

The Response of Groundnut (*Arachis hypogaea* L.) to Timing of Irrigation

I. DEVELOPMENT AND GROWTH

C. M. STIRLING¹, C. K. ONG² and C. R. BLACK

Department of Physiology and Environmental Science, University of Nottingham, School of Agriculture, Sutton Bonington, Loughborough, Leics. LE12 5RD, UK

Received 23 January 1989

ABSTRACT

A timing-of-irrigation experiment was conducted in controlled-environment glasshouses, in which a finite quantity of water was applied to four stands of groundnut (*Arachis hypogaea* L.) at different stages of the growing season. Irrigation schedules were broadly divided into two periods; sowing to pod initiation and pod initiation to final harvest. Within these periods two levels of soil moisture deficit were imposed by withholding or applying limited amounts of irrigation at regular intervals.

Shoot dry matter yields were hardly affected but pod yields were more than 4-fold lower in early- than in late-irrigated stands. Thermal time was used to separate the effects of temperature and water stress on developmental processes. The degree-day requirement for peg initiation was similar in all treatments but late-irrigation delayed pod development by about 200 °Cd. The effect of timing of irrigation on pod yield operated mainly through its influence on the duration of pod production, which was closely linked to the rate and duration of canopy expansion late in the season. The insensitivity of pod yield to early moisture deficits reflected the extreme plasticity of growth and development in groundnut, since most processes resumed rates similar to the pre-stress levels in early-irrigated stands once stress was released.

Key words: Groundnut, irrigation, growth, development.

INTRODUCTION

The majority of the world's groundnut crop is grown under rain-fed conditions in the semi-arid tropics. However, due to a combination of high evaporative demand and variable rainfall, average yields (800–900 kg ha⁻¹) are less than one-third of those achieved under more favourable growing conditions in the USA (FAO, 1980). To ameliorate the effects of uncertain rainfall irrigated groundnut production has increased greatly, with the aim of stabilizing rather than increasing yields. The irrigation water most commonly available to subsistence farmers is ground-water raised from wells or boreholes. However, as the farmer has no means of predicting future rainfall or of controlling the contributions to ground-water reserves received in the preceding year, efficient and economical irrigation schedules are necessary to maximize yields within the resources available.

To optimize irrigation management in terms of yield, it is necessary to establish which stages of growth are most susceptible to water shortage. The influence of timing of irrigation on groundnut yield is well documented. Il'ina (1958) suggested that soil moisture deficits during flowering produced the greatest yield losses. Recent work has established that peg production and pod formation are more sensitive than the pre- and early flowering stages (Nageswara Rao, Sardar Singh, Sivakumar, Srivastava, and Williams, 1985; Baldev Singh, Sandhu, and Aujla, 1986), such that moderate water deficits during early vegetative development do not cause significant yield losses and may even produce slight yield advantages (Pallas, Stansell, and Koske, 1979; Sivakumar and Sarma, 1986).

A variety of methods have been used to study the effects

¹ Present address and to whom correspondence should be sent: Department of Biology, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, UK.

² Present address: International Crop Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh 502324, India.

of timing of irrigation on pod yield. For example, irrigation has either been applied according to the moisture deficit in the top 30 cm of the soil profile (Stansell, Shepherd, Pallas, Bruce, Mintol, Bell, and Morgan, 1976; Boote and Hammond, 1981) or in varying amounts at different phenological stages (Nageswara Rao *et al.*, 1985; Baldev Singh *et al.*, 1986; Nageswara Rao, Williams, Sivakumar, and Wadia, 1988). Consequently, although these studies indicate that the reproductive stage is most drought-sensitive, it is impossible to separate the temporal effect of irrigation from the quantity applied.

To overcome these confounding effects, physiological factors responsible for growth and yield in groundnut of applying a finite quantity of irrigation distributed differently over the growing season were investigated. This paper examines the influence of timing of irrigation on vegetative and reproductive development, whilst effects on ^{14}C -assimilate partitioning and plant water status are described by Stirling, Black, and Ong (1989).

MATERIALS AND METHODS

The experiment was conducted in controlled-environment glasshouses (Monteith, Marshall, Saffell, Clarke, Gallagher, Gregory, Ong, Squire, and Terry, 1983). Environmental control and stand management are described fully by Stirling (1988). Briefly, mean daily air temperature was 27 °C with a diurnal amplitude of ± 7 °C. Maximum saturation deficit was generally maintained between 1.5 and 2.0 kPa, but occasionally rose to 3.0 kPa during periods of severe soil moisture deficits and high irradiance.

Each glasshouse contained a sown area of 30 m² divided into ten sub-plots, each consisting of four half-rows. Three rows at the north end of each house, two rows at the south end and the two end plants in each row were left as a guard area. Groundnut seeds (cv. Kadiri-3), inoculated with *Rhizobium japonicum* (strain 4a/70), were sown by hand on 16 May at 10 cm spacing within rows 35 cm apart to give a population of 28.6 plants m⁻². Before sowing, the soil was treated with N:P:K fertilizer at a rate of 10:100:25 kg ha⁻¹ and irrigated to field capacity. Irrigation was applied through a microporous PVC tube system (Lifecell, Humex, Alderley Edge, Cheshire) buried at a depth of 5.0 cm to minimize evaporative losses during periods when small amounts of irrigation were applied. Drought treatments were maintained when the external water table rose following periods of heavy rain by isolating the glasshouse soil from external soil. This was achieved by excavating the soil to a depth of 0.8 m and installing heavy-duty polythene sheeting. The excavated soil was then replaced according to identifiable layers in which it had been removed.

