

EFFECTS OF SOIL MOISTURE STRESS ON THE WATER RELATIONS AND WATER USE OF GROUNDNUT STANDS

BY C. R. BLACK, D.-Y. TANG,¹ C. K. ONG,² A. SOLON,³ AND L. P. SIMMONDS

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

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SUMMARY

The work described here formed part of a detailed study of the effects of temperature and water stress on growth and development in groundnut (*Arachis hypogaea* L.). Stands of plants were grown in controlled environment glasshouses at mean air temperatures of 25, 28 and 31 °C. Half of each stand was irrigated whenever soil water potential at 10 cm reached –20 kPa. The other half received no further irrigation after sowing, when the soil profile was at field capacity. The effects on plant water status, stomatal conductance and water use were investigated regularly during the growing season.

Leaf water potential (ψ_l), turgor potential (ψ_p) and stomatal conductance (g_l) were already reduced in unirrigated plants by 29 d after sowing (DAS), when leaf area index (LAI) was still below 0.5; g_l was more strongly affected than water status. These differences persisted throughout the season as stress increased. g_l was poorly correlated with ψ_l and ψ_p and of ten exceeded 2 cm s⁻¹ in wilted leaves. LAI was not affected before 40 to 45 DAS but was reduced by 20 to 25 % in unirrigated plants between 60 DAS and final harvest. The decreases in g_l and LAI reduced canopy conductance by up to 40 %. The conservative influence of decreased g_l in unirrigated plants was negated by increases in leaf-to-air vapour pressure difference caused by their higher leaf temperatures. Transpiration rates were therefore similar in both treatments and the lower total water use of the unirrigated stand resulted entirely from its smaller LAI. Unirrigated plants made less vegetative growth but produced more pegs and pods. However, impaired pod-filling reduced pod yields by around 35 %.

Key words: Water stress, *Arachis hypogaea*, irrigation, stomatal conductance.

INTRODUCTION

Groundnut is a sub-tropical grain legume which is widely grown as a pulse or oil crop in North and South America, Africa and Asia under climatic conditions ranging from humid to semi-arid. It is unusual in producing its pods underground, even though the flowers are produced and fertilized above ground. Although it is a C3 plant, groundnut exhibits the extremely high net photosynthetic rates (≤ 50 mg dm⁻² h⁻¹; Zelitch, 1971; Pallas, 1973; Pallas & Samish, 1974) and photosynthetic light saturation levels (≥ 1550 μ E m⁻² s⁻¹; Pallas, 1973; Pallas & Samish, 1974) more typical of C4 plants.

Productivity is extremely high under favourable climatic and agronomic conditions; unshelled pod yields in the United States average 2900 kg ha⁻¹ (FAO

Present address:

1. Institute of Geography, Academia Sinica, Peking, China.
2. ICRISAT, Patancheru, Andhra Pradesh, India.
3. Technical University of Wroclaw, Wroclaw, Poland.

Production Yearbook, 1980) and may reach 7200 kg ha⁻¹ under optimal conditions (McCloud, 1974). However, average yields in developing countries are much lower (500 to 900 kg ha⁻¹) owing to poor pest and disease control, low soil fertility and erratic or inadequate water supplies. Rain-fed crops are particularly at risk since relatively small seasonal variations in the timing and amounts of rainfall cause disproportionately large fluctuations in yield (Bockelée-Morvan *et al.*, 1974; Cheema *et al.*, 1977). Yield appears to be little affected by stress during the vegetative phase (Boote, 1982) and may even be promoted because excessive vegetative growth is prevented (Gorbet & Rhoads, 1975; Vivekanandan & Gunasena, 1976), but is often drastically reduced by drought during flowering or pod-filling (Ochs & Wormer, 1959; Billaz & Ochs, 1961).

Drought affects both vegetative and reproductive growth by reducing assimilate production, since gas exchange is impaired by reduced stomatal conductances (Bhagsari, Brown & Schepers, 1976) and photosynthetic area is restricted by decreased leaf production and expansion (Ong, 1984; Ong *et al.*, 1985). Mild stress promotes peg and pod production, but more severe stress induces floral abortion and decreases both pod production and pod-filling (Ong, 1984) owing to assimilate shortages and inadequate supplies of water and mineral nutrients, which must be absorbed directly from the soil owing to the limited ability of pods to import materials through the xylary connections with the shoot (Wiersum, 1951; Skelton & Shear, 1971). During severe stress, water may be withdrawn from the pods to support transpiration (Bhagsari *et al.*, 1976).

Previous field studies have shown that the transpiration of groundnut crops grown in alfisols may decrease greatly during the week following irrigation (Harris *et al.*, in prep.), even when approximately 70 % of the available soil water remains (Simmonds & Azam-Ali, in prep.), and that reductions in stomatal conductance also occur within a few days of irrigation. The susceptibility to drought of groundnut grown on alfisols may be associated with poor rooting at depth. In this paper we examine how progressive drought, imposed by withholding irrigation, influenced plant water status, stomatal behaviour and transpiration in stands of groundnut grown at differing temperatures in controlled-environment glasshouses, and discuss the significance of the observed stress-induced changes for growth. This work formed part of a larger study of the influence of temperature and water availability on growth and development in groundnut.

MATERIALS AND METHODS

Experimental objectives, treatments and design are described fully elsewhere (Leong & Ong, 1983). Briefly, stands of groundnut, cv. Robut 33-1, were grown in a suite of five controlled-environment glasshouses (Monteith *et al.*, 1983) at mean air temperatures of 19, 22, 25, 28 and 31 °C; temperature was varied diurnally in a sinusoidal manner over a range of ± 5 °C around the mean. Half of the stand in each temperature treatment was trickle-irrigated whenever soil water potential at 10 cm fell below -20 kPa. The other half received no further irrigation after sowing, when 30 mm of water was applied to both irrigated and unirrigated plots to ensure even germination and establishment.

During the first 30 d after sowing (DAS), the humidification system proved incapable of keeping atmospheric saturation deficit (SD) to the intended daytime maximum of 1.5 kPa in the hottest treatments. However, control improved as the canopy expanded and transpiration increased, and maximum SDs were subse-

quently restricted to 2.0 kPa. Most of the data presented in this paper are for the 28 °C treatment, but additional material is drawn from the 25 and 31 °C treatments to illustrate similarities and contrasts. Environmental conditions during the experimental period are summarized in Table 1.

Table 1. (a) *Environmental conditions during experimental period (29 to 77 DAS)*

Treatment		25 °C	28 °C	31 °C
Air temperature (°C)	mean	24.8	27.9	30.9
	max	29.9	32.8	35.2
	min	20.2	23.2	26.2
SD (kPa)	mean	0.92	1.17	1.44
	max	1.45	1.75	1.96
	min	0.40	0.55	0.91

(b) *Soil water deficits (mm) in the wet and dry sub-plots of the 28 °C treatment*

DAS	Wet	Dry
35	0*	15
42	9***	26
46	3**	31
52	16**	41
56	34***	44
63	47***	55
70	39**	60

Note: *, **, and *** indicate that SWD was measured shortly after, midway between or shortly before irrigation.

Water, solute and turgor potentials

Leaf water potentials (ψ_1) were measured using a portable pressure chamber with a rechargeable cylinder (PMS Instrument Co., Oregon, USA). The chamber was taken into the glasshouse to expedite measurements and avoid exposing leaves to large temperature changes after excision. Post-excision water losses were minimized by wrapping single leaflets in polythene before excision and humidifying the air entering the chamber. Individual measurements were completed within 1 to 2 min of excision and leaves of different age and position within the canopy were taken at each sampling time, using three or four replicate leaflets for each.

