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

II. ^{14}C-PARTITIONING AND PLANT WATER STATUS

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ABSTRACT

Finite quantities of water were applied at different growth stages of groundnut stands (*Arachis hypogaea* L.) grown in controlled environment glasshouses. Soil moisture deficits were imposed between sowing and pod initiation or between pod initiation and final harvest by withholding or applying water. Effects on assimilate production and partitioning and plant water relations were examined.

Leaves were the primary sites of $^{14}CO_2$ fixation, though their contribution generally declined late in the season, whereas fixation by stems was initially low but increased sharply when stress was released in the late-irrigated stands. ^{14}C-fixation by stem apices and pegs also rose sharply following irrigation of the late-stressed stands.

Leaves were the primary source of assimilates, though translocation tended to decrease as the season progressed, even in the late-irrigated stands. Stems were initially the major sinks, but their sink activity disappeared almost completely when stress was released in the late-irrigated stands. Assimilate import by stem apices declined progressively and pod sink activity was negligible in the late-stressed stand, but both increased markedly when early-season stress was released.

Leaf water status showed marked diurnal variation, whereas pegs showed less variation and maintained much higher turgor levels, largely because of their lower solute potentials. Marked osmotic adjustment occurred in expanding but not in mature leaves, allowing them to maintain higher turgor levels during periods of severe stress. This adjustment was rapidly lost when stress was released. The observed changes in assimilate production and partitioning preceded detectable changes in bulk turgor levels.

Implications for growth, development and yield are discussed.

Key words: Groundnut, irrigation, partitioning, water status.

INTRODUCTION

The previous paper in this series examined developmental and growth responses of groundnut (*Arachis hypogaea* L. cv. Kadiri-3) to timing of irrigation (Stirling, Ong, and Black, 1989). Large differences in pod yield and harvest index were observed between early- and late-irrigated stands, even though effects on shoot dry matter production were relatively small.

Although, total dry matter production is tightly coupled to the rate of assimilate production, economic yield depends on the balance of assimilate partitioning between reproductive and vegetative structures. To understand why pod yield is highly sensitive to water deficits imposed during reproductive growth, but less sensitive to water deficits experienced during the vegetative phase, it is necessary to elucidate how assimilate production and partitioning is affected by water stress. Whilst studies using dry weight increment as a criterion of growth are useful for following crop development, they provide little information concerning the pattern of carbon flow within individual plants. ^{14}Carbon labelling techniques are now commonly used to study the effects of water deficit on assimilate partitioning, although rarely, if ever, in groundnut.

This paper examines the effects of timing of irrigation

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on ^{14}C-partitioning and plant water status, in an attempt to understand the physiological processes responsible for the remarkable recovery of growth and development in groundnut following the release of early-season moisture deficits reported by Stirling *et al.* (1989).

MATERIALS AND METHODS

The experiment was conducted in controlled-environment glasshouses (Monteith, Marshall, Saffell, Clarke, Gallagher, Gregory, Ong, Squire, and Terry, 1983) and stand management, treatments and environmental control are described by Stirling *et al.* (1989).

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 of 130 mm. 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.

Labelling

^{14}C-labelling and analysis are described in detail by Stirling (1988) but briefly, perspex chambers large enough to accommodate three plants were linked to a closed air-flow system incorporating pumps and fans to enhance air-mixing and $^{14}CO_2$ uptake. Labelled CO_2 was generated inside the assimilation chambers by injecting $NaH^{14}CO_2$ through an air-tight rubber seal into a vial containing excess lactic acid. The chambers were increased in size as the plants grew and the ^{14}C-dose progressively increased from 30 to 75 μCi of $NaH^{14}CO_2$ (specific activity $2{\cdot}11 \times 10^7$ Bq mmol^{-1} (57·1 mCi mmol^{-1}); Radiochemical Centre, Amersham, UK) to avoid excessive dilution. For similar reasons a greater quantity of ^{14}C-activity was applied to the 130/0 stand at 88 d after sowing (DAS) due to its extremely lush vegetative growth relative to other stands.

Plants were labelled between 50 and 97 DAS, on six occasions in the 40/120 and 0/160 stands but on only five in the 130/0 treatment in which severe red spider mite infestation caused some of the crop to be removed on 82 DAS. Twelve plants from each treatment were labelled between 08.00 h and 10.00 h (GMT), except on days of extremely low irradiance when exposure was delayed until midday. After labelling, the chambers were removed and six plants were harvested immediately (0 h), while the remainder were tagged and harvested 24 h later. All above-ground and reproductive structures were removed, placed in polythene bags and stored at 4 °C to minimize redistribution and respiration of ^{14}C-labelled assimilates. Plants were separated into main and branch stems, main and branch stem leaves, stem apices (including expanding leaves), pegs and pods. These components were dried at 80 °C for 48 h, weighed, ground and sample-oxidized (Packard Instrument Co.) to produce a cocktail containing absorbed $^{14}CO_2$. Activity was determined using a Beckman LS 7500 DPM scintillation counter, applying appropriate quench correction.

