THE PHYSIOLOGICAL BASIS FOR YIELD DIFFERENCES BETWEEN FOUR GENOTYPES OF GROUNDNUT (*ARACHIS HYPOGAEA*) IN RESPONSE TO DROUGHT. III. DEVELOPMENTAL PROCESSES†

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SUMMARY

Rates of leaf development in four groundnut genotypes were found to depend primarily on temperature, although there was a linear relation between the thermal time to produce one leaf and mean leaf water potential below − 0.6 MPa. Flower, peg and pod production was analysed in relation to leaf number, since this integrated effects of temperature and water status.

When water was not limited, the ratio of pod number:peg number was about 0.8 for all four genotypes. During drought only one genotype (TMV 2) maintained this value, while for the other genotypes the ratio was approximately 0.15. Genotypes also showed different patterns of development during recovery from drought. TMV 2 maintained relatively high values of partitioning factor throughout the pod-filling period, resulting in the largest harvest index and pod yield. Kadiri 3 achieved the second largest harvest index and pod yield by maintaining production of pegs during drought and only forming pods when stress was relieved.

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

RESUMEN

Los ritmos de desarrollo de la hoja en cuatro genotipos de cacahuete resultaron depender principalmente de la temperatura, aunque existe una relación lineal entre el tiempo térmico para producir una hoja y el potencial hídrico foliar medio por debajo de − 0,6 MPa. Se analizó la producción de la flor, papila y vaina en relación con el número de hojas, puesto que esto integró los efectos de la temperatura y estado hídrico.

Cuando el agua no estaba limitada, la relación de número de vainas:número de papilas fue en el orden de 0,8 para los cuatro genotipos. Durante la sequía, sólo un genotipo (TMV 2) mantuvo este valor, mientras que la relación para los demás genotipos fue aproximadamente 0,15. Los genotipos también mostraron distintos patrones de desarrollo durante la recuperación de la sequía. TMV 2 mantuvo valores del factor de repartición a lo largo de período de relleno de la vaina, dando como resultado el mayor índice de cosecha y rendimiento de vainas. Kadiri 3 logró el segundo índice de cosecha y rendimiento de cosecha, manteniendo la producción de papilas durante la sequía y sólo formando vainas cuando se había aminorado la falta de agua.

INTRODUCTION

Matthews *et al.* (1988a) reported that four contrasting groundnut genotypes produced different pod yields (Y) during drought despite extracting similar amounts of water. These differences could be ascribed partly to differences in the dry matter:water ratio (q) but mainly to differences in the harvest index (h). The differences in h were not associated with different patterns of water use during the season as has been suggested by some authors (e.g. Passioura, 1972).

In this paper we consider how h is influenced by the pattern of reproductive development of the genotypes. Matthews *et al.* (1988a) showed that h could be expressed as the mean value over the season of the 'partitioning factor', p, (dy/dw) weighted by the crop growth rate (dw/dt):

$$h = \frac{\int (dy/dw)(dw/dt)dt}{\int dw/dt . dt} = \frac{\int (p . dw/dt)dt}{W} \tag{1}$$

where W is the total dry weight at final harvest.

In a stand of groundnut, rates of leaf and branch production influence the area of the foliage and its potential for producing assimilates, while rates of flower and seed production define the number of reproductive sinks for these assimilates. Since development is a sequential process, the final number of mature pods depends on a series of previous developmental phases, each of which may be affected to different degrees by drought.

Recent work by Leong and Ong (1983) and Ong (1984) showed that rates of development in groundnut were primarily determined by temperature, and were insensitive to mild water stress. However, the stress which these workers were able to impose in experimental glasshouses was less severe than that often encountered in the semi-arid tropics (SAT).

Leong and Ong (1983) found that rates of development increased linearly between a base temperature, T_b, of 10°C at which rates were zero and an optimum temperature, T_o, of 30°C. Thus, under non-limiting conditions, developmental events occur at a fixed interval of thermal time, θ, (day-degrees, °Cd) defined by the relation:

$$\theta = t(T - T_b) \tag{2}$$

where T is the mean daily temperature and t the duration of a developmental phase, or the time for a discrete event to occur such as the production of one leaf. This concept of thermal time is used here to analyse how patterns of development affected partitioning of dry matter during drought, and how they contributed to differences between the genotypes in p, h and hence final yield.

