Expl Agric. (1988), volume 24, pp. 203–213
Printed in Great Britain

THE PHYSIOLOGICAL BASIS FOR YIELD DIFFERENCES BETWEEN FOUR GENOTYPES OF GROUNDNUT (*ARACHIS HYPOGAEA*) IN RESPONSE TO DROUGHT. II. SOLAR RADIATION INTERCEPTION AND LEAF MOVEMENT†

By R. B. MATTHEWS‡, D. HARRIS, J. H. WILLIAMS§,
and R. C. NAGESWARA RAO§

ODA Microclimatology Group, School of Agriculture, Sutton Bonington,
Loughborough, Leicestershire, England and §*International Crops*
Research Institute for the Semi-Arid Tropics, Patancheru PO,
Andhra Pradesh 502324, India

(Accepted 18 September 1987)

SUMMARY

Four genotypes of groundnut grown with limited irrigation during the post-rainy season in Central India produced similar amounts of dry matter per unit of intercepted solar radiation (e) before pod-filling, although different e values were observed during pod-filling. The relation between cumulative transpiration and intercepted radiation was similar for all genotypes. When drought became severe, fractional radiation interception (f) was reduced by folding of leaves, with little decrease in leaf area (L). The ratio $f/\sqrt{L}$ was used as an index of the degree of leaf folding and was correlated with leaf water potential. The degree of folding varied with genotype and may have contributed to the observed differences in e and the dry matter:water ratio (q). The genotype EC76446(292) had the smallest q and largest $f/\sqrt{L}$ ratio (the poorest radiation avoidance), while Kadiri 3 had the largest q and smallest value of $f/\sqrt{L}$.

R. B. Matthews, D. Harris, J. H. Williams y R. C. Nageswara Rao: *La base fisiológica para diferencias de rendimiento entre cuatro genotipos de cacahuete (*Arachis hypogaea*) como respuesta a la sequía. II. Intercepción de la radiación solar y movimiento de la hoja.*

RESUMEN

Cuatro genotipos de cacahuete cultivados bajo regimen de riego limitado durante la estación después de las lluvias en la India Central produjeron cantidades similares de materia seca por unidad de radiación solar interceptada (e) antes del relleno de la vaina, aunque se observaron distintos valores para (e) durante la etapa del relleno de la vaina. La relación entre la transpiración acumulada y la radiación interceptada era similar para todos los genotipos. Al agravarse la sequía, la intercepción de radiación fraccional (f) fue reducida mediante con el plegado de las hojas, con poca disminución del área foliar (L). Se utilizó la relación $f/\sqrt{L}$ como índice del grado de plegado de la hoja y fue correlacionado con el potencial hídrico foliar. El grado de plegado varió según el genotipo y puede haber contribuido a las diferencias observadas en e y la relación materia seca:agua (q). El genotipo EC76446(292) tuvo la menor q y mayor relación $f/\sqrt{L}$ (el evitar de radiación más pobre), mientras que Kadiri 3 tuvo la mayor q y menor valor para $f/\sqrt{L}$.

INTRODUCTION

This paper is part of a series describing the physiological basis for contrasting yield responses to drought by four groundnut genotypes. In Part I (Matthews

---

† Submitted as Journal Article No. 658 by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT).
‡ Present address: Oxford Forestry Institute, Oxford University, South Parks Road, Oxford, England.

et al., 1988) it was shown that despite similar amounts of water being transpired, the dry matter:water ratios (q) and, in particular, harvest indices (h) varied significantly between genotypes, resulting in dramatic differences in their pod yields (Y). A second approach is to examine differences in dry matter produced (W) by each genotype in terms of the solar radiation intercepted (S) and the amount of dry matter produced per unit of radiation intercepted (e), where $W = eS$.