Immediately after measuring ψ_1 , the leaflets were placed in small glass vials, frozen with liquid freon and stored deep-frozen for later determination of solute potential (ψ_s) by dewpoint hygrometry, using a Wescor HR 33T dewpoint hygrometer and C52 chambers. Duplicate measurements were made for each sample, using sap expressed after thawing. Turgor potential (ψ_p) was obtained by difference between ψ_s and ψ_1 . Errors in the estimation of ψ_s introduced by apoplastic dilution were assumed to be negligible since measured values of ψ_s and ψ_1 agreed closely in fully wilted leaves, where ψ_p is zero.

Leaf and canopy conductances

Stomatal resistance (r_s) was measured using two automatic diffusion porometers (Delta-T Devices, Mark II) and the values obtained converted to their

Table 2. *Influence of porometer cup orientation on measured conductances (cm s⁻¹)*

Cup orientation	Time (GMT)					
	1115			1345		
	<i>g_s</i> (abaxial)	<i>g_s</i> (adaxial)	<i>g_l</i>	<i>g_s</i> (abaxial)	<i>g_s</i> (adaxial)	<i>g_l</i>
Parallel to midrib	1.12 ± 0.18	1.45 ± 0.23	2.57 ± 0.33	1.31 ± 0.08	1.31 ± 0.05	2.62 ± 0.11
Transverse to midrib	0.80 ± 0.13	1.02 ± 0.11	1.82 ± 0.19	1.06 ± 0.07	1.23 ± 0.06	2.29 ± 0.12

All measurements were made on 29 DAS using irrigated plants from the 28 °C treatment; values are means of 16 measurements ± SE.

reciprocal, stomatal conductance. The values for the upper and lower leaf surfaces were summed to provide total leaf conductance (*g_l*). Tests were made using groups of 16 replicate leaflets to determine whether the orientation of the porometer cup on the leaflet influenced the values obtained; the long axis of the cup was aligned either parallel to or across the midrib. Table 2 demonstrates that the measured conductances for both surfaces may be reduced substantially when the cup is oriented across the midrib, presumably because stomatal density, and hence water loss, is lower in this area. All measurements were therefore made with the cup parallel to but excluding the midrib.

The porometers were allowed to cycle on their calibration plates for 15 min before measurements began, were calibrated before and after each set of measurements and placed in shade between measurements. Separate calibrations were used for each house. Several preliminary runs were made on leaves to ensure full equilibration of cup and leaf temperatures before commencing measurements. Unless otherwise stated, all values presented are means for four to six leaflets of similar age and orientation in the canopy.

Canopy conductance (*g_c*), a measure of the combined conductance of all the transpiring leaves, was calculated using the approach adopted by Jarvis, James & Landsberg (1976), Squire (1979) and Squire & Black (1982), and based on measurements of the profiles of leaf conductance and leaf area index (LAI) within the canopy. LAI was obtained by growth analysis.

Boundary layer resistance (r_a)

The rate of evaporation from artificial leaves cut from green blotting paper was used to estimate *r_a*. These leaves, of similar size and shape to groundnut leaves, were saturated, blotted to remove excess water and suspended at various heights in the canopy and positions in the glasshouse, using a support attached to a sensitive electronic balance. The artificial leaves were weighed immediately and again after 3 and 6 min. Leaf temperature, air temperature and ambient saturation deficit were recorded twice during this period using miniature thermocouples and a ventilated Assman psychrometer. *r_a* (s m⁻¹) was obtained by dividing the mean difference in water vapour concentration between leaf and air (g m⁻³) by the mean evaporation rate (g m⁻² s⁻¹). Values of *r_a* were typically 75 to 80 s m⁻¹ at the surface of the canopy, rising to 140 s m⁻¹ 30 cm below the surface.

Transpiration rate

The transpiration rates of individual leaves (*E_l*) or canopy layers were

calculated using the relation:

$$E_1 = \frac{x_1 - x_a}{r_s + r_a}$$

where x_1 and x_a are the concentrations of water vapour at the leaf surface and in the surrounding air. The mean transpiration rates for individual canopy layers were multiplied by the corresponding leaf area indices and summed to provide an estimate of total canopy transpiration (E_t ; g m⁻² of ground area h⁻¹).

Soil water status

Tensiometers were used for timing irrigation, water being applied whenever tensiometer readings at 10 cm in the irrigated plots exceeded -20 kPa. Three neutron probe access tubes were installed in every plot and used to monitor soil water content at 10 cm intervals to a depth of 1.2 m; measurements were made at 4 to 7 d intervals between 35 and 70 DAS in the 28 °C treatment and three week intervals in the other treatments. The water content of the profile was expressed as a soil water deficit (SWD), calculated by subtracting the average profile water content of a specific treatment from the value obtained in the appropriate wet sub-plot immediately after irrigation on 35 DAS. Soil water deficits in the wet and dry sub-plots of the 28 °C treatment are shown in Table 1.

The use of tensiometers installed at a single depth for timing irrigation proved unsatisfactory since insufficient water was applied at each irrigation to recharge the profile fully. The soil below 40 cm therefore dried steadily during the season and SWD increased gradually (Table 1). However, SWD was always smaller than in the unirrigated plot, even at the end of a drying cycle, and the maximum recorded SWD of 47 mm (Table 1) immediately preceded an irrigation of 20 mm.

RESULTS

The diurnal courses of g_1 and ψ_1 were influenced by systematic spatial variation within the glasshouses; until midday g_1 was significantly higher and ψ_1 significantly lower on the eastern side of the house, but thereafter the position was reversed. This pattern occurred in both irrigated and unirrigated plants, was most pronounced under sunny conditions and resulted from the presence of an axially oriented, perforated polythene ventilation duct in the apex of each house. The duct cast a shadow approximately 70 cm wide, within which irradiance was reduced by about 15 %. The shaded band moved from west to east across the stand as solar position changed during the day. Sampling errors associated with the spatial variation introduced by the ventilation duct were minimised in this study by invariably sampling plants distributed throughout the stand, and were subsequently eliminated entirely by replacing the duct with two large, horizontally rotating fans, which reduced shading and improved air circulation.

Diurnal trends

Figures 1 and 2 show typical diurnal time-courses for the principal environmental and physiological variables. Measurements of g_1 were not possible before 29 DAS (Fig. 1) because the leaflets were too small; 71 DAS (Fig. 2) was approximately three weeks before final harvest, when the canopy was fully developed.