MATERIALS AND METHODS

Four groundnut genotypes with contrasting drought tolerance were grown on a moderately deep red Alfisol in the post-monsoon season at the International

Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India. Three genotypes, TMV 2, NC Ac 17090 (hereafter referred to as NC) and EC 76446 (292) (referred to as EC) had an upright-bunch sequential branching growth habit while the fourth, Kadiri 3, was a semi-spreading alternate branching type. After sowing, the genotypes were irrigated lightly until 17 days after sowing (DAS) to ensure uniform establishment. Subsequently they received water only at 72 and 107 DAS. Full details are given by Matthews *et al.* (1988a).

From 18 DAS, 10 plants of each genotype were sampled every week from each plot, and the numbers of pegs, pods and leaves were counted. Plants were subsequently used for dry weight measurements as described by Matthews *et al.* (1988a). The numbers of flowers per plant and the time taken for the stands to begin flower, peg and pod production were determined by daily observation.

Dry-bulb air temperature above the crop was measured using an aspirated psychrometer unit (Delta-T Devices) and the soil temperature at 5 cm depth was measured in each plot using thermocouples. Temperatures were logged automatically every half-hour throughout the experiment.

Bulk leaf water potential, ψ_1, was measured twice weekly between 54 and 91 DAS and weekly thereafter, using a hydraulic jack (Rajendrudu *et al.*, 1983). Values of ψ_1 were obtained every two hours for individual fully-expanded leaflets taken from the top, middle and bottom layers of the canopy in each plot, and combined to give a mean value.

RESULTS

The relation between main stem leaf number and accumulated thermal time (calculated using air temperature and $T_b = 10°C$) is shown in Fig. 1. Rates of leaf appearance were estimated by linear regression of the data within each of the five periods shown. The reciprocals of these rates are the thermal times, θ, (°Cd) required to produce one leaf (Table 1). In general, θ was larger during periods when drought was allowed to develop. Some information is lost by calculating regressions; in particular, leaf production rates for the weeks after the irrigations at 72 and 107 DAS were very similar to the rates calculated during the first period when stress was minimal, suggesting that leaf production was very responsive to hydration. Genotypes maintained consistent rankings throughout, and separation between genotypes became more pronounced with time and level of stress.

The relation between θ and mean leaf water potential (ψ_1), measured at 0800 local time for all periods in Fig. 1, showed a strong correlation between the two variables with no significant differences between genotypes (Fig. 2). The dotted line indicates the mean thermal time of the four genotypes calculated during the period 18–46 DAS when stress was minimal.

The numbers of days and degree-days taken by each genotype to begin flower, peg and pod production is shown in Table 2. Soil temperature at 5 cm depth was used to calculate θ, since the meristems responsible for all three
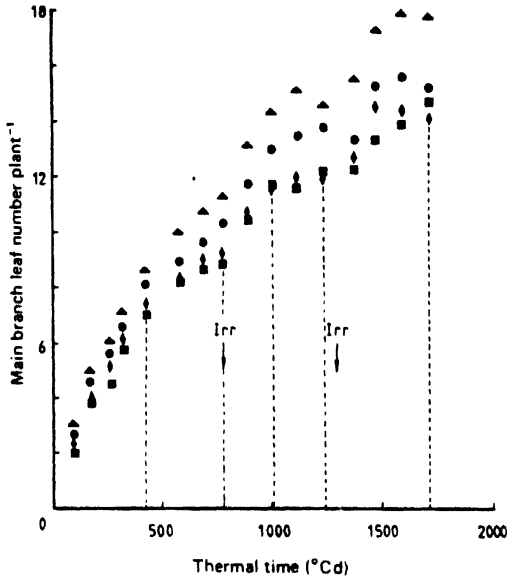
Fig. 1. Relation between the number of leaves per plant (up the main stem) and accumulated thermal time for the four groundnut genotypes, ●, TMV 2; ▲, Kadiri 3; ◆, NC Ac 17090; and ■, EC 76446 (292). 'Irr' indicates time of irrigation.

