf area of all the cultivars increased with temperature. At all temperatures, *L* was highest in Oasis and lowest in Sanio. Differences between cultivars were significant and increased with temperature.

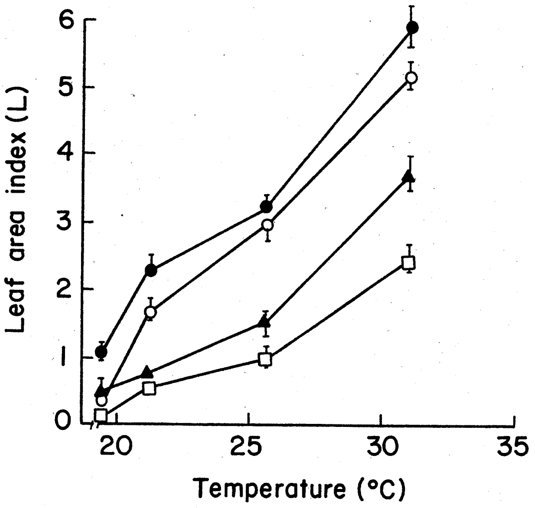

FIG. 2. Leaf area index at 35–37 d after sowing versus mean temperature.

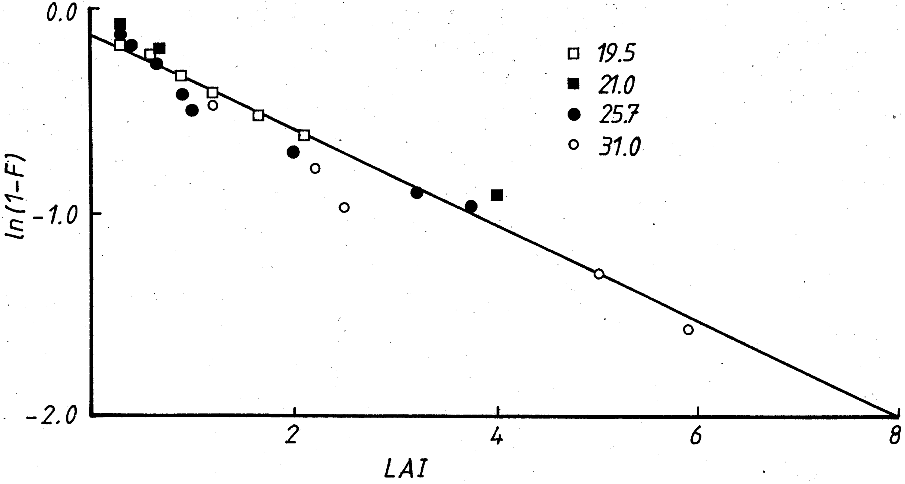

FIG. 3. Dependence of fractional light interception, F, plotted as $\ln(1-F)$, on leaf area index for millet, cv. Oasis. Data from the four temperature treatments are indicated on the figure.

The dependence of the fractional interception of radiation (F) on leaf area is shown in Fig. 3 for cv. Oasis, where log $(1-F)$ is plotted against L, using the equation:

$$F = 1-\exp(-K_t L) \tag{1}$$

where K_t is the transmission coefficient for the crop (Squire *et al.*, 1984). K_t values were 0·23, 0·27, 0·35 and 0·47 for Oasis, Chadi, Kala and Sanio, respectively, consistent with the observed differences in the canopy structure of these cultivars. The lowest correlation coefficient (r) was 0·93, significant at $P < 0{\cdot}001$.

The time-course of dry matter production by all four cultivars shows that the ranking of cultivars is consistent at all four temperatures (Fig. 4). The final dry weight (grammes per