The water status and stomatal conductances of unirrigated plants were already

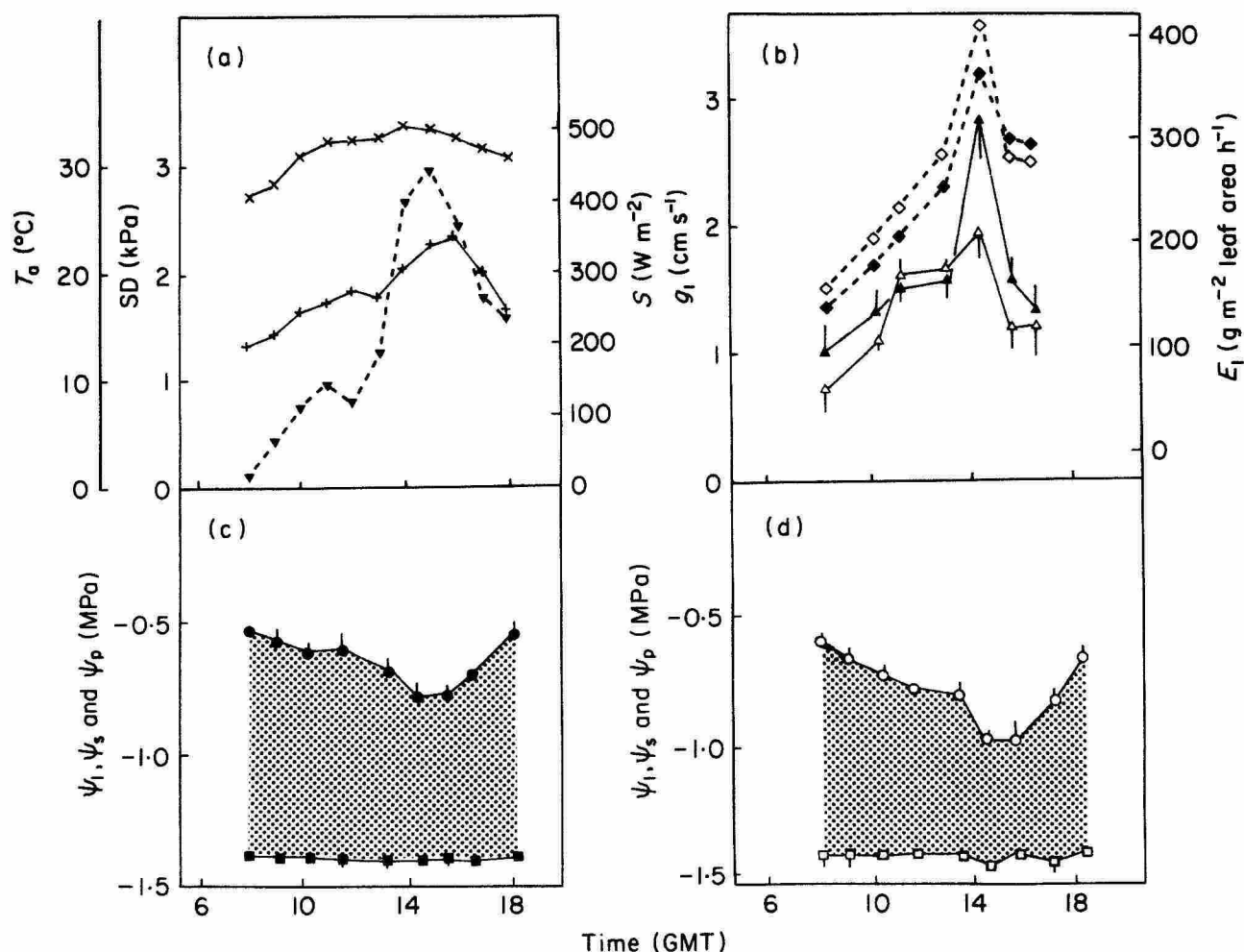


Fig. 1. Diurnal time-courses on 29 DAS in the 28 °C treatment. (a) T_a (x), S (▼) and SD (+) in the glasshouse; (b) g_1 (▲, △) and E_1 (◆, ◇); (c) and (d) ψ_1 (●, ○), ψ_s (■, □) and ψ_p (stippled areas). In this and subsequent figures, irrigated and unirrigated plants are denoted by closed and open symbols respectively and single standard errors are shown.

affected by 29 DAS, when LAI was still below 0.5. g_1 was closely correlated with irradiance (S), particularly in irrigated plants, and was generally slightly lower in the unirrigated plants, the daily mean reduction in g_1 being 13%. However, the lower conductances of the unirrigated plants were more than compensated for by increases in leaf to air vapour pressure difference (vpd), brought about because leaf temperature was typically about 1.5 °C higher than in irrigated plants. As a direct consequence, transpiration rate (E_1) was higher than in the irrigated plants, except during late afternoon.

ψ_1 and ψ_p were both slightly lower in unwatered plants, in keeping with their higher transpiration rates; the minima between 1400 and 1500 GMT corresponded closely to the period of maximum isolation, SD and transpiration. Thereafter, ψ_1 and ψ_p recovered rapidly as E_1 decreased, returning almost to their early morning values by 1800 GMT. ψ_s showed no significant diurnal variation or difference between treatments.

Broadly comparable results were obtained on 71 DAS (Fig. 2). Owing to a data-logger malfunction, no environmental means are available for 1500 GMT; the values of T_a and SD for this hour are therefore spot-measurements derived from Assman psychrometer records. g_1 was already relatively high by 0500 GMT, even though S was still extremely low, and similar precocious opening was frequently observed. Thereafter, g_1 followed a bimodal time-course in both treatments, with a distinct stomatal closure around midday when S and SD were still