Table 1. *Thermal time (°Cd) required to produce one leaf*

Period (DAS)	TMV 2	Kadiri 3	NC	EC
18–46	65	63	69	70
46–74	162	129	199	203
74–88	86	72	89	77
88–102	296	353	473	—
102–123	194	100	100	155

Table 2. *Time to the start of the reproductive phases (DAS) for four ground-nut genotypes, with equivalent thermal times (°Cd) in brackets*

	TMV 2	Kadiri 3	NC	EC	SE
Flowering	38 (479)	43 (534)	39 (492)	41 (510)	4.8
Pegging	63 (813)	64 (828)	75 (996)	69 (905)	10.8
Podding	75 (996)	75 (996)	78 (1024)	82 (1077)	6.9

processes appear to respond to soil temperature rather than air temperature (Leong and Ong, 1983).

Flowering began between 38 and 43 DAS at a time when plants were still small. As neutron probe measurements (Matthews *et al.*, 1988a) showed that the range of soil water deficit was only 21–27 mm, plants were not exposed to significant stress at this stage and the thermal time to flowering of Kadiri 3 (534 °Cd) is very close to the value (538 °Cd) obtained by Leong and Ong (1983) for this genotype.
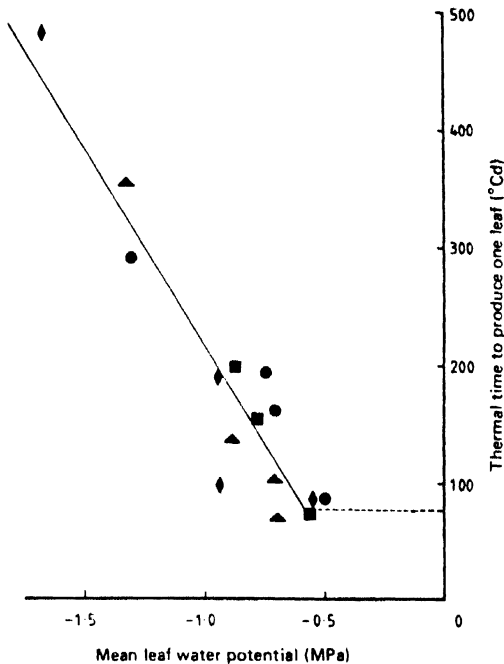
Fig. 2. Relation between the thermal time required to produce one leaf and mean leaf water potential. Regression equation, y = 33.11 x − 115 (r² ≈ 0.88). Dotted line represents genotype mean for the period 18–46 DAS (minimal stress). Symbols as in Fig. 1.

The thermal times to the onset of pegging (813-996 °Cd) and podding (996-1077 °Cd) were considerably longer than the estimates of Leong and Ong (1983) for unstressed Kadiri 3 (669 °Cd and 720 °Cd, respectively). Between the start of flowering and the first production of pegs and pods, plant water potentials fell to around − 1.1 MPa and the soil water deficit reached 52 mm. It is therefore probable that shortage of water before the irrigation at 72 DAS delayed reproductive development, but the extent to which it influenced each process is difficult to assess because of the sequential nature of development and the change of stress with time.

The course of flower production with time (Fig. 3) shows that rate of flowering was sensitive to irrigation, particularly in Kadiri 3. The flush of new flowers after the irrigation at 72 DAS suggests that the number produced before that irrigation was limited by drought. Until the irrigation at 72 DAS, the earlier a genotype flowered the faster its flower production rate.

However, expressed on the basis of leaf number, flower production was virtually identical in all genotypes except Kadiri 3 (Fig. 4a). In all genotypes, flowering began only when six or seven leaves had been produced on the main stem, but Kadiri 3 subsequently produced fewer flowers per leaf than the others until after the irrigation at 72 DAS. Peg production data were more variable,
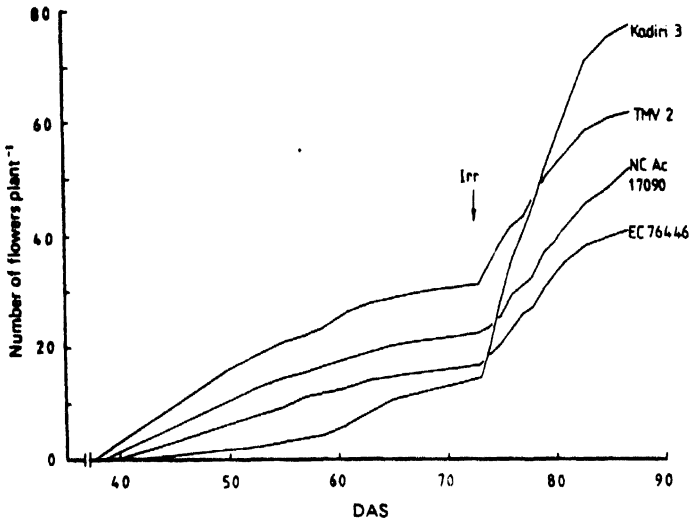
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Fig. 3. Cumulative total number of flowers per plant.