To impose irrigation treatments varying in timing, four glasshouses were each ascribed a unique irrigation schedule. These were broadly divided into two periods: (A) sowing to pod initiation; and (B) pod initiation to final harvest. Within each period two levels of soil water deficit were imposed, either by withholding irrigation or by applying predetermined quantities of water at regular intervals. Four equal quantities of irrigation were applied to each treatment at fortnightly intervals during the first period, A and five equal irrigations were applied at weekly intervals during the second period, B. It had been intended that all treatments should receive a total of 160 mm of irrigation but glasshouse 2 effectively received only 20 and 30 mm at 28 and 42 d after sowing (DAS) due to rapid drainage, providing a total

TABLE 1. Summary of the timing of irrigation (days after sowing, DAS) and amount received (mm) in each treatment

DAS	Treatment			
	130/0	120/40	40/120	0/160
16	40	30	10	0
28	20	30	10	0
42	30	30	10	0
56	40	30	10	0
79	0	8	24	32
85	0	8	24	32
93	0	8	24	32
101	0	8	24	32
109	0	8	24	32

of 130 mm (Table 1). The treatments have been defined as 0/160, 40/120, 120/40 and 130/0 according to the quantity and timing of irrigation in each.

Soil temperature was measured at a depth of 1.0 cm using three copper-constantan thermocouples spaced at 1.0 m intervals across each house. Meristem temperature was monitored by using fine thermocouples inserted into the main stem just below the newly emerged stem leaf and repositioned weekly. The three soil and meristem thermocouples in each treatment were connected in parallel to give mean values. Leaf water potential (ψ_1) was measured between 08.00 h and 09.00 h GMT using a portable pressure chamber (PMS Instrument Co., Oregon USA). This measurement was made on the youngest fully-expanded leaf at approximately weekly intervals between 34 and 105 DAS, using three replicate leaflets per treatment.

Growth analysis samples, each consisting of ten plants, were removed at regular intervals between 30 DAS and final harvest. Severe infestation by red spider mite in the 130/0 stand made it necessary to remove some of the crop on 82 DAS, and hence only nine harvests were possible as opposed to ten in other treatments. One plant was sampled randomly from each of the ten sub-plots at each harvest, ensuring that no plant was removed from a position adjacent to that of a previously harvested plant. Developmental measurements were recorded for each of the ten plants, which were then divided into their individual components and oven-dried at 80 °C for 48 h. Total leaf area per plant was calculated as the product of leaf dry weight and specific leaf area (SLA). SLA was derived from the dry weight of 40 leaf discs per treatment, each 0.79 cm² in area. Plant population was recorded at weekly intervals in all treatments and at final harvest 50 plants were removed to determine final yield.

RESULTS

The numbers of leaves and pods present at final harvest were greater in late- as opposed to early-irrigated stands (Table 2a), but no consistent effect on branch or peg numbers was observed.

Vegetative development

Early season soil moisture deficits greatly reduced main stem extension (Fig. 1a). Treatment effects were largest around 79 DAS, when main stem height was reduced by 67% and 72% in the 0/160 and 40/120 treatments relative to the 130/0 stand. Stem extension increased sharply after irrigation at 79 DAS in the 0/160 stand but not in the 40/120 stand.

Previous studies of groundnut indicate that develop-

TABLE 2. The influence of timing of irrigation on (a) plant morphology and (b) components of yield at final harvest

Standard errors of the mean are shown in brackets.

Component numbers	Treatment			
	130/0	120/40	40/120	0/160
Main stem	17.9	17.1	19.3	21.1
leaves	(±3.7)	(±2.1)	(±4.2)	(±2.7)
Total	67.2	88.4	99.3	109.2
leaves	(±13.5)	(±14.7)	(±24.0)	(±17.7)
Branches	5.1	6.2	5.9	6.9
	(±1.3)	(±1.0)	(±0.8)	(±1.0)
Pegs	54.8	33.1	48.3	76.5
	(±25.2)	(±9.6)	(±19.8)	(±18.4)
Pods	12.8	14.5	18.9	39.8
	(±12.0)	(±5.7)	(±12.7)	(±9.1)

Component numbers	Dry weight (g m ⁻²)			
	130/0	120/40	40/120	0/160
Stems	469	445	289	455
	(±106)	(±154)	(±81)	(±116)
Leaves	238	275	236	339
	(±74)	(±81)	(±68)	(±71)
Pods	55	85	118	258
	(±74)	(±81)	(±68)	(±71)
Total dry matter (excluding roots)	762	805	643	1049
	(±230)	(±330)	(±266)	(±264)
Harvest Index (%)	7	11	18	25

mental rates are linearly related to temperature between a base, T_b , of 10 °C and an optimum, T_o , of 28–30 °C (Leong and Ong, 1983). The calculation of thermal

time is based on the linear rate/temperature response of developmental processes between T_b and T_o and can be used to predict developmental events in a crop's lifecycle, or as a means of analysing the influence of environmental factors other than temperature on developmental rates (Gallagher, 1979; Leong and Ong, 1983). Thermal time is related to temperature by the equation.

$$\theta = (T - T_b)t$$

where θ is the thermal time (degree-days, °Cd), T_b is the base temperature, (°C), T is the prevailing temperature, (°C; where $T_b \leq T \leq T_o$), and t is the time (d). In the present study, thermal time was calculated using shoot meristem temperature, with which vegetative developmental rates are closely correlated (Peacock, 1975) and was used to take account of the effect on developmental rates of the systematic variations in meristem temperature caused by watering regimes. Development was analysed in two stages, broadly defined as periods when the bulk of irrigation was either withheld or applied.