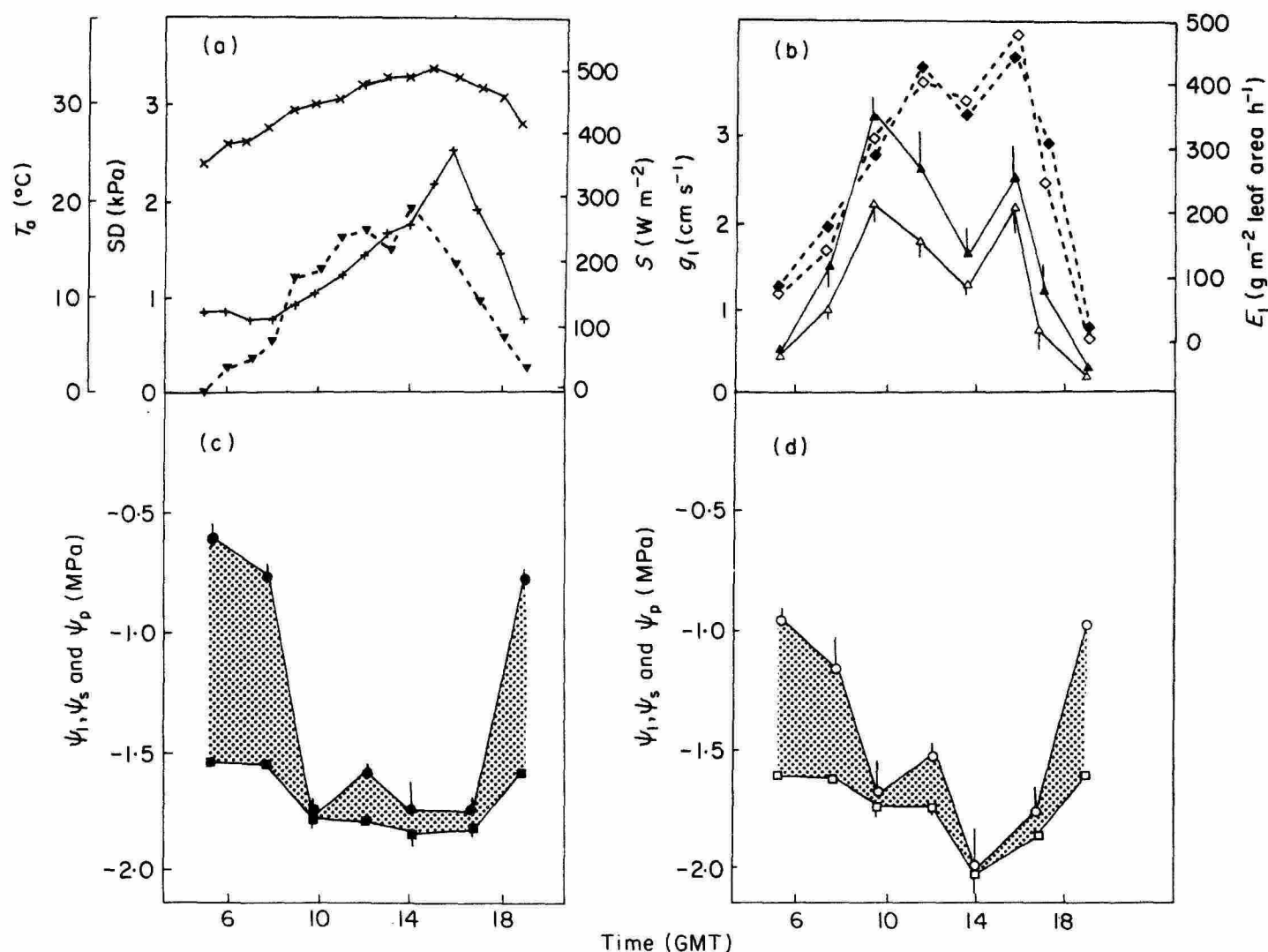


Fig. 2. Diurnal time-courses on 71 DAS in the 28 °C treatment. Symbols as in the legend for Figure 1.

increasing. The correlation between g_1 and S was much poorer than on 29 DAS (Fig. 1), and the reductions in g_1 in the unirrigated treatment [Fig. 2(b)] and ψ_1 and ψ_p in both treatments [Fig. 2(c) and (d)] were much more severe.

With respect to E_1 , the large reductions of g_1 in unirrigated plants were again largely negated by opposing differences in vpd since leaf temperatures were up to 1.5 and 4.0 °C above those of irrigated plants and air temperature respectively. E_1 [Fig. 2(b)] was therefore generally similar in both treatments, and indeed was slightly greater in the unirrigated plants during early afternoon; the daily mean value for E_1 was only 2.6 % lower in the unirrigated plants, despite a reduction of 27.3 % in the corresponding value for g_1 .

Foliar water status bore a close inverse relationship to g_1 and especially E_1 (Fig. 2). ψ_1 and ψ_p were 0.3 to 0.4 MPa higher in irrigated plants at dawn and dusk, but fell rapidly and to similar levels in both treatments during the morning as transpiration increased. A transient slight recovery in ψ_1 and ψ_p during the midday depression of E_1 preceded a further decline, which was greater in the unirrigated plants, in accord with their more rapid transpiration. ψ_1 and ψ_p again recovered rapidly and almost completely as E_1 decreased. The diurnal variation in ψ_s and the small differences between treatments resulted from changes in hydration rather than solute content (unpublished results).

Seasonal trends

Figure 3 shows the seasonal trends in ψ_1 , ψ_s and g_1 at 0800, preceding the usual

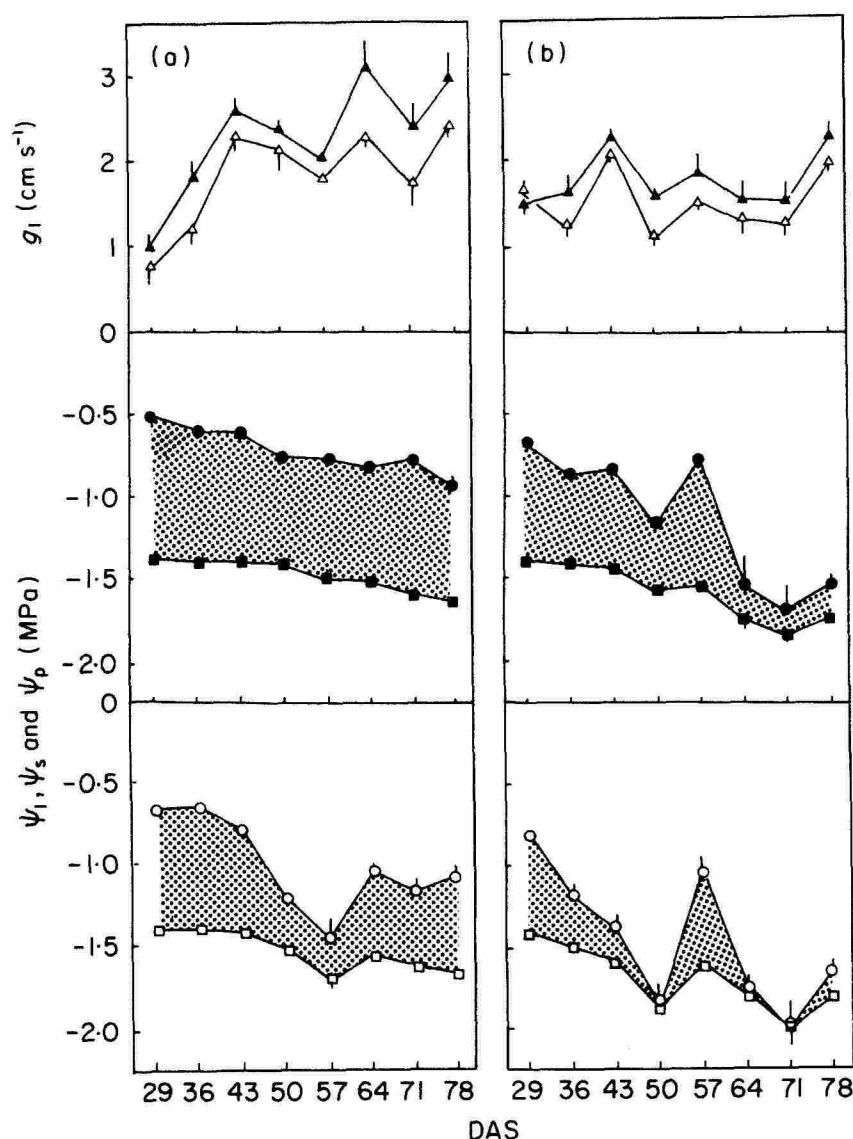


Fig. 3. Seasonal trends in the 28 °C treatment for g_1 (\blacktriangle , \triangle), ψ_1 (\bullet , \circ) ψ_s (\blacksquare , \square) and ψ_p (stippled areas) at 0800 GMT (a) and 1330 GMT (b).

rapid diurnal decline in water status, and 1330 GMT, which normally coincided with the period of maximum stress. Although predawn values of ψ_1 and ψ_s would have provided a better measure of overnight recovery, appropriate data are not available for all sampling dates.

In the irrigated plants, ψ_1 at 0800 GMT declined by approximately 0.35 MPa during the season but ψ_p remained virtually constant owing to a concurrent decrease in ψ_s . Turgor was consistently lower in the unirrigated plants, where the seasonal decline ψ_1 was only partially compensated for by reductions in ψ_s . With the exception of 57 DAS, ψ_1 and ψ_p were generally much reduced by 1330 GMT, especially in the unirrigated plants, and stress increased in severity as the season progressed. The improvement in water status between 0800 and 1330 GMT on 57 DAS resulted from the arrival of dense cloud after a bright morning. The irrigated plants retained substantial midday turgor until 64 DAS, shortly after pod-filling began. Except on 29 DAS, g_1 was always lower in unirrigated plants and decreased between 0800 and 1330 GMT (Fig. 3). The largest differences between treatments were during the latter part of the season at 0800 GMT.