but again Kadiri 3 produced the fewest pegs per leaf until later in the season (Fig. 4b). Similarly, the relation between pod number and leaf number (Fig. 4c) was approximately the same for all genotypes except Kadiri 3 over a wide range of leaf numbers, irrespective of water status, and only Kadiri 3 responded to irrigation at 107 DAS.

Yields are determined by the number of mature pods produced and their final size. Pod numbers depend on the numbers of pegs produced and the proportion of these pegs that become pods, while peg number is determined by the number of flowers and the proportion of flowers which become pegs. Finally, the number of flowers depends on the number of leaves subtending reproductive nodes and the number of flowers in each. The effects of drought and genotype on these proportions or 'partial reproductive efficiencies' are shown in Fig. 5.

Kadiri 3 and EC began producing pegs once they had produced similar numbers of flowers and then maintained similar rates of peg production per flower (Fig. 5a). However, Kadiri 3 eventually produced more pegs than EC because it produced more flowers. Both TMV 2 and NC had produced more flowers by the time they started producing pegs compared to the other two genotypes, but subsequently the rate of peg production per flower was higher in TMV 2 than in NC. On average TMV 2 produced almost three times as many pegs per flower as did NC.

The relation between the number of pods and the number of pegs (Fig. 5b) falls into two categories. The first group of points (line A) includes all data for NC, EC and Kadiri 3 (except for data from 109 DAS) after stress was relieved by the irrigation at 107 DAS, together with *all* data for TMV 2. The second
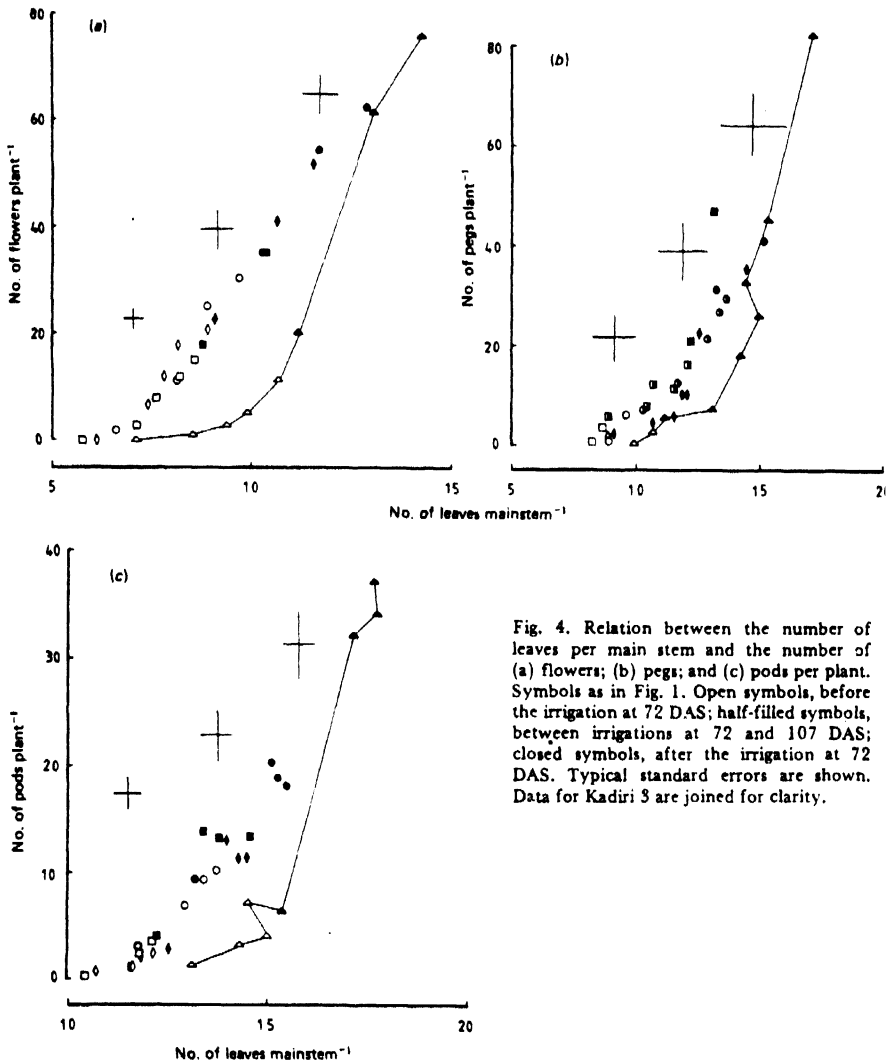
Fig. 4. Relation between the number of leaves per main stem and the number of (a) flowers; (b) pegs; and (c) pods per plant. Symbols as in Fig. 1. Open symbols, before the irrigation at 72 DAS; half-filled symbols, between irrigations at 72 and 107 DAS; closed symbols, after the irrigation at 72 DAS. Typical standard errors are shown. Data for Kadiri 3 are joined for clarity.