Total counts were calculated for each plant component and expressed as a percentage of the total activity recovered from the plant. To examine treatment effects on assimilate partitioning, the net gain or loss of ^{14}C-activity in each component is expressed as the difference between % ^{14}C-activity recovered at time 0 and after a 24 h translocation period. Roots were not included in the analysis because of high variability within the ^{14}C-data (Stirling, 1988). However, omission of these data would not substantially bias the overall pattern of ^{14}C-distribution within shoot and reproductive structures since the ^{14}C-activity recovered in roots never exceeded 5% of the total plant dpm.

Water relations

Tissue water (ψ_w) and solute (ψ_s) potentials were measured using a portable pressure chamber (PMS Instrument Co., Oregon, USA) and a freezing point osmometer (Roebling), respectively. The water status of pegs, expanding and first fully-expanded leaves was measured at approximately 4 h intervals between 04.00 h and 20.00 h. Intensive diurnal measurements were made only in the extreme 130/0 and 0/160 treatments between 41 and 88 DAS with the ψ_s measurements largely being confined to the period between 08.00 h and 16.00 h, while the more rapid ψ_w measurements were extended to the extremes of the light period. At each sampling time, triplicate samples were taken from similar positions within the crop stand. To minimize post-excision water losses, individual leaflets and pegs were enclosed in a humidified polythene bag before being excised and sealed in the pressure chamber. After measuring ψ_w, samples were placed in small glass vials, rapidly frozen using liquid freon and stored deep-frozen for subsequent measurements of ψ_s. After thawing, duplicate measurements of ψ_s were made on sap extracted by microcentrifugation from each replicate sample, from which the mean was calculated. Turgor potential (ψ_p) was calculated as the difference between corresponding mean values of ψ_s and ψ_w at each sampling time.

RESULTS

Distribution of ^{14}C-activity at time 0

Leaves were the major site of ^{14}C-fixation in all treatments for most of the measurement period (Fig. 1) and substantially more of the activity was recovered from branch rather than main stem leaves due to their larger combined dry weight. The decrease in CO_2 fixation as leaves age and become increasingly shaded may explain the general decline in % ^{14}C-recovery from branch leaves in all stands late in the season. Nevertheless, % ^{14}C-recovery from branch leaves increased at 88 DAS following the release of water stress at 79 DAS in the 0/160 stand (Fig. 1c), although the corresponding values for main stem leaves continued to decline, as also occurred in the 40/120 treatment (Fig. 1b). In general, % ^{14}C-recovery from stems increased in all stands towards the end of the measurement period, particularly in branch stems in the late-irrigated treatments.

^{14}C-fixation by the stem apices remained below 5% of total plant activity in the 130/0 stand (Fig. 1a), but increased substantially after 79 DAS in the late-irrigated 40/120 and 0/160 stands (Fig. 1b, c). Similarly, pegs invariably contained less than 3% of total plant dpm in the 130/0 stand, but contributed as much as 15·9% of

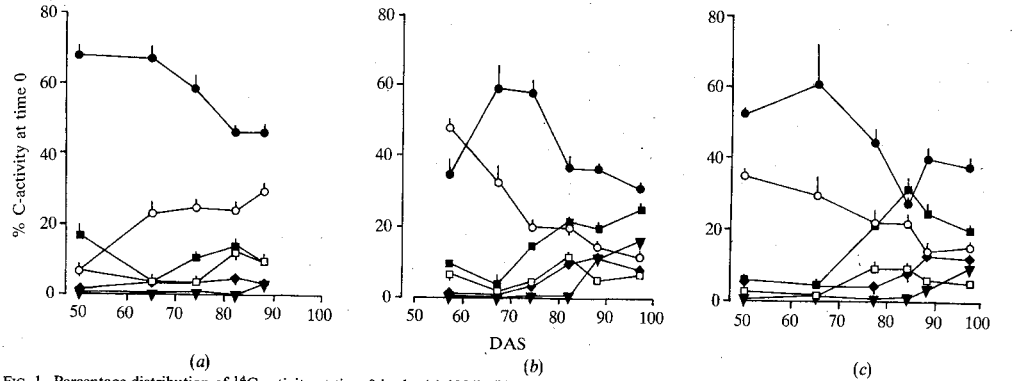

FIG. 1. Percentage distribution of ^{14}C-activity at time 0 in the (a) 130/0, (b) 40/120 and (c) 0/160 stands. Symbols are: ▼, stem apices; ○, main stem leaves; ●, branch stem leaves; □, main stem; ■, branch stem and ◆, pegs. Bars show double standard error of the mean in this and subsequent figures.