The reciprocal of the slope of the regressions between main stem height and thermal time (Fig. 1b) gives the thermal time required per unit increase in height, assuming a base temperature of 10 °C. During the early part of the season main stem extension was closely coupled to thermal time in the 130/0 and 120/40 stands requiring 21.3 °Cd cm⁻¹, but a clear departure from this relation was evident in the crops receiving little or no irrigation during the first 79 d. This departure is described by a separate linear regression (2) requiring 66.7 °Cd cm⁻¹ for stem extension, approximately one-third of the rate observed in the early-irrigated stands. Following irrigation at 79 DAS, the thermal time required for main stem

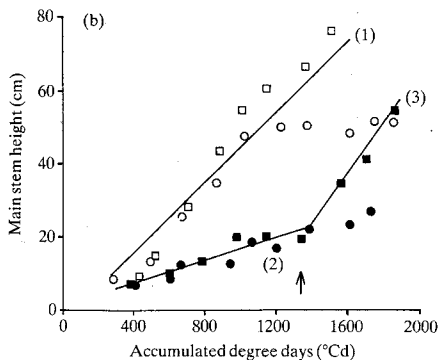
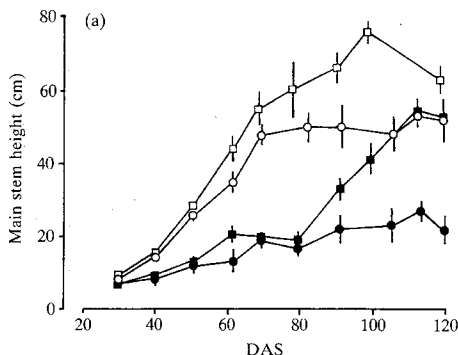


FIG. 1. (a) Seasonal time-courses of main stem extension and (b) the relation between stem height and thermal time in the 130/0 (□), 120/40 (○), 40/120 (●) and 0/160 (■) treatments. In (a) vertical bars indicate double standard errors of the mean. In (b) linear regressions are fitted to (1) all data for the 130/0 treatment and prior to the onset of stress at 69 d after sowing (DAS) in the 120/40 stand, (2) the 0/160 and 40/120 stands up to 79 DAS and (3) the 0/160 stand after 79 DAS. The equations (± standard errors) are: (1) $y = -3.00 (\pm 10.02) + 0.05 (\pm 0.01)x$; $r^2 = 0.87$; (2) $y = 1.70 (\pm 2.74) + 0.02 (\pm 0.001)x$; $r^2 = 0.85$; (3) $y = -69.83 (\pm 0.27) + 0.07 (\pm 0.001)x$; $r^2 = 0.99$. The arrow indicates the first irrigation in the 0/160 stand in this and subsequent Figures.

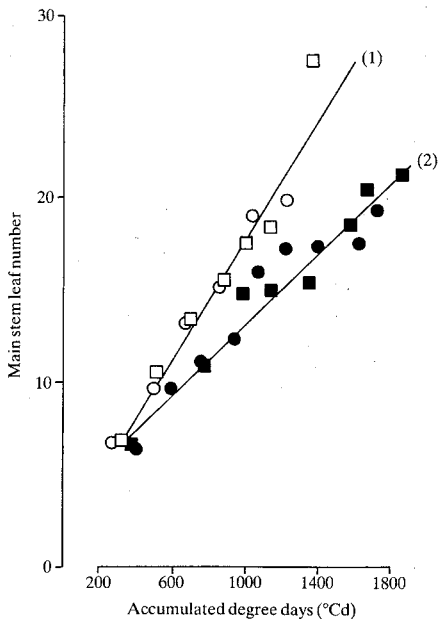


FIG. 2. Relation between main stem leaf appearance and accumulated degree-days ($^{\circ}\text{Cd}$) before the onset of leaf senescence in the 130/0 (\square), 120/40 (\circ), 40/120 (\bullet) treatments and final harvest in the 0/160 (\blacksquare) stand. Regressions (\pm s.e.m.) for (1) the early and (2) late-irrigated stands are: (1) $y = 1.78 (\pm 1.74) + 0.02 (\pm 0.001)x$; $r^2 = 0.95$; (2) $y = 4.00 (\pm 1.32) + 0.01 (\pm 0.001)x$; $r^2 = 0.94$.

extension decreased more than 4-fold to $14.7^{\circ}\text{Cd cm}^{-1}$ in the 0/160 crop, but remained virtually unchanged in the 40/120 stand. Similarly, stem extension continued at a relatively constant rate in the 130/0 stand until 98 DAS but virtually ceased in the 120/40 crop following the last major irrigation at 56 DAS.

A similar analysis of leaf appearance on the main stem (Fig. 2) showed that, prior to the onset of leaf senescence at 82 and 90 DAS in the 120/40 and 130/0 stands, new leaves were produced at relatively constant intervals of 58.8°Cd . This value is virtually identical to that of 56°Cd obtained at the same time of year in an earlier glasshouse experiment using the same cultivar grown with irrigation (Leong and Ong, 1983). As for main stem extension, the rate of leaf appearance was reduced by early water shortage, with new leaves appearing at an interval of 100°Cd in the 0/160 and 40/120 stands. Although leaf appearance rate did not increase greatly following irrigation at 79 DAS, the extended duration of leaf production in late-irrigated stands resulted in a greater number of leaves being present at final harvest (Table 2a).