group of points includes all data from the period of stress before the irrigation at 107 DAS for NC, EC and Kadiri 3, when very few pegs were initiated and fewer developed into pods (line B).

TMV 2 was able to maintain a peg production efficiency of about 0.8 whether stressed or not, but the other three genotypes had an efficiency of only about 0.15 during drought. After the irrigation this increased to 0.8, although Kadiri 3 took longer to reach this figure because irrigation produced a further flush of flower, peg and pod production, hence the anomolous point at 109 DAS (see also Fig. 3). However, many of the new pods produced after
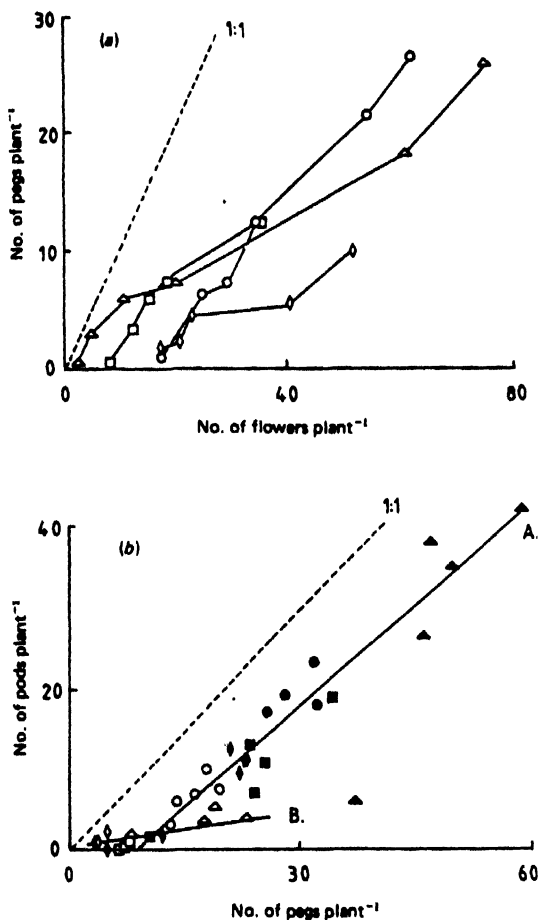
Fig. 5. Partial reproductive efficiencies: (a) relation between the number of pegs and the number of flowers per plant; and (b) relation between the number of pods and the number of pegs per plant. Symbols as in Fig. 1. Open symbols represent harvests before, and closed symbols after, the irrigation at 107 DAS. Regression equations (± standard errors): for A, $y = 0.814$ (± 0.06) $x - 6.4$ (± 3.9), $r^2 = 0.71$, and for B, $y = 0.149$ (± 0.04) $x - 0.5$ (± 0.9), $r^2 = 0.58$.

the irrigation at 107 DAS did not contribute to economically useful yield, because there was not enough time for them to develop into mature pods containing kernels before final harvest at 137 DAS. Only TMV 2 (with 1.9 g plant^{-1}) and Kadiri 3 (1.4 g plant^{-1}) produced mature kernels.