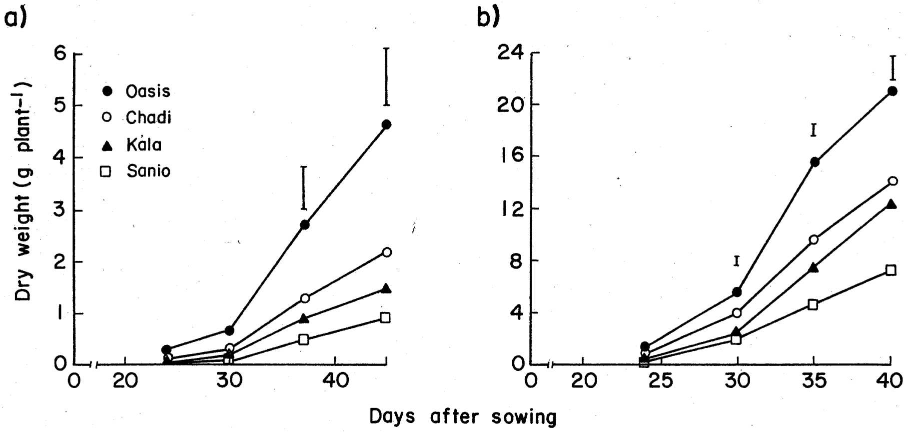

FIG. 4. (a) The time-course of dry matter production at 19·5 °C and (b) the time-course of dry matter production at 31 °C. For clarity, the vertical scale in Fig. 4a is ×4 that in Fig. 4b.

plant) increased from 4·6, 2·2, 1·5 and 0·9 g at 19·5 °C to 15·3, 9·0, 8·0 and 7·5 g at 26 °C and to 21·2, 14·0, 12·5 and 7·4 g at 31 °C for the cultivars Oasis, Chadi, Kala and Sanio, respectively. Averaged over the whole period, Oasis produced dry matter at a rate of 0·1 g d^{-1} $plant^{-1}$ at 19·5 °C, but at a rate of 0·5 g d^{-1} $plant^{-1}$ at 31 °C. The corresponding values for Sanio were 0·02 and 0·19 g d^{-1} $plant^{-1}$.

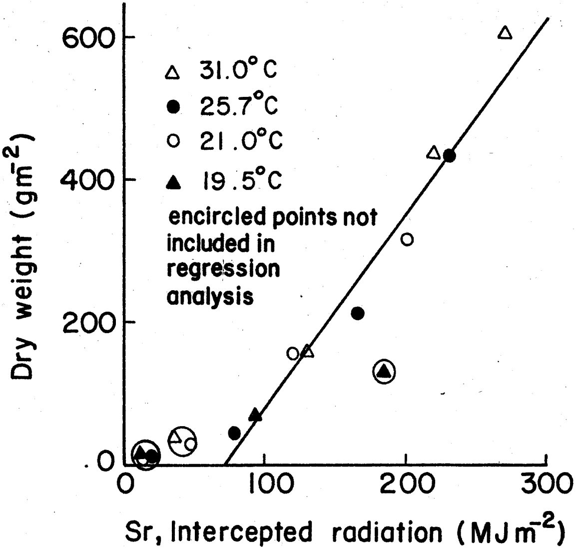

FIG. 5. Dry weight versus intercepted radiation for cv. Oasis.

The relation between the dry matter of the shoots and the accumulated intercepted radiation (*S*) of cv. Oasis is shown in Fig. 5. *S*, expressed in terms of photosynthetically active radiation (*PAR*), was obtained from the equation:

$$S = \text{incident radiation} \times 0{\cdot}6\ F \tag{2}$$

where 0·6 was the transmission coefficient for the glasshouses. Radiation was accumulated from 10 d onwards. For each cultivar, the accumulated dry matter (g m^{-2}) increased linearly with *S* at all temperatures and the lowest value of *r* was 0·90 at $P = 0{\cdot}001$. However, the initial points and most of the values obtained at 19·5 °C were outside the linear part of the graph and were, therefore, excluded from regression. Values of *e* at 19·5 °C, based on final harvests, were usually less than half of the values at higher temperatures. The slopes of these graphs give the mean efficiency of energy conversion (*e*) as 2·75, 1·62, 1·29 and 1·03 g MJ^{-1} for Oasis, Chadi, Kala and Sanio, respectively (for a standard population of 28·6 plants m^{-2}); the corresponding errors of the slopes were 0·18, 0·18, 0·12 and 0·16 g MJ^{-1}.

Figure 6 shows a plot of the dry weight of cultivars (at 35/37 DAS) against temperature. Dry matter increased with mean temperature for all cultivars in a manner similar to that for leaf area, but the proportion of the differences is larger than that for *L*.