The rate of dry matter accumulation (dw/dt) depends both on the leaf area index (L) of a crop, and on the orientation of this area with respect to the sun. Because photosynthetic rate per unit leaf area in groundnut usually shows a curvilinear response to increases in irradiance (Pallas and Samish, 1974), the rate of photosynthesis per unit of intercepted light increases as irradiance decreases. It follows that if the angle between the normal to a leaf plane and the solar beam increases, photosynthesis becomes more efficient but less radiation is intercepted. Less energy has to be dissipated by either evaporation or re-radiation; consequently leaf temperatures may be lower. This may be advantageous in the semi-arid tropics (SAT) where transpiration is often limited by drought, and without evaporative cooling leaf temperatures can often rise several degrees higher than air temperature (Gates, 1968) to a level at which severe tissue damage may occur (Sullivan *et al.*, 1977).

Some crop species, such as groundnut and cowpea, are able to respond to drought by paraheliotropism - folding and orienting their leaves - thereby reducing the intensity of radiation received. A corresponding increase in q has been reported in some species (Mooney *et al.*, 1977) and a lowering of the mean temperature of leaf tissue in others (Babu *et al.*, 1983; Shackell and Hall, 1979; Ehleringer and Forseth, 1980).

In this paper the contribution made by each of the components in the equation $W = eS$ to differences in dry matter produced by each of the genotypes is examined, and the possible influence of paraheliotropism on these components is considered.

MATERIALS AND METHODS

Four genotypes of groundnut (*Arachis hypogaea*) with a range of yield responses to drought were grown in a medium deep alfisol at ICRISAT, Patancheru, in Central India. Two of the genotypes, TMV 2 and Kadiri 3, are commonly grown by Indian farmers, while the other two, NC Ac 17090 and EC 76446(292) (hereafter referred to as NC and EC) are genotypes with large differences in performance in the ICRISAT drought screening programme. The crops were irrigated until 20 days after sowing (DAS) to ensure uniform establishment, then received no further water until 72 DAS and again at 107 DAS. Full details of the design and management of the experiment are given by Matthews *et al.* (1988).

At weekly intervals, a sample of ten plants was taken from each plot to determine leaf area and shoot dry matter. Three plants were selected at random from each sample and their leaf areas measured using a leaf-area meter (LICOR 3000). The leaf area for the whole sample was then estimated by dividing the total leaf weight of the sample by the specific leaf weight of the sub-sample. Leaf area index was calculated by multiplying this value by the population density. Dry weights of the 10 plants were then measured after drying for 48 h at 105°C. The coefficient of 1.65 used by Duncan *et al.* (1978) to adjust dry weights for the higher energy content of pods, based on the energy content of mature pods from well-irrigated crops, is inappropriate in the present droughted stands because of the lower ratios of kernel weight to pod weight obtained. Using the shelling percentage of well-irrigated crops, a revised conversion coefficient of 2.4 was therefore calculated for kernel tissue weights alone.

Whole spectrum solar radiation, both incident upon and transmitted through the foliage, was measured using tube solarimeters (Delta-T Devices) and their output recorded with a data-logger (Campbell Scientific Inc.) at half-hourly intervals throughout the season. The fraction of incident radiation intercepted by the crop (f) was estimated as the difference between incident and transmitted fluxes.

Bulk leaf water potential (ψ_1) of leaves in the top, middle and bottom layers of the canopy was measured using a hydraulic jack (Rajendrudu *et al.*, 1983) twice weekly from 54 to 91 DAS and weekly thereafter. Values from each layer were combined to give a mean value.

RESULTS

The relation between the energy-adjusted shoot dry matter and cumulated intercepted radiation for each genotype during the season, the slope of which is e, is shown in Fig. 1. Until pod filling, when about 300 MJ m^{-2} of radiation had been intercepted, there were no significant genotypic differences between the values of e, the mean value being 0.40 ± 0.07 g MJ^{-1}. However, from around the start of pod-filling at about 75 DAS, e declined for all genotypes. This implies a change in the efficiency of conversion of radiation into dry matter during pod filling, although it is possible that leaf damage from insects towards the end of the season may have contributed to these lower values. There were significant differences in e between genotypes during this stage; values (in g MJ^{-1}), estimated from the slopes of the regressions for each of the genotypes, were: TMV 2, 0.29 ± 0.05; Kadiri 3, 0.39 ± 0.05; NC, 0.35 ± 0.05; and EC, 0.27 ± 0.02. At the end of the season, all genotypes had intercepted the same amount of solar radiation but had produced different amounts of dry matter.