The consequences for partitioning of dry matter to pods of these varietal differences in development are shown in Fig. 6. High values of p for TMV 2 reflect the early and continued commitment to pod growth of this genotype. The rate of increase of p in Kadiri 3 was similar to that in TMV 2, but p was lower throughout the pod-filling phase because rapid pod filling began later.
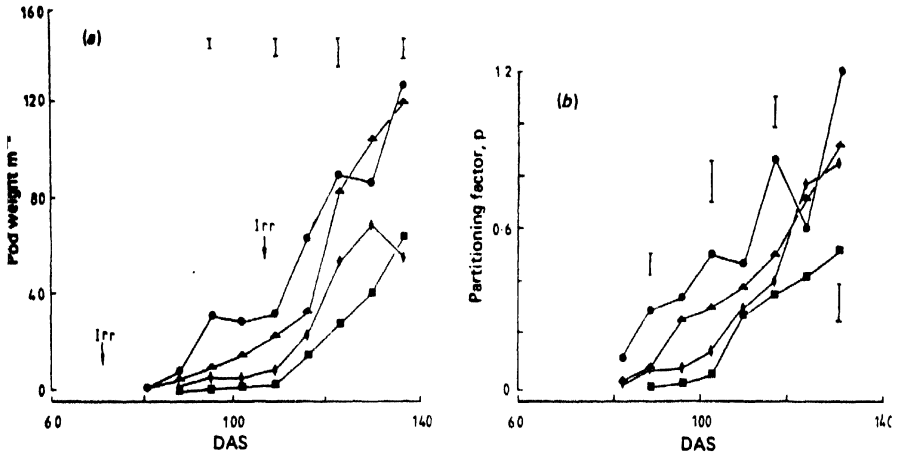
Fig. 6. Time course of (a) pod weight; and (b) partitioning factor, p (see text). Symbols as in Fig. 1.
Vertical bars are standard errors of the mean.

Delays in pod filling were even more marked in NC and EC. Towards the end of the season there was a rapid increase of p in NC, but this occurred too late to improve final yield.

DISCUSSION

At the levels of drought achieved in this field experiment, development was slowed more than in glasshouse trials described by Leong and Ong (1983) and Ong (1984). It was not possible to analyse flower, peg and pod production directly in terms of plant water potential, because all these processes depend to a certain extent on the state of ontogeny of the plant. In addition, none of these processes was measured for long enough to compute reliable mean rates of production with respect to water potential. However, leaf number was measured throughout the experiment, and leaf production rate was found to be very sensitive to drought. The thermal time required to produce one leaf increased linearly with decreasing leaf water potentials below a threshold of about −0.6 MPa. This relation was the same for all genotypes, despite large differences in leaf number at any one time. Leaf number could therefore be used as a common basis for the analysis of other developmental processes since it expressed the combined influence of temperature and water deficit on ontogeny.

Kadiri 3 was clearly different from the upright-bunch genotypes, as a consequence of its different growth habit and longer time to maturity. Rates of flower production per leaf were similar in all the upright-bunch genotypes (Fig. 4a), as were rates of peg and pod production per leaf (Figs 4b and c). In each of these cases, the semi-spreading Kadiri 3 produced more leaves before it

started producing flowers, pegs and pods. Subsequently, the rate of flower, peg and pod production per leaf was smaller than in the other genotypes until after irrigation. It appears from Fig. 4b that the number of pegs per leaf increased after irrigation in all genotypes, suggesting that this stage of development was relatively more sensitive to plant water deficit than was the flowering or podding.

The yield strategy of TMV 2 was to produce and fill pods at a moderate but constant rate, irrespective of changes in the intensity of drought. This is consistent with the pattern of flowering, pegging and podding described here. In complete contrast, the drought sensitive character of Kadiri 3 resulted in a late flush of pods which could not mature in the time available. Final pod yields in the dry treatment ranged from TMV 2 and Kadiri 3 (125 and 122 g m^{-2}, respectively) to NC and EC (93 g m^{-2} and 63 g m^{-2}, respectively) (Matthews *et al.*, 1988a). The higher yield of TMV 2 compared with NC appears to be a consequence of the greater number of leaves, and therefore pods, in the former. Leaf number alone cannot account for the very low yield of EC. In this genotype, weight per pod was also small, either through a lack of assimilate or through poor allocation of assimilate to pods, reflected in relatively low values of p (Fig. 6b).