Leaf area increased steadily throughout the season in all treatments (Fig. 3a) but was consistently greatest in the 130/0 stand, which achieved a maximum value of $0.3 \text{ m}^2 \text{ plant}^{-1}$ prior to the onset of senescence at 98 DAS. Leaf senescence occurred in all except the 0/160 stand, which attained a final leaf area of $0.29 \text{ m}^2 \text{ plant}^{-1}$. Thermal time analysis (Fig. 3b) showed that pre- and post-irrigation rates of leaf area development in the extreme 130/0 and 0/160 treatments changed in a similar manner to those for main stem extension, with early water shortage decreasing the rate of expansion. The thermal time required for leaf

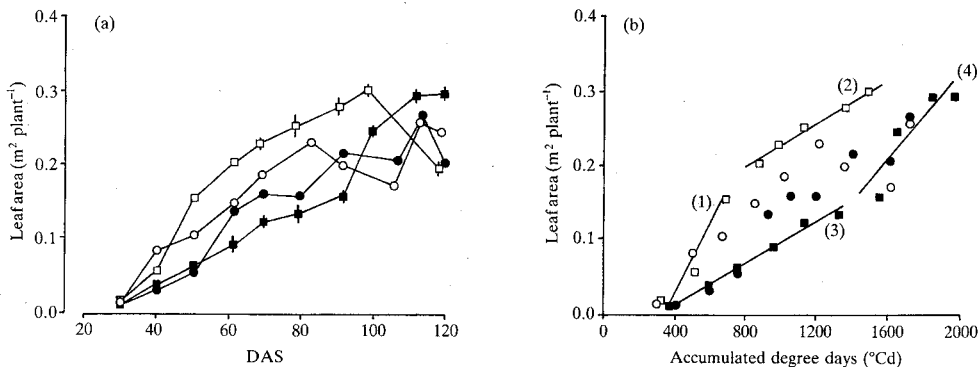


FIG. 3. (a) Seasonal time-courses of leaf area development and (b) the relation between leaf area development and thermal time in the 130/0 (\square), 120/40 (\circ), 40/120 (\bullet) and 0/160 (\blacksquare) treatments. Regressions (\pm s.e.m.) for the 130/0 (1 and 2) and 0/160 (4 and 3) treatments during periods with (1 and 4) and without (2 and 3) irrigation are: (1) $y = 0.12 (\pm 0.00) + 0.004 (\pm 0.000)x$; $r^2 = 0.96$; (2) $y = 0.08 (\pm 0.01) + 0.0002 (\pm 0.000)x$; $r^2 = 0.99$; (3) $y = 0.04 (\pm 0.01) + 0.0001 (\pm 0.000)x$; $r^2 = 0.98$; (4) $y = 0.23 (\pm 0.10) + 0.0003 (\pm 0.000)x$; $r^2 = 0.89$.

area expansion increased from 0.27 to 0.66 °Cd cm⁻² as water stress increased after 56 DAS in the 130/0 stand, but decreased from 0.73 to 0.36 °Cd cm⁻² following irrigation in the 0/160 stand. In general, leaf area expansion in the 120/40 and 40/120 stands remained intermediate to that of the extreme 130/0 and 0/160 treatments throughout most of the season.

Although developmental processes are often highly sensitive to temperature, other factors, notably water stress, may influence development at least as strongly (Pallas *et al.*, 1979; Ong, Black, Simmonds, and Saffell, 1985). To examine this interaction the degree-day requirement per unit leaf area expansion (°Cd cm⁻²) was related to leaf water potential (Fig. 4). Most of the data points

represent values for periods when irrigation was either applied or withheld in the 130/0 and 0/160 stands. Since limited water potential measurements were made in the intermediate treatments, only the early-season response in the 40/120 stand can be included in the analysis. Each water potential value represents the average of three replicate measurements made on the youngest mature leaf between 08.00 h and 09.00 h GMT on each of the four separate sampling dates.

Despite large differences between treatments in the degree-day requirement for leaf area development by individual plants (Fig. 3b), Fig. 4 shows a close correlation between the thermal requirement for leaf area expansion and ψ_1 . Thus, when differences in developmental stage are accounted for by using thermal time, the rate of leaf area expansion is directly related to ψ_1 , with leaf area expansion probably being reduced at low water potentials by inhibition of cell division (McCree and Davies, 1974), cell enlargement (Acevedo, Hsiao, and Henderson, 1971), or both (Slatyer, 1973).

Reproductive development

Thermal analyses of the effects of the treatments on reproductive development were performed using soil temperature at 1.0 cm depth, close to the reproductive primordia (Leong and Ong, 1983). In Fig. 5a, linear regressions were fitted to the data from the extreme 130/0 and 0/160 stands, analysed over two periods which broadly coincided with the imposition of or release from treatment effects. Peg development began at similar developmental stages in all treatments between 580 and 650 °Cd, similar to the value of 699 °Cd reported by Leong and Ong (1983). Irrigation at 79 DAS reduced the thermal time required for peg production from 23.3 to

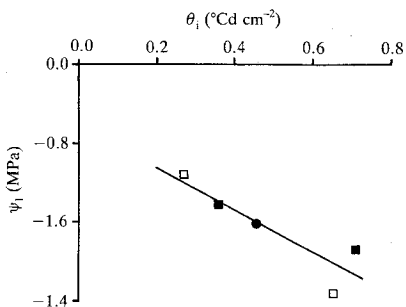


FIG. 4. Relationship between the thermal time requirement per unit increment in leaf area, θ , (°Cd cm⁻²) and mean water potential in the expanding leaf between 08.00 h and 09.00 h GMT in the 130/0 (□); 40/120 (●) and 0/160 (■) treatments. The regression equation (\pm s.e.m.) is: (1) $y = -0.10 (\pm 0.18) - 3.50 (\pm 0.28)x$; $r^2 = 0.98$.