the total in the late-irrigated treatments at 97 DAS. The late-season increase in the activity recovered from the vegetative and reproductive meristems in the 40/120 and 0/160 stands might have been caused by rapid ^{14}C-translocation between harvest and separation of the plant components, which appears unlikely in view of the short time-scale involved, or, more probably, by a substantial increase in photosynthetic activity during reproductive development.

Translocation of ^{14}C-activity

Translocation from the branch leaves was initially high in the 130/0 stand, ranging from 32 to 28% of the activity present at time 0 between 50 and 74 DAS (Fig. 2a), but declined to about 10% at 88 DAS as water stress increased after the final irrigation at 56 DAS. Increasing water stress had no systematic effect on the corresponding values for main stem leaves. ^{14}C-translocation from branch and main stem leaves also decreased progressively

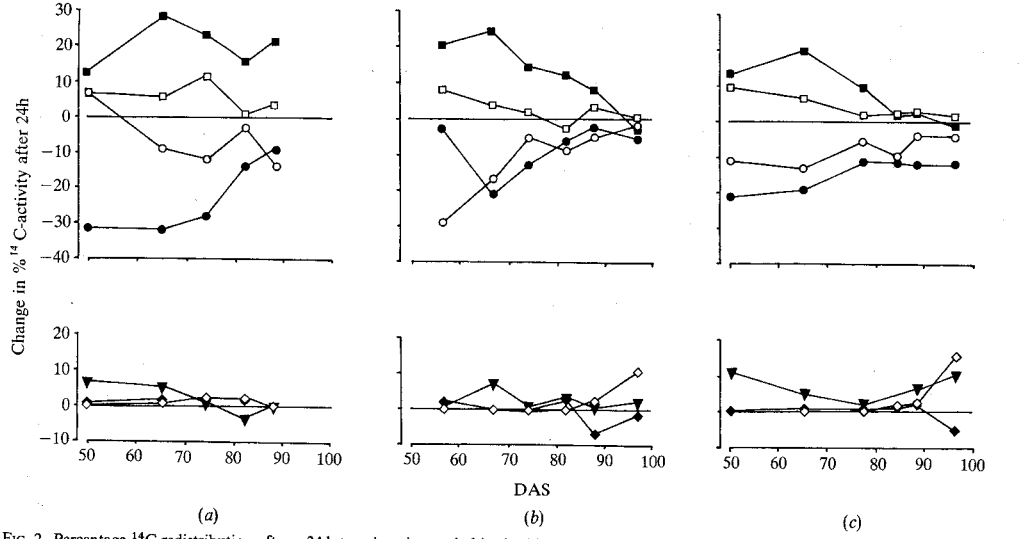

FIG. 2. Percentage ^{14}C redistribution after a 24 h translocation period in the (a) 130/0, (b) 40/120 and (c) 0/160 stands for ▼, stem apices; ○, main stem leaves; ●, branch stem leaves; □, main stem; ■, branch stem; ◆, pegs and ◇, pods.

in the early-stressed 40/120 and 0/160 stands (Fig. 2b, c), although irrigation of the 0/160 stand at 79 DAS arrested this decline for branch leaves.

Stems, particularly branch stems, were the most important sinks for ^{14}C-assimilate throughout the season in the late-stressed 130/0 stand (Fig. 2a), but were major sinks only during the period of early-season water stress in the 40/120 and 0/160 stands (Fig. 2b, c). In these stands stem sink activity was lost almost entirely when water stress was released at 79 DAS. However, the concurrent increases in ^{14}C-fixation at time 0 (Fig. 1b, c) suggests that the stems may have become more self-sufficient for assimilates and, therefore, have had less need to import assimilates late in the season.

^{14}C-import by the stem apices declined progressively in the early-stressed 0/160 stand, but increased rapidly once stress was released at 79 DAS (Fig. 2c). The more limited irrigation of the 40/120 stand after 78 DAS produced no equivalent recovery in apical sink activity (Fig. 2b) and in the late-stressed 130/0 treatment there was a pronounced decline in sink activity (Fig. 2a) towards the end of the season. By 88 DAS small differences in allocation to the pods were evident and by 97 DAS values for the late-irrigated 40/120 and 0/160 stands had reached 11% and 15% (Fig. 2b, c). The specific activity (% dpm g^{-1} dry weight) for pods after 24 h was up to six times greater in the late-irrigated stands than in the 130/0 stand at 88 DAS, suggesting that the greater ^{14}C-assimilate partitioning to pods in the former treatments was not simply a consequence of their greater pod dry weights.