Figure 4 shows the relation between the mean values of g_1 at 0800 and 1330 GMT and the corresponding data for ψ_1 and ψ_p . The linear regressions were fitted to the data for 36 to 77 DAS and the correlation coefficients with ψ_1 and ψ_p were

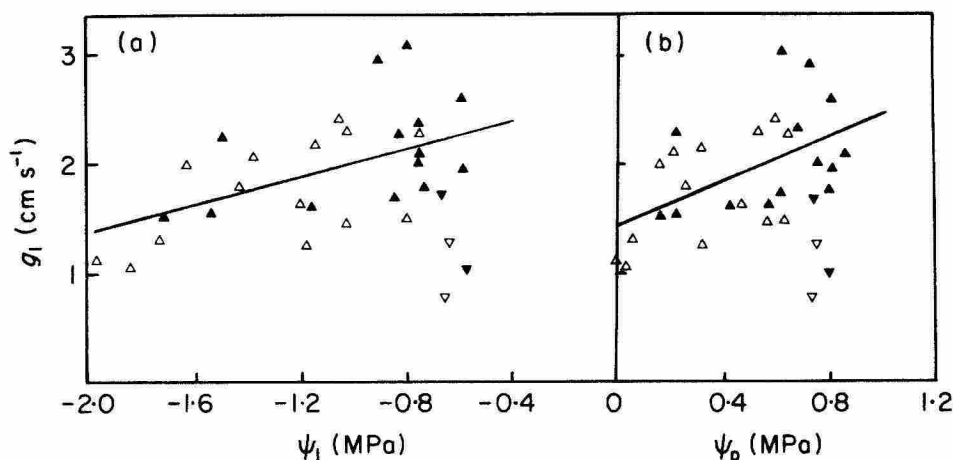


Fig. 4. Relation between mean g_1 at 0800 and 1330 GMT and the corresponding values of (a) ψ_1 and (b) ψ_p in the 28 °C treatment for the period 29 to 77 DAS. Closed symbols represent irrigated plants and \blacktriangle and ∇ denote data for 29 DAS, immediately preceding flowering. The linear regressions are fitted to the data obtained during the reproductive phase (\blacktriangle , \triangle); the regressions are (a) $y = 2.63 - 0.062x$; $r = 0.50$ and (b) $y = 1.45 + 0.10x$; $r = 0.53$.

respectively 0.50 and 0.53. Although the correlations were significant ($P < 0.005$), the data show considerable scatter, possibly because water stress was not sufficiently severe to eliminate stomatal responses to other influential variables such as irradiance, which varied greatly from day to day. Inclusion of the data for 29 DAS reduced r values to 0.25 and 0.33, indicating that stomatal behaviour may have changed after flowering began on 32 and 30 DAS in the irrigated and unirrigated plants respectively; insufficient data are available for the period before flowering to test this theory rigorously.

Profiles within the canopy

Figures 1 to 4 all show data for the youngest expanded leaf (leaf 2) which is more susceptible to environmental variations than older, partially shaded leaves. Typical diurnal variations in the profiles of ψ_1 , ψ_p and g_1 are shown in Figures 5 to 7. Stress increased rapidly in the early morning and ψ_1 and ψ_p reached their daily minima by 0930 GMT in the irrigated plants [Fig. 5(a)], but continued to decrease until 1330 GMT in the unirrigated plants [Fig. 5(b)]. Stress was most severe near the top of the canopy and differences in ψ_1 of 1.0 to 1.2 MPa between leaves 2 and 10 were common during the period of peak irradiance; leaf 2 was often 0.3 to 0.4 MPa more stressed than the expanding leaf immediately above (Fig. 5) or leaf 3 (data not shown). Water status recovered rapidly as S declined, ψ_1 increasing by 0.5 to 1.0 MPa between 1615 and 1815 GMT. Turgor levels were only slightly greater in the irrigated plants, except during the early morning.

Unirrigated plants were consistently more stressed than irrigated plants in the 28 °C [Figs 3, 5 and 6(b)] and 31 °C treatments, but the converse often applied at 25 °C [Fig. 6(a)]. The more favourable water status and higher conductances of the unirrigated plants in this treatment probably resulted from restrictions imposed on light interception and transpiration by the much larger drought-induced reduction of LAI at 25 °C (3.3 vs 1.6) than at either 28 °C (4.5 vs 3.7) or 31 °C (5.0 vs 3.9) at this time.

g_1 showed great diurnal variation, particularly near the surface of the canopy where values frequently reached 2.5 to 3.0 cm s⁻¹ under sunny conditions (Fig. 7). When evaporative demand was high, g_1 in the youngest expanded leaf (leaf 2) was lower than in the significantly less stressed leaf 3 (cf. Fig. 5). Below leaf 3, g_1