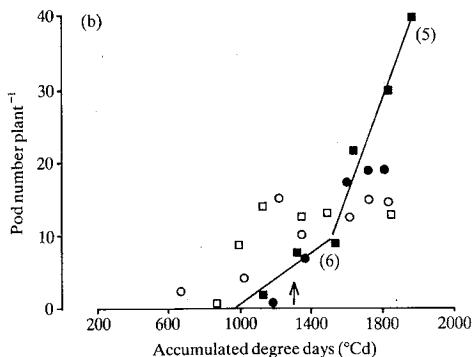
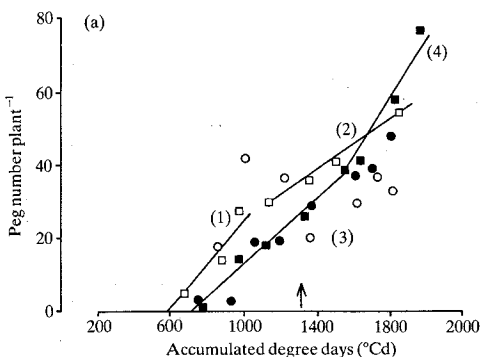


FIG. 5. Relationship between (a) peg and (b) pod number per plant and accumulated degree-days. In (a) the linear regressions (\pm s.e.m.) for the 130/0 (1 and 2) and 0/160 (3 and 4) treatments during periods with (1 and 3) and without (2 and 4) irrigation are: (1) $y = -35.24 (\pm 11.65) + 0.02 (\pm 0.01)x$; $r^2 = 0.93$; (2) $y = -9.27 (\pm 4.10) + 0.03 (\pm 0.003)x$; $r^2 = 0.99$; (3) $y = -28.93 (\pm 6.83) + 0.04 (\pm 0.01)x$; $r^2 = 0.96$; (4) $y = -77.81 (\pm 18.25) + 0.08 (\pm 0.01)x$; $r^2 = 0.95$. In (b) the linear regressions (\pm s.e.m.) for the 0/160 stand (5 and 6) during periods with (5) and without (6) irrigation are: (5) $y = -91.70 (\pm 18.03) + 0.07 (\pm 0.01)x$; $r^2 = 0.96$; (6) $y = -17.10 (\pm 7.67) + 0.02 (\pm 0.01)x$; $r^2 = 0.94$. Symbols are: □, 130/0; ○, 120/40; ●, 40/120 and ■, 0/160 treatments.

13.2 °Cd in the 0/160 stand; and no recovery was evident in the 40/120 stand, which maintained a relatively constant value of 25.1 °Cd throughout the season. Following the last major irrigation at 56 DAS θ increased from 16.7 to 33.3 °Cd per peg in the 130/0 crop, although no clear relation was found between peg number and thermal time in the 120/40 stand ($r^2=0.35$).

The onset of pod development (Fig. 5b) was delayed in the late-irrigated stands, requiring between 1 000 and 1 200 °Cd, compared with *c.* 600–900 °Cd in the early-irrigated crops. However, this delay was more than offset by the greatly increased rate of pod appearance following irrigation at 79 DAS, when the value of θ calculated from the regressions fitted to the data for the 0/160 stand declined from 70.1 to 14.9 °Cd per pod. In contrast, the earlier pod development in the 120/40 and 130/0 stands was followed by its virtual cessation after 78 DAS (*c.* 1 200 °Cd), when pegging also slowed greatly (Fig. 5a).

Pod number was closely correlated with leaf area in the 0/160 stand (Fig. 6a), whilst the early-irrigated stands produced fewer pods per unit leaf area. Pod and peg numbers were linearly related in the 0/160 and 40/120 stands, but the correlation was poor in the early-irrigated stands ($r^2=0.40$), largely because fewer pegs developed pods late in the season (Fig. 6b). The reduced pod number per plant was not simple a consequence of fewer pegs because the 130/0 stand produced more pegs but fewer pods than the 120/40 or 40/120 stands. Late-season drought may reduce cell turgor and hence peg elongation (Boote, Varnell and Duncan, 1976), which would be more critical in taller stands where pegs must travel further to reach the soil.

Growth

Pod dry weight at final harvest (Table 2b) was positively correlated with the quantity of irrigation applied

after 78 DAS, increasing by a factor of almost five between the 130/0 and 0/160 stands. In contrast, leaf and stem weights were little affected by the timing of water stress, although failure to respond to irrigation after 79 DAS produced the lowest stem weight in the 40/120 stand. The absence of any marked difference in final shoot weight (with the exception already noted) suggests that the greater pod yields in the late-irrigated crops were largely a result of increased partitioning of assimilates to reproductive structures, a view supported by the much greater harvest index of the 0/160 stand relative to the 130/0 stand.

The rate of biomass production (excluding roots) was substantially reduced by early-season water deficits (Fig. 7a), resulting in a reduction in dry matter of *c.* 50% at around 1 200 °Cd relative to the last-stressed stands. Irrigation at 79 DAS promoted rapid growth in the 0/160 stand, which had the largest plants at final harvest because dry matter production continued after growth had ceased in the early-irrigated stands. In contrast, irrigation at 79 DAS produced no marked recovery in the 40/120 stand, which attained the lowest final dry matter content. The distribution of shoot dry matter between leaves and stems differed greatly between the extreme 130/0 and 0/160 treatments (Fig. 7b). Stem growth was more vigorous in the 130/0 stand, in which it comprised 50% of total dry matter (excluding roots) at 1357 °Cd, as compared with 49% at 1328 °Cd in the 0/160 stand. The proportion of shoot dry matter present in leaves as opposed to stems was much greater in the 0/160 stand than in the 130/0 treatment.