Many authors (e.g. Underwood *et al.*, 1971; Boote *et al.*, 1976; Vivekanandan and Gunasena, 1976; Pallas *et al.*, 1979) have reported that temporary water stress during the reproductive phase reduced pod number to a greater extent than weight per pod at final harvest. This is true only when sufficient water is available later in the season to allow adequate production of assimilates. Underwood *et al.* (1971) and Lenka and Misra (1973) reported that drought during the pod-filling phase reduced weight per pod.

In the present work, it was difficult to identify which, if any of the reproductive processes was most sensitive to drought, although peg production was perhaps stimulated most by irrigation (Fig. 4b). This may have been an artefact of the timing of the irrigations, and no firm conclusions are possible. However, Ong (1984) showed that the rate of peg production declined rapidly at pre-dawn water potentials below −0.8 MPa. In the present experiment, much of the pegging activity took place when ψ_1 (measured 2 h after sunrise) was between −0.9 and −1.6 MPa.

Billaz and Ochs (1961) found that numbers of fruit set were least when drought was imposed between 50 and 80 DAS. It is significant that the bulk of pegs are produced during this period. Several authors (Lenka and Misra, 1973; Lin *et al.*, 1963; Fourrier and Prevot, 1958) have found that flower numbers were reduced by drought, and this reduction was greatest when drought was imposed near the period of peak flower production. However, flower number itself may not be a reliable indicator of potential peg production which also depends on successful fertilization of flowers. Several workers (Lee *et al.*, 1972; Bhatia *et al.*, 1984) have reported that water stress impairs fertilization in groundnut. Although irrigation produces a further flush of flowers (see Fig. 3 and Ono *et al.*, 1974; Boote *et al.*, 1976) and enhances peg formation, yield

will increase only if the resulting extra pods are filled. If such an irrigation is late or of only temporary benefit, then these later pods will not reach maturity. In such a case, drought during the pegging phase could be critical.

Much of the work on drought-sensitive phases in groundnut has assumed that the effect of water stress operates within each phase separately, and that water is not limited during earlier or subsequent phases. This is unrealistic in crops grown in the SAT on stored water where long periods of drought of progressively increasing intensity may be experienced. When irrigation is available it often relieves drought for only a short time. There are thus many possible interactions between plant water status and stage of growth, and although groundnut has some ability to compensate later for poor growth early in the season, it is often not possible to delay harvesting to take advantage of this compensation. The difference between TMV 2 and Kadiri 3 illustrates this point. Without the final irrigation it is unlikely that Kadiri 3 would have filled any pods, whereas at least some yield would have been obtained from TMV 2.

CONCLUSION

All four groundnut genotypes used similar quantities of water and solar radiation, but produced different amounts of dry matter (W) and pod weights (Y); the efficiency of resource use and partitioning to reproductive structures were therefore identified as the main sources of variation in yield (Matthews *et al.*, 1988a). As the relation between transpired water and intercepted radiation was similar for all genotypes, variation in the dry matter:water ratio (q) was assumed to be responsible for differences in the dry matter:radiation quotient (e) (Matthews *et al.*, 1988b).

There were small differences between genotypes in the timing and rates of water extraction from different depths and in early root growth (Matthews *et al.*, 1988a) but it was not possible to establish a link between these and the variations in q or h. However, subtle differences in the pattern of water extraction may have explained conflicting results from some of the genotypes when grown in conditions different from those in the present work, emphasizing the need to match carefully genotype with environment.

There was some evidence that differences in q were dependent on canopy architecture. Genotypes able to fold their leaves to reduce the intensity of solar radiation on their foliage also had higher values of q (Matthews *et al.*, 1988b). It was suggested that leaf movement may allow flexibility in maximizing radiation interception when water is plentiful, and minimizing radiation interception and maximizing q when water is scarce.

Variation in h accounted for the largest proportion of variation in Y, suggesting that the fastest progress might be made by selecting for this character. The results presented in this paper show that differences in the onset, rate and duration of reproductive growth were the cause of the variation in h. Three 'strategies' were apparent. The first involved early production of flowers, pegs and pods, with subsequent filling of the pods at a mode to but ----

constant, rate despite the drought. In the second, reproductive development started late, but many pegs were produced which developed into pods once water again became available late in the season. Similar yields were obtained from these two differing strategies. The third strategy resulted in poor yields because reproductive development was sensitive to drought, and the onset of rapid pod growth was delayed to such an extent that almost no kernels were produced by final harvest.

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

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

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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