The relation between the dry matter:radiation quotient, e, and the dry matter:water ratio, q, can be expressed as $e = qr$, where r is a coefficient with units in kg water MJ^{-1}. The differences in e between the genotypes were primarily a consequence of variations in q rather than r. Indeed, when transpired water was plotted against cumulative intercepted radiation (Fig. 2), the slope

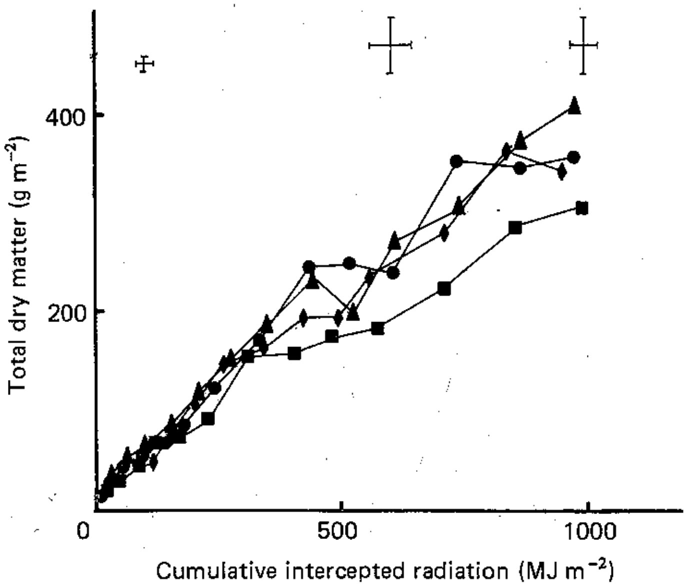

Fig. 1. Relation between accumulated shoot dry matter and intercepted radiation for the four groundnut genotypes, ● TMV 2, ▲ Kadiri 3, ◆ NC Ac 17090 and ■ EC 76446 (292). Typical standard errors are shown.

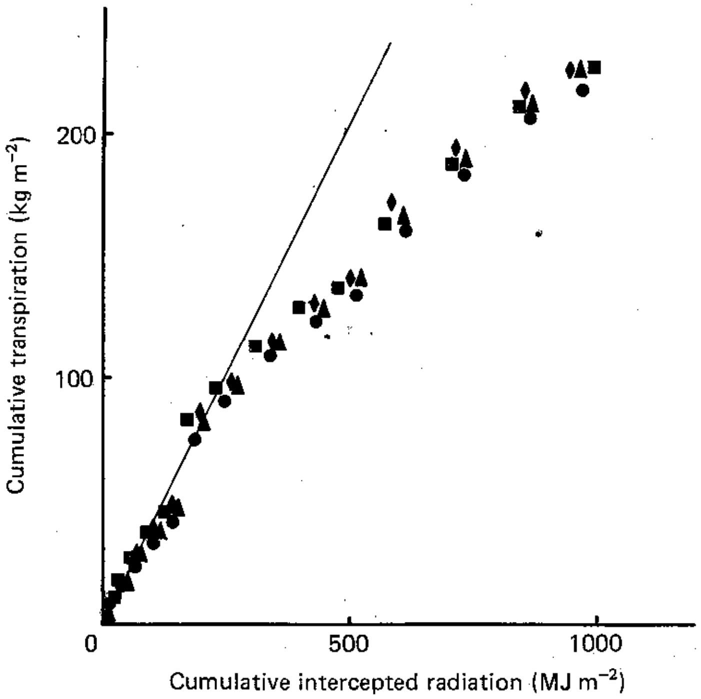

Fig. 2. Relation between intercepted radiation and transpired water. Line represents the latent heat of water (0.408 kg water MJ^{-1}). Symbols as for Fig. 1.