Timing of irrigation greatly affected pod growth (Fig. 8a). Late irrigation increased the thermal time required for the initiation of pod-fill for about 860 °Cd in the early- to about 1 140 °Cd in the late-irrigated stands.

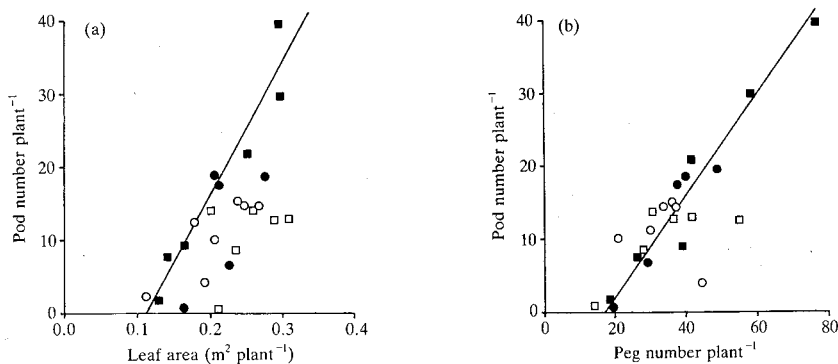


FIG. 6. Relation between pod number per plant and (a) leaf area and (b) peg number per plant. In (a) the linear regression (\pm s.e.m.) for the 0/160 treatment is: $y = -20.15 (\pm 7.06) + 183.97 (\pm 25.22)x$; $r^2 = 0.93$; and in (b) the equation for the regression fitted to the data for the 40/120 and 0/160 treatment is: $y = -11.29 (\pm 4.14) + 0.68 (\pm 0.06)x$; $r^2 = 0.93$.

Symbols are: \square , 130/0; \circ , 120/40; \bullet , 40/120 and \blacksquare , 0/160 treatments.

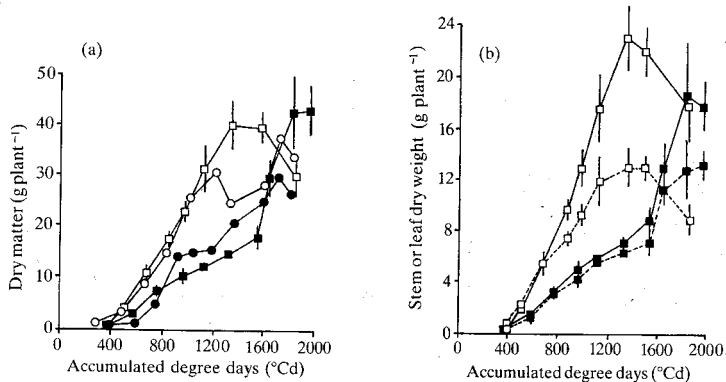


FIG. 7. Relation between (a) dry matter production (excluding roots) and (b) stem (solid lines) or leaf (broken lines) dry weight and accumulated degree-days. For clarity, standard errors are omitted for the 120/40 (○) and 40/120 (●) stands as these were similar to the 130/0 (□) and 0/160 (■) stands, respectively.

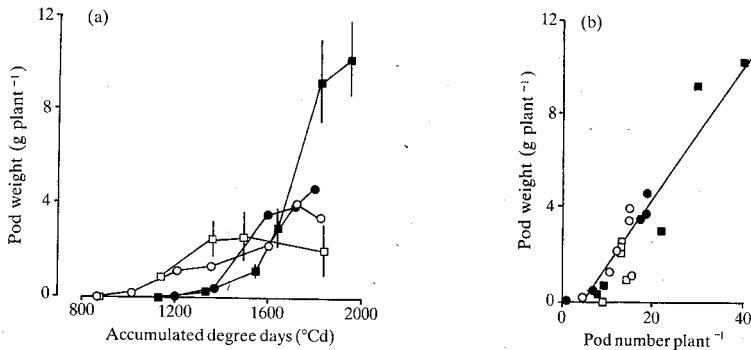


FIG. 8. (a) Effect of timing of irrigation on pod growth with thermal time and (b) relation between final pod weight and pod number per plant. For clarity, standard errors are omitted for the 120/40 (○) and 40/120 (●) stands as these were similar to the 130/0 (□) and 0/160 (■) stands respectively. In (b) the equation for the regression (\pm s.e.m.) fitted to all treatments is: $y = -1.29 (\pm 1.10) + 0.28 (\pm 0.02)x$; $r^2 = 0.87$.

Both values exceed the value of 720 °Cd reported for the same cultivar grown under irrigated glasshouse conditions (Leong and Ong, 1983). However, as irrigation was withheld from all stands between 56 and 79 DAS, it is possible that water shortage during this period may have delayed pod development in all treatments.

As well as delaying pod production, early season drought slowed initial pod growth relative to the 130/0 and 120/40 stands (Fig. 8a). However, following irrigation at 79 DAS, pod growth rapidly recovered to rates greater than in the 130/0 stand, reflecting concurrent increases in the rates of leaf area expansion (Fig. 3) and peg and pod development (Fig. 6) in the 0/160 and, to a lesser extent, the 40/120 stand.