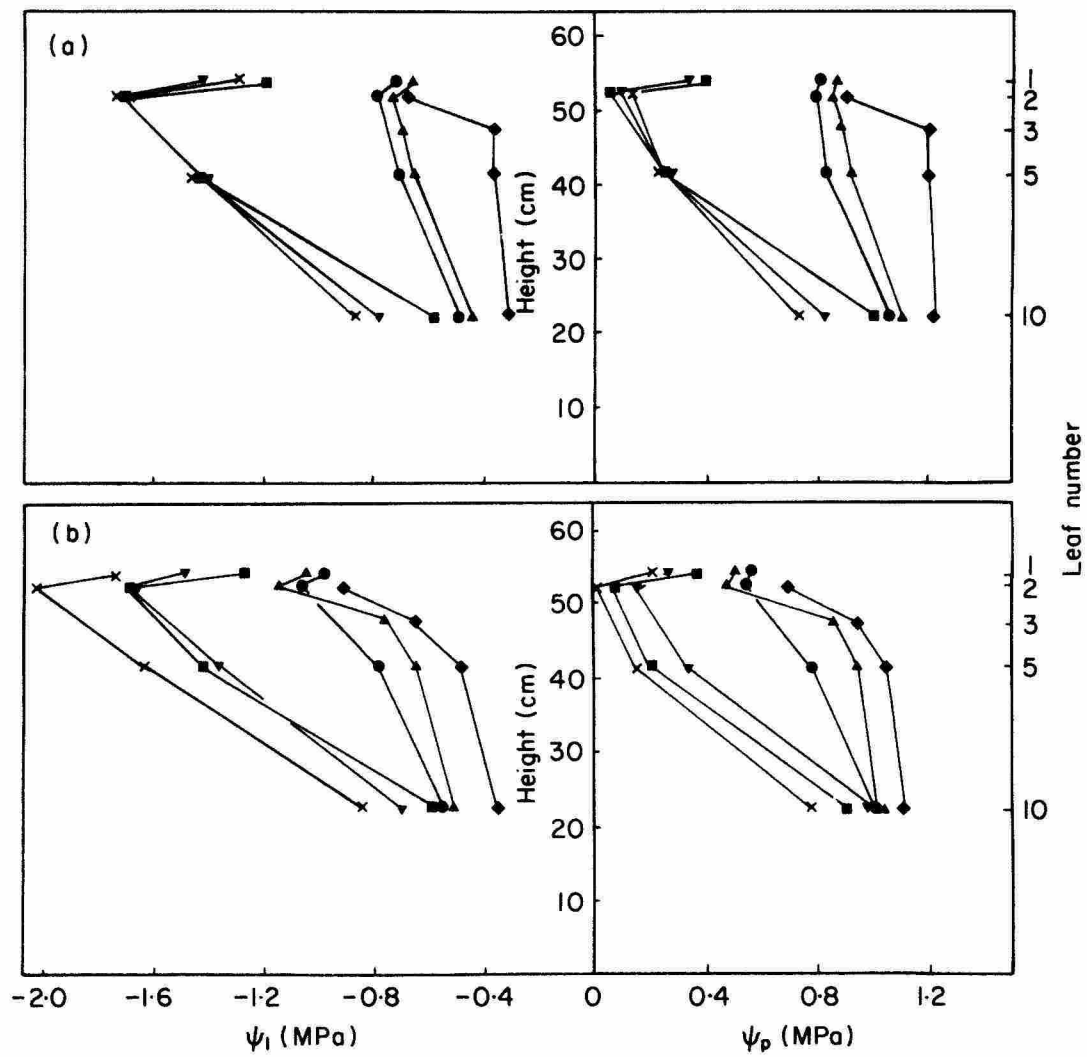


Fig. 5. Diurnal variation in the profiles of ψ_l and ψ_p in (a) irrigated and (b) unirrigated plants from the 28 °C treatment on 71 DAS. Symbols are: ◆, 0500; ▲, 0745; ■, 0930; ×, 1330; ▼, 1615; and ●, 1815 GMT. Standard errors are omitted for clarity but are of similar size to those in Figures 2, 6 and 7.

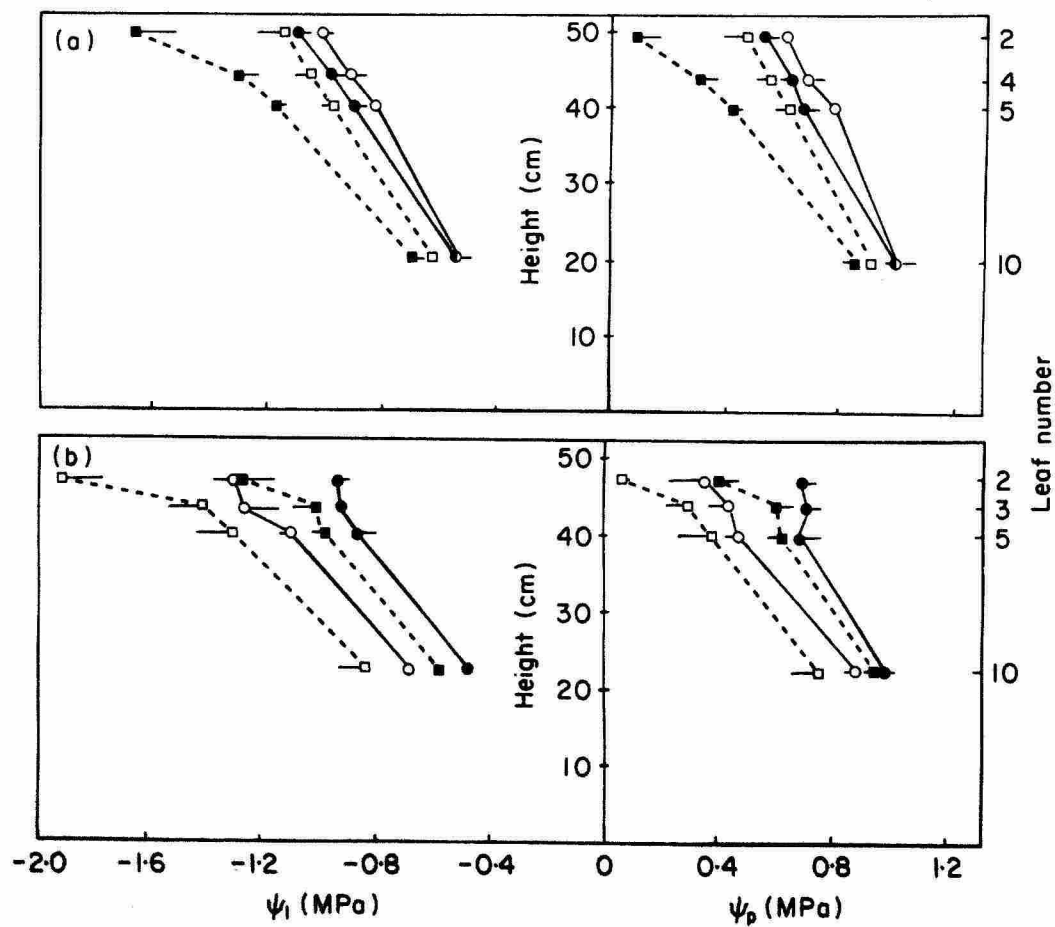


Fig. 6. Profiles of ψ_l and ψ_p at 1100 (●—●), (○—○) and 1530 GMT (■---■), (□---□) in the 25 (a) and 28 °C (b) treatments on 64 DAS.

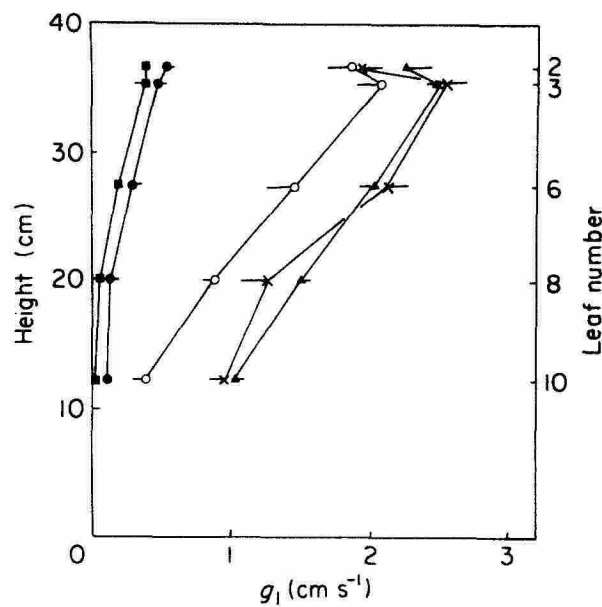


Fig. 7. Diurnal variation in the profiles of g_1 in irrigated plants from the 25 °C treatment on 55 DAS. Symbols are: ●, 0600; ×, 0930; ▲, 1230; ○, 1530 and ■, 1800 GMT.

decreased progressively as mutual shading increased and irradiance decreased. The expanding leaf (leaf 1) was too small for g_1 to be measured. The absolute values and diurnal variation in the conductances of the uppermost five expanded leaves remained similar as the season progressed and the canopy grew to a height of 70 to 80 cm. However, the number of older, heavily shaded leaves with maximum conductances of 0.2 to 0.5 cm s⁻¹ increased steadily since no senescence was observed even when LAI reached 8 to 10. Profiles of g_1 were similar in unirrigated plants in the 28 and 31 °C treatments, but conductances for specific leaves were typically 10 to 20 % lower.