of the plot being r, there was little difference between genotypes. The line representing the latent heat of water (0.408 kg MJ^{-1}) is also shown; when water was not limiting at the beginning of the season, the values of the genotypes closely approached this line, but as water became scarce, they deviated significantly from it. The mean value of r over the season was 0.208 kg MJ^{-1}, about half that for the latent heat of water, implying that only about half of the intercepted radiation was dissipated as latent heat of vaporization, the remainder contributing in part to a rise in sensible heat of the vegetation.

There were differences in L between genotypes in the first part of the growing period, with EC consistently smaller and Kadiri 3 larger than the others. Towards the end of the season, damage to foliage by insect attack increased the variability in the measurements. The rate of increase of L slowed towards the end of each drying cycle and increased substantially after each irrigation as a result of renewed leaf production and expansion (Harris *et al.*, 1988).

Changes in fractional interception (f) throughout the season are shown in Fig. 3. Differences between the genotypes were small and not consistent throughout, so that for clarity only the mean of the four genotypes is shown. For comparison, the mean L is also shown. At no time did the canopy close completely; the highest value of f was 0.75, achieved by EC at 120 DAS. The onset of drought had a marked influence on f. From emergence, f increased steadily until about 50 DAS, after which the rate of increase declined as leaf growth was restricted by the decreasing availability of soil water. After the irrigation at 72 DAS, f increased rapidly at first as the leaves unfolded and the rate of leaf production and expansion increased, but began to fall sharply 10 days after the irrigation. As there was little change in L at this stage, this reduction in fractional interception was due to leaf folding and changes in leaf

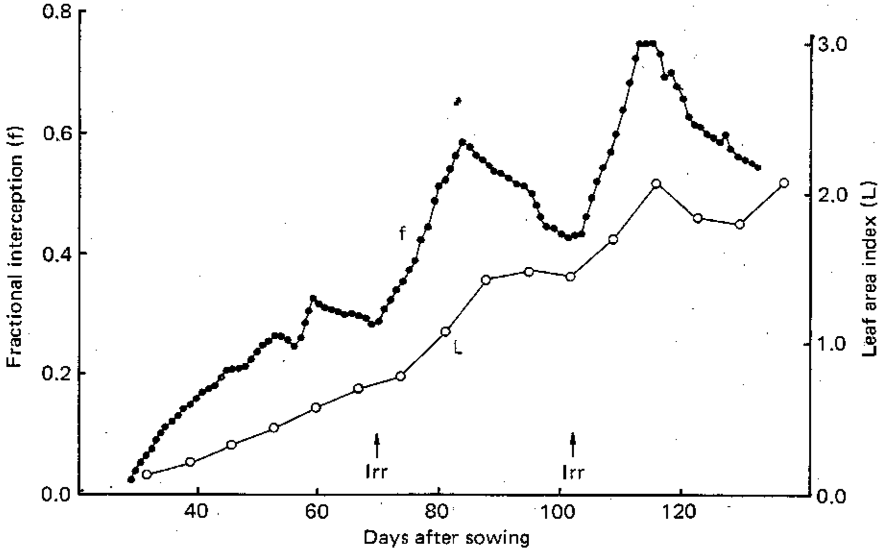

Fig. 3. Seasonal changes in fractional interception and leaf area index; 'Irr' denotes irrigation. Typical standard errors shown.

orientation, which allowed light to penetrate the canopy and reduced the radiation load on individual leaves. A similar pattern occurred after the irrigation at 107 DAS.