The greater proportion of dry matter invested in stems of early- as opposed to late-irrigated stands (Table 2b)

may have limited assimilate availability for pod growth late in the season. Regression analysis of all treatments showed that the fraction of dry matter present in the pods (*HIP*) bore a close inverse relationship to the fraction of dry matter in the stems (*HIS*) at final harvest, where $HIP = 0.66 - 0.96 HIS$ ($r^2 = 0.98$). Ong (1984) reported a similar negative correlation between *HIP* and *HIS* in irrigated groundnut grown in glasshouses. This relationship may indicate that the greater stem growth in early-irrigated stands increased competition for assimilates between vegetative and reproductive organs, thereby producing large differences in *HIP* between treatments at final harvest.

However, the lower pod yields in the early- as opposed to late-irrigated stands were predominately due to effects on pod development, rather than the filling of individual

Pods. This is confirmed by the close linear relationship between pod weight and pod number per plant in all stands (Fig. 8b), which suggests that assimilate supply to individual pods was not a major limitation on pod yield.

DISCUSSION

The results indicate that late-season drought is more detrimental to final pod yield in groundnut than early-season stress, in agreement with the findings of Nageswara Rao *et al.* (1985; 1988), Baldev Singh *et al.* (1986) and Sivakumar and Sarma (1986). The lower pod yields in early-irrigated stands were mainly attributable to effects of timing of irrigation on pod development. Several authors (Boote *et al.*, 1976; Vivekanandan and Gunasena, 1976; Harris, Matthews, Nageswara Rao, and Williams, 1988) have reported that water stress during reproductive development primarily reduced pod number rather than mean pod weight at final harvest. However, this may not be the case when water becomes limited during the later stages of pod growth, since mean pod weight in the 130/0 stand was approximately 40% lower than in the other treatments, probably because water stress and premature leaf senescence reduced assimilate availability late in the season (Stirling, 1988; Stirling *et al.*, 1989).

Thus, pod growth in the late-irrigated stands was apparently delayed until stress was released at 79 DAS, when renewed leaf area expansion probably ensured adequate assimilate availability throughout pod-fill. Moisture deficits during the reproductive phase may impair pod growth in several ways. Firstly, water stress may induce flower abortion or sterility (Bolhuis, Frinking, Leenwaugh, Rens, and Starisky, 1965), thereby reducing the rates of peg and pod development. This view is supported by the fact that the early-irrigated stands, which began to suffer moisture deficits soon after peg initiation, continued to produce pegs throughout the season, but more slowly than the late-irrigated stands. Secondly, late drought may reduce turgor within the pegs and hence their ability to penetrate dry soil (Underwood, Taylor, and Hoveland, 1971), which might partially explain why the 0/160 stand produced only 28% more pegs, but 68% more pods than the 130/0 treatment (Table 2a). Finally, once initiated, pod growth may be restricted by inadequate supplies of assimilates (Lenka and Misra, 1973; Stirling *et al.*, 1989), moisture (Boote *et al.*, 1976) or calcium (Skelton and Shear, 1971).

The insensitivity of pod yield to early moisture deficits reflects the high plasticity of growth and development in groundnut. The developmental processes determining the number of leaves, pegs and pods apparently suffered no lasting effect of early drought and in most cases resumed rates similar to the pre-stressed levels in the 130/0 stand. The close relationship between pod number and leaf area in the late-irrigated stands (Fig. 8b) suggests that it is important to maintain canopy development throughout

pod initiation in order to obtain high yields. It appears that pod development and growth is regulated by current assimilate availability and it is clear that the recovery of leaf area development following irrigation in the 0/160 stand (Fig. 3) was associated with a concurrent increase in the rate of pod production (Fig. 5b) and hence final pod yield, relative to the other treatments. More limited irrigation of the 40/120 than of the 0/160 stand after 78 DAS may have intensified the degree of competition for assimilates during reproductive growth with the result that assimilates were preferentially allocated to rapidly growing pods at the expense of stems late in the season (Stirling *et al.*, 1989). This would explain the virtual absence of recovery of main stem extension in the 40/120 stand following irrigation at 78 DAS (Fig. 1b).

The present study has confirmed the usefulness of the thermal time concept in predicting developmental events in groundnut. For example, the values of θ for leaf appearance on the main stem (58.8 °Cd) and the onset of rapid canopy expansion (c. 300 °Cd) in the early-irrigated stands were virtually identical to those previously cited by Leong and Ong (1983). Furthermore, although the values of θ for most developmental processes were found to be highly sensitive to water stress, present and earlier results indicate that the timing of peg initiation is relatively insensitive to environmental factors other than temperature (Stirling, 1988). Thus, in all but the most extreme environments, thermal time calculations may be used to predict the onset of peg initiation and hence the optimum time for irrigation to induce early pod development, thereby ensuring that at least some pods are filled by final harvest. Alternatively, with appropriate meteorological records, irrigation could be used to adjust the sowing date so that the critical stage of peg development has a high probability of coinciding with periods of rainfall.

ACKNOWLEDGEMENTS

We thank the University of Nottingham (C.M.S) and the UK Overseas Development Administration (C.K.O) for financial support, ICRISAT for providing seeds and our colleagues for environmental control.

LITERATURE CITED

- ACEVEDO, E., HSIAO, T. C., and HENDERSON, D. W., 1971. Immediate and subsequent growth responses of maize leaves to changes in water status. *Plant Physiology*, **8**, 631–3.
- BALDEV SINGH, B. S., SANDHU, K. L., and AJULA, T. S., 1986. Groundnut response to irrigation and sowing times on a deep loamy sand in a subtropical monsoon region. *Field Crops Research*, **13**, 355–66.
- BOLHUIS, G. G., FRINKING, H. D., LEENWAUGH, J., RENS, R. G., and STARISKY, G., 1965. Occurrence of flowers with short style in groundnut (*Arachis hypogaea*). *Oleagineux*, **20**, 293–6.
- BOOTE, K. J., and HAMMOND, L. C., 1981. Effect of drought on vegetative and reproductive development of peanut. *Proceedings of American Peanut Research Education Society, Abstract*, **13**, 86.