DISCUSSION

The measurements of leaf area and light interception showed that *L* increased with mean temperature between 19·5 °C and 31 °C in all cultivars, consistent with work on the same

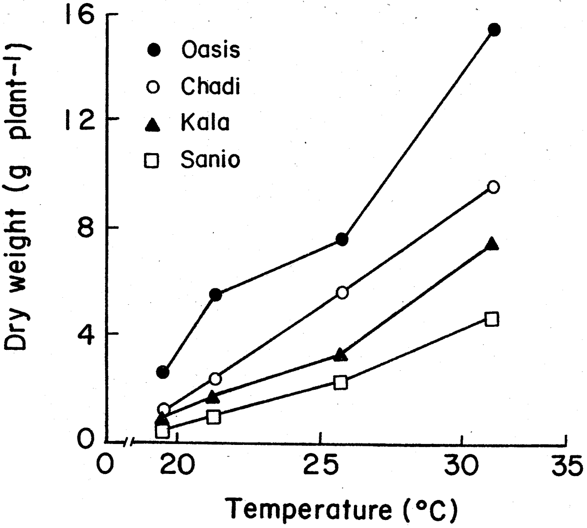

FIG. 6. Dry weight in g/plant 35–37 d after sowing versus temperature.

species by Hart and Wells (1965), Pearson (1975) and Squire *et al.* (1984), and also with work on other crops, e.g. *Vicia faba* (Dennett and Auld, 1980) and sugar beet (Milford and Riley, 1980). The optimum temperature, T_o, for leaf area development of these cultivars was at least 31 °C, consistent with an estimate by Ong (1983) that T_o is between 28 °C and 33 °C for millet development and with the temperature responses for developmental processes in the same cultivars, reported by Mohamed *et al.* (1988*a*, *b*). The slow rate of canopy development at low temperatures is accompanied by a reduction in photosynthetic rate, particularly below 24 °C (McPherson and Slatyer, 1973; Pearson and Derrick, 1977) and the retention of an increasing percentage of photosynthate in the leaves as temperature declines from day/night temperatures of 33/28 °C to 18/13 °C (Pearson, Bishop, and Vesk, 1977; Pearson and Derrick, 1977). There is also a reduction in meristem activity below 19/24 °C (Pearson, 1975).

The four cultivars showed large differences in the rates of canopy development and their relative rankings were the same at each temperature tested. Their transmission coefficients varied from 0·23 to 0·47, so were close to a value of 0·30 reported by Squire *et al.* (1984) for cv. BK 560. Monteith (1975) reported transmission coefficient values of 0·49 and 0·43 for the related crops sorghum and rye grass. Light interception is governed mainly by the leaf area, leaf geometry and optical properties of leaves. The leaf area depends on the speed with which leaves are produced (leaf appearance rate), how fast they grow (leaf extension rate) and the length of time for which they grow (duration of expansion). All of these are temperature-dependent processes. The results described here and by Mohamed *et al.* (1988*b*) have shown that the ranking of leaf appearance rate was Oasis > Chadi > Kala > Sanio and that leaf extension rates followed the same order. However, determination of the duration of expansion was beyond the scope of this study.

The differences in dry matter production at different temperatures were consistent with the differences in leaf area development. The severity of growth suppression by low temperatures differed between cultivars and is consistent with their sensitivity to low temperature. For example, the growth rate of Oasis at 19·5 °C is about 20% of that at 31 °C, whereas that of Sanio is only 10%. Sanio has already been shown to have a higher T_b (Mohamed *et al.*, 1988*a*, *b*) than other cultivars.

Estimates of the efficiency of dry matter production (*e*) differed by almost a factor of 3 between cultivars from 1·0 to 2·7 g MJ^{-1}. At 19·5 °C the observations were consistent with a lower value of (*e*), as reported for cv. BK 560 by Squire *et al.* (1984).

The measurements reported in this and the two preceding papers have shown that the germination behaviour of pearl millet cultivars is strongly associated with subsequent field performance. We suggest that selection of germplasm based on heat tolerance during germination could be usefully applied to millet and may be equally applicable to other crops, and that the thermal gradient plate has potential as a cheap, reliable and efficient tool for screening germplasm as well as for the investigation of physiological changes (Cole, 1972).

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