Radiation interception and leaf area

Canopy development in groundnut can be divided into four distinct stages. The first stage begins immediately after emergence, when each plant is a discrete unit and leaves do not merge with those of neighbouring plants. The second stage begins when plants begin to merge within rows, leading to the third stage when the shape of the canopy approximates a half-cylinder with its axis along the row and with a radius equal to the height of the plant (Fig. 4). The fourth stage begins when rows begin to merge and the canopy completely covers the ground. The duration of the first stage depends on the intra-row distance between plants, and does not last long. It was found that, for a 35 X 10 cm spacing, plants began to merge within rows when L was about 0.2, and approximated a complete half-cylinder when L was about 0.6. As full canopy closure was never achieved (Fig. 3), the following analysis is restricted to the third stage, for values when L was equal to or greater than 0.6.

If the leaf area in a length x of a crop row is L′ and the distance between rows is s, the leaf area index L is:

$$L = L'/(x.s).$$

If r is the effective radius of a row treated as a half-cylinder, then the volume of the row of length x is $\pi r^2 x/2$ and the leaf area density γ (leaf area per unit volume) is:

$$\gamma = \frac{L'}{\pi r^2 x/2} = \frac{2.L.s}{\pi r^2}.$$

It follows that provided plants expand in such a way that γ remains constant, L will be proportional to r^2. Similarly, for a given solar angle the fraction of incident radiation (f) intercepted by a row will be proportional to r, and hence to $\sqrt{L}$. This relation is valid only when the canopy is equivalent to a half-cylinder and cannot be assumed to hold before plants meet completely within rows, because no light is intercepted in the gaps between them.

The relation between f and $\sqrt{L}$ for each of the four genotypes was generally

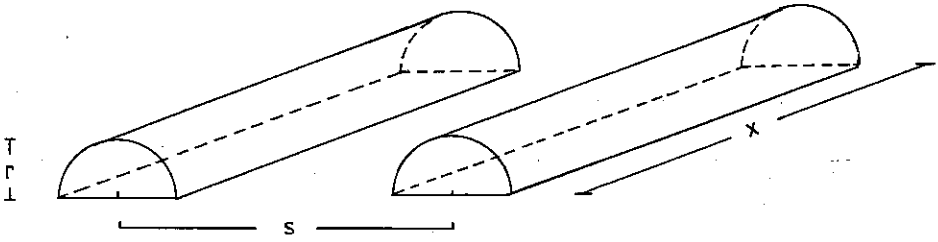

Fig. 4. Schematic representation of a row of groundnut, showing parameters used in calculations.

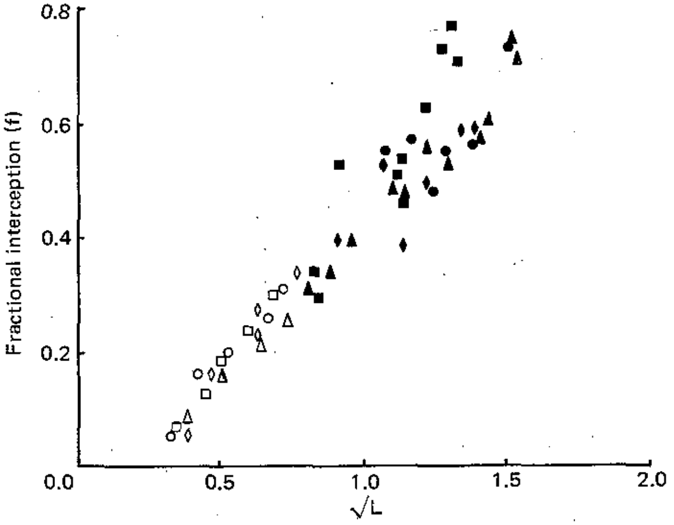

Fig. 5. Relation between fractional interception and $\sqrt{L}$. Symbols as for Fig. 1.

linear (Fig. 5), in agreement with the theory. Changes in the ratio of f to $\sqrt{L}$ during the season can be ascribed to changes in leaf area density. If the leaves fold due to stress, resulting in less interception for a given L, the 'effective' volume of the canopy decreases. Therefore, we have used the ratio $f/\sqrt{L}$ as an index of the degree of leaf folding. A small value for this ratio indicates a high degree of paraheliotropism. The mean values of $f/\sqrt{L}$ over the third phase of canopy development were: TMV 2, 0.446 ± 0.057; Kadiri 3, 0.419 ± 0.031; NC, 0.425 ± 0.046; and EC, 0.453 ± 0.071. Thus Kadiri 3 was able to shed more radiation for a given L than EC.