Canopy conductance and transpiration

Diurnal time-courses of canopy conductance (g_c) and transpiration rate per unit ground area (E_t) on 71 DAS are shown in Figure 8. The trends for g_c [Fig. 8(a)] closely resemble those for g_1 (Fig. 2), demonstrating that the responses of leaf

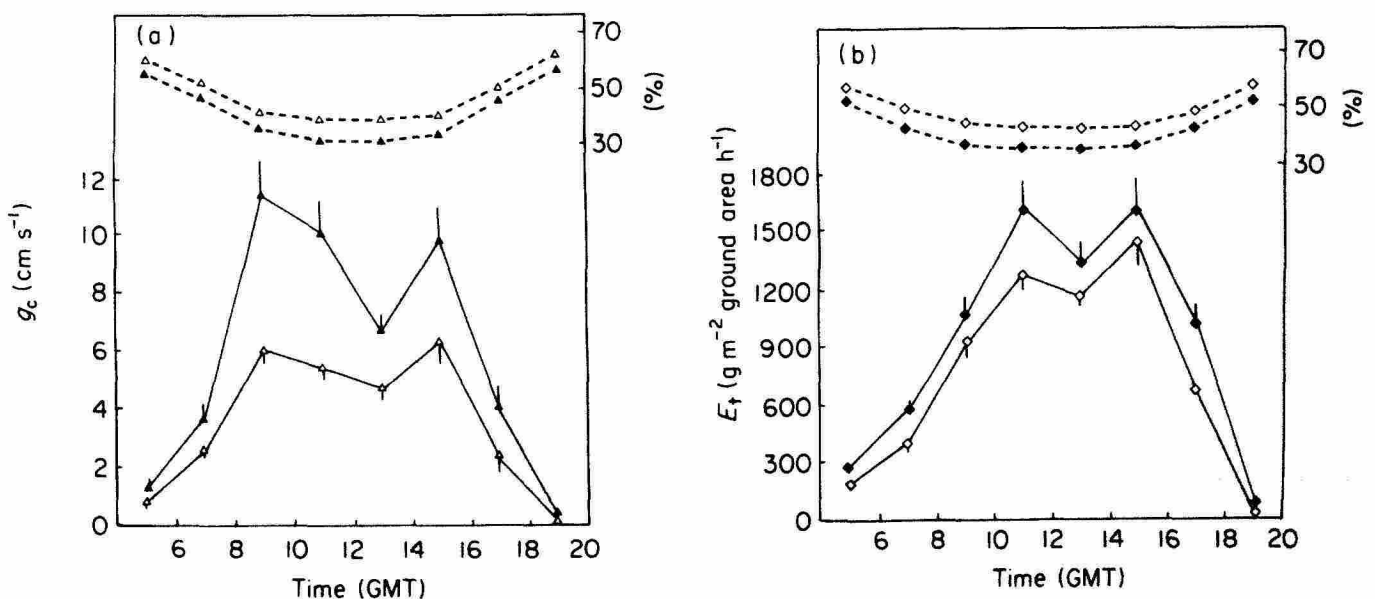


Fig. 8. Diurnal variation in (a) g_c (▲, △) and (b) E_t (◆, ◇) in the irrigated (closed symbols) and unirrigated stands (open symbols) grown at 28 °C on 71 DAS. Dashed lines show the fraction of g_c and E_t contributed by the five youngest mature leaves.

2 were typical of the leaves dominant in determining g_c . g_c was much lower in the unirrigated stand owing to reductions in both g_1 (cf. Fig. 2) and LAI (5.5 vs 4.35); the latter effect resulted from reduced leaf expansion rather than decreased leaf production or premature senescence (Leong & Ong, 1983).

Expanding leaves (leaf 1) were not included in the calculations of E_t [Fig. 6(b)] since their conductances could not be measured. However, this omission is unlikely to introduce serious errors as these leaves were small, folded about their midrib, protecting the adaxial surface, and were held parallel to direct sunlight. As in single leaves (Fig. 2), the differences in transpiration rate between treatments were much smaller than those in conductance.

DISCUSSION

Foliar water status, conductance and transpiration

Differences in water status between irrigated and unirrigated plants were small but consistent (Figs 1 to 3, 5), and seasonal minimum water potentials were respectively -1.7 and -2.0 MPa. Ong *et al.* (1985) also found water status in groundnut to be relatively unaffected by a range of soil and atmospheric stress, with minimum ψ_1 varying according to treatment between -1.5 and -2.0 MPa. Reports for field crops indicate that ψ_1 rarely falls below -1.3 MPa in well-watered plants, but commonly reaches -3 to -4 MPa and occasionally -6 to -8 MPa during severe drought (Allen, Boote & Hammond, 1976; Gautreau, 1977; Pallas, Stansell & Koske, 1979). Variation in tissue hydration was the principal cause of temporal and between-treatment differences in ψ_p since there was no systematic variation in ψ_s between treatments and long term osmotic adjustment, as assessed from measurements of ψ_s at zero ψ_p , was small (0.3 to 0.4 MPa), despite the marked seasonal decrease in ψ_1 and ψ_p (Fig. 3). In groundnut, as in other species, the capacity for osmotic adjustment depends on the nature of the stress imposed; mild stress induces little or no adjustment, as in this study, but progressive severe stress may stimulate substantial solute accumulation (Ong *et al.*, 1985).

Two factors minimised the differences in water status between treatments. Firstly, the irrigated plants were less well watered than intended (Table 1). Secondly, groundnut is capable of rooting to depths exceeding 90 cm by 70 DAS and may eventually extract water to 150 to 250 cm (Stansell *et al.*, 1976; Hammond *et al.*, 1978; Robertson *et al.*, 1980; Boote, 1982). The unirrigated plants may therefore have gained access to free water deep in the profile, a view supported by two pieces of evidence. Analysis of the neutron probe data shows that water was being extracted to a depth of 70 cm by 45 DAS, but that no soil drying occurred below 80 to 90 cm at any time, probably because of the proximity of standing water. Water tables were not monitored in the glasshouses but periodic observations in nearby dipwells revealed free water within 1 m of the soil surface. Estimates of water use efficiency in the dry sub-plot of the 28 °C treatment, calculated from the mean rates of soil drying and crop growth between 35 and 70 DAS, also suggest that large quantities of water were drawn from the water table, since the values obtained exceeded those expected for groundnut by at least three-fold.

The rapid recovery of foliar water status when stress is relieved (Figs 1 and 2) appears to be common in groundnut, even after sustained severe stress. For example, Allen *et al.* (1976) observed almost complete stomatal reopening in heavily wilted leaves after 1 h of cloud cover and Pallas *et al.* (1979) reported that

the stomatal resistances of plants subjected to prolonged drought returned to normal one day after irrigation; water status and net photosynthesis may also return to near normal within 1 to 2 d of rewatering. The capacity for rapid, almost full recovery from stress may be an important adaptive response in groundnut.

Withholding irrigation had little effect on E_1 (Figs 1 and 2) because the potential conservative influence of the large reductions in g_1 was almost totally negated by opposing increases in vpd (Table 3). The important influence of vpd is emphasised

Table 3. *Relative contributions of g_1 , vpd and LAI to the observed reductions in E_1 and E_t in the unirrigated stand on 71 DAS (Cf. Figs 2 and 8)*

	1 g_1	2 vpd	3 LAI	4 E_1 or E_t
Leaf 2	-13.8	+11.8	—	-2.6
Canopy	-11.4	+12.0	-17.7	-17.5

Columns 1 to 3 show the predicted affect of each variable, had it been the only factor to differ between treatments, and column 4 shows their combined effect. The values are daily means and are expressed relative to the irrigated control as percentage changes in transpiration rate.

by the continued increase in E_1 and E_t between 0900 and 1100 GMT on 71 DAS, despite substantial reductions in g_1 and g_c (Figs 2 and 8). These results clearly demonstrate the dangers of attributing conservative benefits to decreases in conductance without a full knowledge of the other variables influencing transpiration, particularly in the semi-arid environments where groundnut is often grown.