- VARNELL, R. J., and DUNCAN, W. G., 1976. Relationship of size, osmotic concentration and sugar concentration of peanut pods to soil water. *Proceedings of Soil and Crop Science Society Florida*, **35**, 47–50.
- FAO PRODUCTION YEARBOOK, 1980. Volume 33, FAO, United Nations, Rome.
- GALLAGHER, J. N., 1979. Field studies of cereal leaf growth. I. Initiation and expansion in relation to temperature and ontogeny. *Journal of Experimental Botany* **30**, 625–36.
- HARRIS, D., MATTHEWS, R. B., NAGESWARA RAO, R. C., and WILLIAMS, J. H., 1988. The physiological basis for yield differences between four genotypes of groundnut (*Arachis hypogaea* L.) III. Developmental processes. *Experimental Agriculture*, **24**, 215–26.
- IL'INA, A. J., 1958. Definition of the periods of high sensitivity of peanut plants to soil moisture. *Soviet Plant Physiology*, **5**, 253–8.
- LENKA, D., and MISRA, P. K., 1973. Response of groundnut (*Arachis hypogaea* L.) to irrigation: *Indian Journal of Agronomy*, **18**, 492–7.
- LEONG, S. K., and ONG, C. K., 1983. The influence of temperature and soil water deficit on the development and morphology of groundnut (*Arachis hypogaea* L.). *Journal of Experimental Botany*, **34**, 1551–61.
- MCCREE, K. J., and DAVIES, S. D., 1974. Effect of water stress and temperature on leaf size and on size and number of epidermal cells in grain sorghum. *Crop Science*, **14**, 751–5.
- MONTEITH, J. L., MARSHALL, B., SAFFELL, R. A., CLARKE, D., GALLAGHER, J. N., GREGORY, P. J., ONG, C. K., SQUIRE, G. R., and TERRY, A., 1983. Environmental control of a glass-house suite for crop physiology. *Journal of Experimental Botany*, **34**, 309–321.
- NAGESWARA RAO, R. C., SARDAR SINGH, SIVAKUMAR, M. V. K., SRIVASTAVA, K. L., and WILLIAMS, J. H., 1985. Effect of water deficit at different growth phases of peanut. I. Yield responses. *Agronomy Journal*, **77**, 782–6.
- WILLIAMS, J. H., SIVAKUMAR, M. V. K., and WADIA, K. D. R., 1988. Effect of water deficit at different growth phases of peanut. II. Response to drought during preflowering phase. *Agronomy Journal*, **80**, 431–8.
- ONG, C. K., 1984. The influence of temperature and water deficit on the partitioning of dry-matter in groundnut (*Arachis hypogaea* L.) *Journal of Experimental Botany*, **35**, 746–55.
- BLACK, C. R., SIMMONDS, L. P., and SAFFELL, R. A., 1985. Influence of saturation deficit on leaf production and expansion in stands of groundnut (*Arachis hypogaea* L.) grown without irrigation. *Annals of Botany*, **56**, 528–36.
- PALLAS, J. E., JR, STANSELL, J. R., and KOSKE, T. J., 1979. Effects of drought on Florunner peanut. *Agronomy Journal*, **71**, 853–8.
- PEACOCK, J. M., 1975. Temperature and leaf growth in *Lolium perenne*. II. The site of temperature perception. *Journal of Applied Ecology*, **12**, 115–23.
- SIVAKUMAR, M. V. K., and SARMA, P. S., 1986. Studies on water relations of groundnut. In *Agrometeorology of groundnut*. Proceedings of an International Symposium. ICRISAT Sahelian Centre, Niamey, Niger, 21–26 August 1985. Pp. 83–98.
- SKELTON, B. J., and SHEAR, G. M., 1971. Calcium translocation in the peanut (*Arachis hypogaea* L.). *Agronomy Journal*, **63**, 409–12.
- SLATYER, R. O., 1973. The effects of internal water status on plant growth, development and yield. In *Plant response to climatic factors*. Ed. R. O. Slatyer, Proceedings of Uppsala Symposium, 1970. UNESCO, Paris. Pp. 177–91.
- STANSELL, J. R., SHEPHERD, J. L., PALLAS, T. E., JR., BRUCE, R. R., MINTON, N. A., BELL, D. K., and MORGAN, L. W., 1976. Peanut response to soil water variables in the Southeast. *Peanut Science*, **3**, 44–8.
- STIRLING, C. M., 1988. Environmental effects on partitioning and development on groundnut. Ph.D. Thesis, Nottingham University.
- BLACK, C. R., and ONG, C. K., 1989. The response of groundnut (*Arachis hypogaea* L.) to timing of irrigation. II. ¹⁴C-partitioning and plant water status. (In prep.).
- UNDERWOOD, C. V., TAYLOR, H. M., and HOVELAND, C. S., 1971. Soil physical factors affecting peanut pod development. *Agronomy Journal*, **63**, 953–4.
- VIVEKANANDAN, A. S., and GUNASENA, H. P. M., 1976. Lysimetric studies on the effect of soil moisture tension on the growth and yield of maize (*Zea mays* L.) and groundnut (*Arachis hypogaea* L.). *Beitrage Tropischen Landwirtschaft und Veterinarmedizin*, **14**, 369–78.