To examine in more detail how the onset of drought influences light interception, we considered the drying cycle between the irrigations at 72 and 107 DAS. The changes in $f/\sqrt{L}$ over this drying period, using L estimated by interpolation for days between weekly samples, are shown in Fig. 6. Throughout the whole of the period, L exceeded 0.6, so the assumption of the canopy approximating a half-cylinder, and hence the $f/\sqrt{L}$ ratio as an index of orientation, is valid.

For the first 10 days, there was an increase in $f/\sqrt{L}$ as existing leaves unfolded. However, unfolding was observed to occur within one to two days after release of stress, suggesting that the increase in $f/\sqrt{L}$ should have occurred over a much shorter time interval. The production of new leaves should not change $f/\sqrt{L}$ since any increase in leaf area is associated with an increase in interception. However, interpolation from the weekly samples may have overestimated L in the first few days, because of a time lag in leaf production after the release of stress, resulting in lower $f/\sqrt{L}$ values than in reality over this period. The exact length of time during which $f/\sqrt{L}$ increased is therefore uncertain.

It is clear, however, that the ratio rapidly decreased as drought became more severe, and fell in most genotypes to about 70% of its peak value. There were

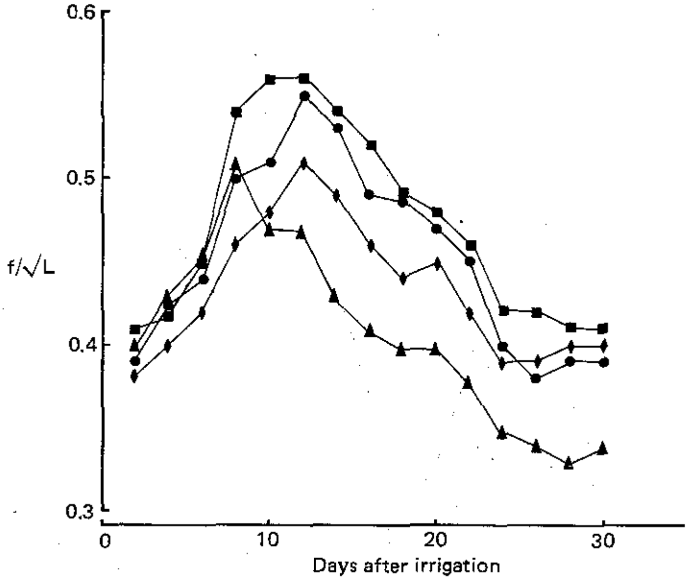

Fig 6. Changes in the ratio $f/\sqrt{L}$ during the period between irrigations at 72 and 107 DAS. Symbols as for Fig 1.

also significant genotypic differences, EC having a higher ratio than Kadiri 3, indicating that the former is less able to reduce its radiation load during stress. A similar analysis for the period from the irrigation at 107 DAS to final harvest was not attempted because of the confounding effects of defoliation by insects.

The relation between $f/\sqrt{L}$ and mean leaf water potential ψ_1 measured periodically during the drying cycle (Fig. 7) shows that the ratio is very sensitive to changes of potential in the range -0.8 to -1.2 MPa, below which a further decrease in ψ_1 has little effect. There were no significant differences between