The maximum stomatal conductances in groundnut of 3 to 4 cm s⁻¹ (Figs 1 and 2; Black & Squire, 1979) are exceptionally high compared to many temperate species, and conductances exceeding 2 cm s⁻¹ are common even in wilted leaves (Fig. 2). Visible wilting first occurred when ψ_1 reached -1.4 to -1.7 MPa, depending on the stage of the season, but net photosynthesis (P_n) showed little response until ψ_1 exceeded -1.4 MPa (unpublished results). Bhagsari *et al.* (1976) also found that P_n in potted groundnut and soybean plants was not affected by increasing stress until shortly before wilting began, but declined to 8 to 13 % of watered controls by the time ψ_1 reached -3.0 MPa; they concluded that the major effect of drought on P_n was exerted through stomatal closure. These results suggest that g_1 is often higher than is necessary to satisfy photosynthetic CO₂ requirements, even in stressed plants, a conclusion which may provide an explanation for observations that groundnut benefits from being intercropped with taller cereals, since the resultant shading would reduce transpiration and minimise water stress.

The ability to maintain high stomatal conductances at low water potentials (Figs 2 and 4) is a common adaptive response to drought which is usually attributed to the maintenance of turgor by osmotic adjustment (Brown *et al.*, 1976; Turner *et al.*, 1978). However, little osmotic adjustment was found either in this experiment or in millet, which also maintains stomatal opening in wilted leaves during the reproductive phase (Hensen *et al.*, 1982a, b). Changes in stomatal behaviour from a water-conserving to an assimilate-maximizing strategy after reproduction begins have now been observed in several species (Hensen *et al.*, 1982b). When this occurs, ψ_1 and ψ_p become functions of g_1 rather than the converse, and low ψ_1 is induced by rapid transpiration whenever high g_1 , S and SD coincide (cf. Figs 1 to 2 and 5 to 7). These results demonstrate clearly that the turgor relations of the stomatal

complex which control stomatal aperture were largely independent of bulk ψ_1 or ψ_p .

Canopy development and water use

In the absence of other limitations, the rate of leaf expansion in groundnut is extremely sensitive to foliar water status, declining by approximately 10% for every 0.1 MPa reduction in ψ_p (Ong, 1984; Ong *et al.*, 1985). Persistent small differences in water status may therefore induce large changes in final leaf size, since the duration of expansion is almost unaffected by water stress. The number of leaves produced may also be greatly reduced by stress (Ong *et al.*, 1985). The consequences for canopy development depend on the severity of the stress imposed. In this experiment, LAI was not affected until after 40 to 45 DAS, but was reduced by 20 to 25% between 60 DAS and final harvest in the unirrigated stands grown at 28 or 31 °C; LAI nevertheless still reached 7 to 8. Much larger reductions are induced by more severe stress (Ong *et al.*, 1985), seriously delaying or preventing the establishment of full ground cover. In these circumstances, assimilation is limited by incomplete light interception as well as impaired photosynthetic activity.

Total water use by the irrigated and unirrigated stands on 71 DAS, calculated from the areas under the curves in Figure 8(b), was 7.4 and 6.2 mm d⁻¹ respectively. Maximum evapotranspiration rates of 5.3 to 6.0 mm d⁻¹ are also found in field crops (Kassam *et al.*, 1975; Vivekanandan and Gunasena, 1976; Stansell *et al.*, 1976), and *mean* values of 5.6 to 7.45 mm d⁻¹ have been recorded between 53 and 83 DAS under conditions of high evaporative demand (Mantell & Goldin, 1964); LAIs were similar to those reported here. The lower daily water use of the unirrigated stand was entirely attributable to its smaller LAI, rather than decreased stomatal conductance, owing to the compensatory effect of increased vpd (Table 3). Regulation of water use through control of LAI rather than g_1 is possible when drought is imposed slowly and has the advantage of permitting high stomatal conductances and assimilation rates to be sustained in the remaining foliage for extended periods. In extreme cases, g_1 and ψ_1 may even be *higher* than in irrigated plants (cf. Fig. 6), with stomatal closure occurring only as a last resort (Squire & Black, 1982).

The contribution of the five youngest expanded leaves (leaves 2 to 6) to g_c and E_t varied diurnally and was larger in the unirrigated stand (Fig. 8). The decreased contribution of leaves 2 to 6 around midday resulted from a relative increase in the stomatal conductances of the older leaves and reflected the improvement in light penetration into the canopy caused by the wilting and nastic folding movements of the younger leaves. These responses serve to reduce insolation during periods of high irradiance. Leaves 2 to 6 comprised 23 and 28% of the total LAI and contributed 34 and 42% of E_t in the wet and dry stands respectively during the period of peak transpiration. Previous research has shown that the top 42% of the leaf area in a groundnut stand intercepted 74% of the incident light and accounted for 63% of the CO₂ assimilated (Boote *et al.*, 1980).

In groundnut, canopy closure occurs at an LAI of 2.5 to 3.0 and fractional light interception reaches 90 to 95% when LAI is 4.0 to 4.5. Diurnal reorientation of the upper leaves therefore causes diurnal variation in fractional light interception when LAI is small. When LAI is large, as on 71 DAS, fractional interception is unaffected, but the area of maximum light interception moves deeper into the canopy, probably to the detriment of carbon assimilation, since photosynthetic

activity is maximal in two-week-old leaves but declines sharply in leaves older than four weeks (Trachtenburg & McCloud, 1976; Pallas & Samish, 1974). The shift in the area of maximum light interception to the older, less active leaves is therefore likely to have temporarily decreased the photosynthetic capacity of the canopy, although this effect proved impossible to quantify owing to concurrent changes in other influential variables such as foliar water status.

Effects on growth and yield

Although LAI and total shoot dry weight were reduced by 20 to 25 and 11 to 13 % respectively in unirrigated plants, these decreases in vegetative growth were not necessarily reflected in reproductive processes. For example, peg and pod numbers in the 28 °C treatment were 40 and 30 % greater in the unirrigated stand, where reduced stem extension permitted an increased number of pegs to reach the soil and produce pods. Total pod yield in the dry stand was nevertheless reduced from 1060 to 657 kg ha⁻¹ owing to impaired pod-filling (Ong, 1984), a process which may be adversely affected by several factors in droughted plants. Reduction of minimum ψ_1 to -2.0 MPa during the reproductive phase (cf. Figs 2 and 3) is sufficient to reduce whole canopy CO₂ fixation by 32 % (Ong *et al.*, 1985), and Ong (1984) has further reported that the partitioning of the available assimilates to the pods was greatly reduced in the unirrigated stand. Additional limitations imposed by the inability of pods to obtain sufficient water and mineral nutrients when the surrounding soil is dry (Wiersum, 1951; Skelton & Shear, 1971) were probably unimportant in this experiment because volumetric soil water contents at 10 and 20 cm in the dry stand were never less than 20 and 25 %, equivalent to a soil water potential no lower than -1.0 MPa. Thus it is clear that although mild water stress during the vegetative phase may be beneficial (ICRISAT, 1981; Boote, 1982), sustained, relatively mild stress during reproduction, particularly at pod-filling, may greatly reduce yields.

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