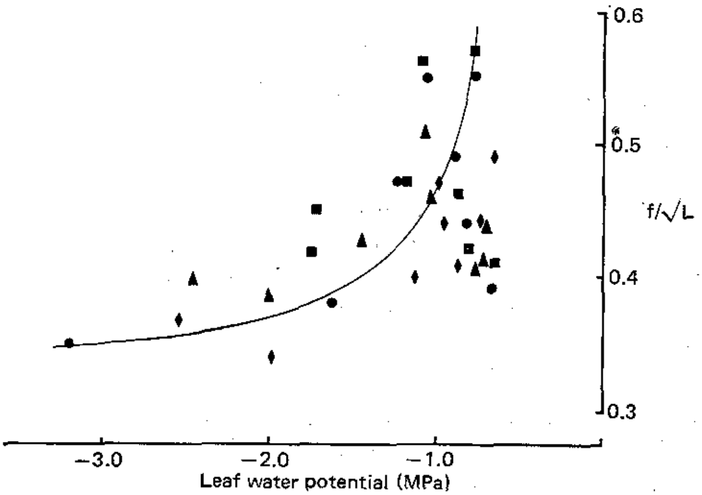

Fig. 7. Relation between the ratio $f/\sqrt{L}$ and leaf water potential (ψ_1). Symbols as for Fig. 1.

genotypes in this relation. Genotypic differences in the ability to fold leaves, thereby reducing radiation load, may be related to differences in plant water status, but this requires further investigation.

DISCUSSION

As all genotypes had intercepted the same amount of solar radiation at the end of the season, differences in final dry matter production were due to the differences in e that became apparent at the start of pod-filling (Fig. 1). Moreover, the close relation between cumulative transpiration and intercepted radiation suggests that these differences in e were due to the differences in q reported in Part I.

There was a correlation between the values of q and the degree of paraheliotropism exhibited by the genotypes. The genotype EC had the smallest value of q and the largest $f/\sqrt{L}$ ratio (Fig. 6), while Kadiri 3 with the largest q had the smallest $f/\sqrt{L}$ ratio, i.e. the greatest degree of paraheliotropism. However, as the drying cycle progressed the differences in $f/\sqrt{L}$ were maintained (Fig. 6), indicating that the higher q of Kadiri 3 was associated with more acutely angled leaves in all conditions of water availability. Similar increases in q as leaves became more vertical were found in *Atriplex hymenelytra* (Mooney *et al.*, 1977), apparently because photosynthetic rates were saturated at higher light intensities but transpiration rates were not.

The implications of these differences for selection are important. A genotype such as EC may be able to maximize light interception when water is plentiful, but it would be at a disadvantage under drought, since it would not have the ability to shed a proportion of incoming solar radiation by folding its leaves. Kadiri 3, on the other hand, by reducing the radiation intensity on its leaf surfaces, would be able to reduce water loss without a proportional decrease in photosynthesis, thereby optimizing the use of a scarce resource.

Various reports have indicated that paraheliotropism may also help to reduce leaf temperatures. Wainwright (1977) found that orientation by stressed leaves of desert lupin could reduce the solar radiation they absorbed by up to 40%. Shackell and Hall (1979) observed that the leaf folding in cowpeas reduced leaf temperatures by up to 5.5°C. However, in the present study, despite the observed variation in paraheliotropism, no consistent differences in leaf temperature were found between the genotypes. This may have been because any small differences in temperature as a result of leaf folding were swamped by a strong upward sensible heat flux from the very hot soil (in excess of 55°C). If this was so, it would suggest that the role of paraheliotropism in reducing canopy temperatures is of little consequence for droughted crops growing near a hot dry soil surface. It is more likely that leaf folding helps to minimize damage to the photosynthetic apparatus from high light intensities in the presence of high temperature (Ludlow and Bjorkman, 1984). This requires further investigation.

The degree of folding was influenced by leaf water potential (Fig. 7), the most sensitive range falling between −0.8 and −1.2 MPa. A similar relation between stomatal conductance and leaf water potential was observed in groundnut grown in the field (Bennett *et al.*, 1984). The presence of mechanisms for both stomatal closure and leaf movement may provide a capability for optimizing water loss and restricting leaf temperature over a greater range of environmental conditions than would be possible with either of these characteristics alone.

The observed changes in leaf orientation indicate that groundnut has mechanisms which optimize energy interception when water is freely available but maximize q when water becomes limiting. Grancher and Bonhomme (1972) also showed that leaves of cowpea seedlings were orientated towards the sun in the morning when conditions were favourable for photosynthesis, but not in the afternoon, thus preventing high leaf temperatures as water stress developed later in the day. Though little studied, the capacity of both diaheliotropism and paraheliotropism to increase plant productivity when water is available and to improve the chance of survival during drought may contribute significantly to legume adaptation to the semi-arid areas of the world.

Acknowledgements. This work was sponsored by the UK Overseas Development Administration and ICRISAT. Special thanks must go to G. N. Ramchandram, Prabodhan Reddy and Arjun Rao for technical assistance in carrying out the work. We also acknowledge the advice of Professor J. L. Monteith and other members of the ODA unit during the preparation of this manuscript.

Note. Reference to commercial products in this paper does not imply endorsement or recommendation by ICRISAT in preference to other similar products.

REFERENCES

Babu, V. R., Murty, P. S. S., Reddy, G. H. S. & Reddy, T. Y. (1983). Leaflet angle and radiation avoidance by water-stressed groundnut (*Arachis hypogaea* L.) plants. *Environmental and Experimental Botany* 23:183–188.

Bennett, J. M., Boote, K. J. & Hammond, L. C. (1984). Relationships among water potential components, relative water contents, and stomatal resistance of field-grown peanut leaves. *Peanut Science* 11:31–35.

Duncan, W. G., McCloud, D. E., McGraw, R. L. & Boote, K. J. (1978). Physiological aspects of peanut yield improvement. *Crop Science* 18:1015–1020.

Ehleringer, J. & Forseth, I. (1980). Solar tracking by plants. *Science* 210:1094–8.

Gates, D. M. (1968). Transpiration and leaf temperatures. *Annual Review of Plant Physiology* 12:21–238.

Grancher, C. V. & Bonhomme, R. (1972). The use of solar energy by a crop of *Vigna sinensis.* I. Theoretical study of the effect of leaf heliotropism on the interception of radiation. *Annales Agronomiques* 23:407–417.

Harris, D., Matthews, R. B., Nageswara Rao, R. C. & Williams, J. H. (1988). The physiological basis for yield differences between four genotypes of groundnut (*Arachis hypogaea*) in response to drought. III. Developmental processes. *Experimental Agriculture* 24:215–226.

Ludlow, M. M. & Bjorkman, O. (1984). Paraheliotropic leaf movement in Siratro as a protective mechanism against drought induced damage to primary photosynthetic reactions: damage by excessive light and heat. *Planta* 161:505–518.

Matthews, R. B., Harris, D., Nageswara Rao, R. C., Williams, J. H. & Wadia, K. D. R. (1988). The physiological basis for yield differences between four genotypes of groundnut (*Arachis hypogaea*) in response to drought. I. Dry matter production and water use. *Experimental Agriculture* 24:191–202.

Mooney, H. A. Ehleringer, J. & Bjorkman, O. (1977). The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra. Oecologia*, Berlin 29:301–310.

Pallas, J. E. Jr & Samish, Y. B. (1974). Photosynthetic response of peanut. *Crop Science* 14:478–482.

Rajendrudu, G., Singh, M. & Williams, J. H. (1983). Hydraulic press measurements of leaf water potential in groundnuts. *Experimental Agriculture 19:287–293.*

Shackell, K. A. & Hall, A. E. (1979). Reversible leaf movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. *Australian Journal of Plant Physiology* 6:265–76.

Sullivan, C. Y., Norcio, N. V. & Eastin, J. D. (1977). Plant responses to high temperatures. In *Genetic Diversity in Plants*, 301–317 (Eds A. Muhammad, R. Aksel and R. C. von Borstel). New York, USA: Plenum Press.

Wainwright, C. M. (1977). Suntracking and related leaf movements in a desert lupin (*Lupinus arizonicus*). *American Journal of Botany* 64:1032–1041.