Plant water status

At 65 DAS ψ_w, ψ_s and ψ_p were all substantially higher in both expanding and mature leaves in the 130/0 than in the 0/160 stand throughout the day (Fig. 3a, b). In both stands all water relations parameters reached their minimum around 13.30 h, soon after irradiance (S) and vapour pressure deficit (D) reached their daily maxima. ψ_w recovered almost to the early morning values by 19.30 h. Although early season-moisture deficits greatly reduced turgor in both expanding and mature leaves in the 0/160 stand (Fig. 3b), peg ψ_p was similar in both stands throughout the day and consistently much higher than in either expanding or mature leaves.

At 72 DAS, 7 d before stress was released in the late-irrigated treatments, ψ_w and ψ_p initially declined rapidly in the 130/0 stand as S and D increased (Fig. 4a). The ensuing slight recovery in the water status of expanding leaves and pegs coincided with the decline in S after 13.30 h caused by dense cloud. In the 0/160 stand ψ_w and ψ_s for all components were already much lower than in the 130/0 stand at dawn and showed little recovery until late in the observation period (Fig. 4b). The expanding leaf was most sensitive to moisture deficits in the 130/0 stand, with ψ_w and ψ_s declining to minima of $-1{\cdot}80$ and $-1{\cdot}85$ MPa as ψ_p fell to 0·05 MPa (Fig. 4a). In the 0/160 stand increasingly severe moisture deficits between 65 and 72 DAS reduced the daily minimum ψ_w in the expanding leaf from $-2{\cdot}02$ to $-2{\cdot}77$ MPa (Figs. 3b, 4b), although the concurrent but larger decline in ψ_s from $-2{\cdot}04$ to $-3{\cdot}17$ MPa led to an improvement in ψ_p of 0·38 MPa. The first fully expanded leaf in the 0/160 stand appeared to suffer the most severe stress at this stage, since turgor fell rapidly after 07.00 h and remained near zero for much of the day (Fig. 4b). Although ψ_w values were much lower in the 0/160 stand, turgor remained similar in pegs and higher in expanding leaves than in the 130/0 stand for most of the measurement period.

ψ_w and ψ_s increased markedly in all components of the 0/160 stand following irrigation at 79 DAS, and the extent of the increase in ψ_s suggests a substantial disappearance of solutes between 72 and 82 DAS (Figs 4b, 5b). Values of ψ_p between 13.00 h and 14.00 h were 0·40 and 0·26 MPa higher in mature leaves and pegs, but 0·19 MPa lower in expanding leaves on 72 DAS (Figs 5b, 4b). The improvement in the water status of mature leaves and pegs may have been amplified by the unusually low irradiances experienced on 82 DAS, which may also account for the observed increase in turgor in all components of the 130/0 stand, even though irrigation was discontinued after 56 DAS (Fig. 5a).

Irradiances were much higher on 88 DAS and D increased rapidly to reach maximum values at 15.00 h of 3·04 kPa in the 130/0, but only 1·50 kPa in the 0/160 stand. ψ_w bore a close inverse relation to S in the 0/160 stand, but was already low at dawn and showed much less variation in the 130/0 stand (Fig. 6). ψ_s also showed relatively little diurnal variation and ψ_w and ψ_p values for pegs were much lower in the 130/0 stand at all times. The partial maintenance of turgor in expanding leaves in the 130/0 stand, despite its total loss in mature leaves at midday (Fig. 6a) closely resembles the pattern seen in response to early-season moisture deficits (Fig. 4b).

DISCUSSION

^{14}C production and partitioning

A notable effect of timing of irrigation was the substantial increase in $^{14}CO_2$ fixation by stems apices and pegs in late- as opposed to early-irrigated stands during reproductive development (Fig. 1). Concurrent increases in the rates of canopy expansion and reproductive development late in the season were reported by Stirling *et al.* (1989). The increased contribution of branch stems to $^{14}CO_2$ fixation during reproductive growth in all stands (Fig. 1) was reflected by the greater partitioning of shoot dry matter to stems as opposed to leaves at this time (Stirling *et al.*, 1989). However, the sharp increase in $^{14}CO_2$ fixation by branch stems in the 0/160 stand between 65 and 84 DAS (Fig. 1c) occurred at a time when the ratio of stem to leaf weight remained virtually unchanged (Stirling

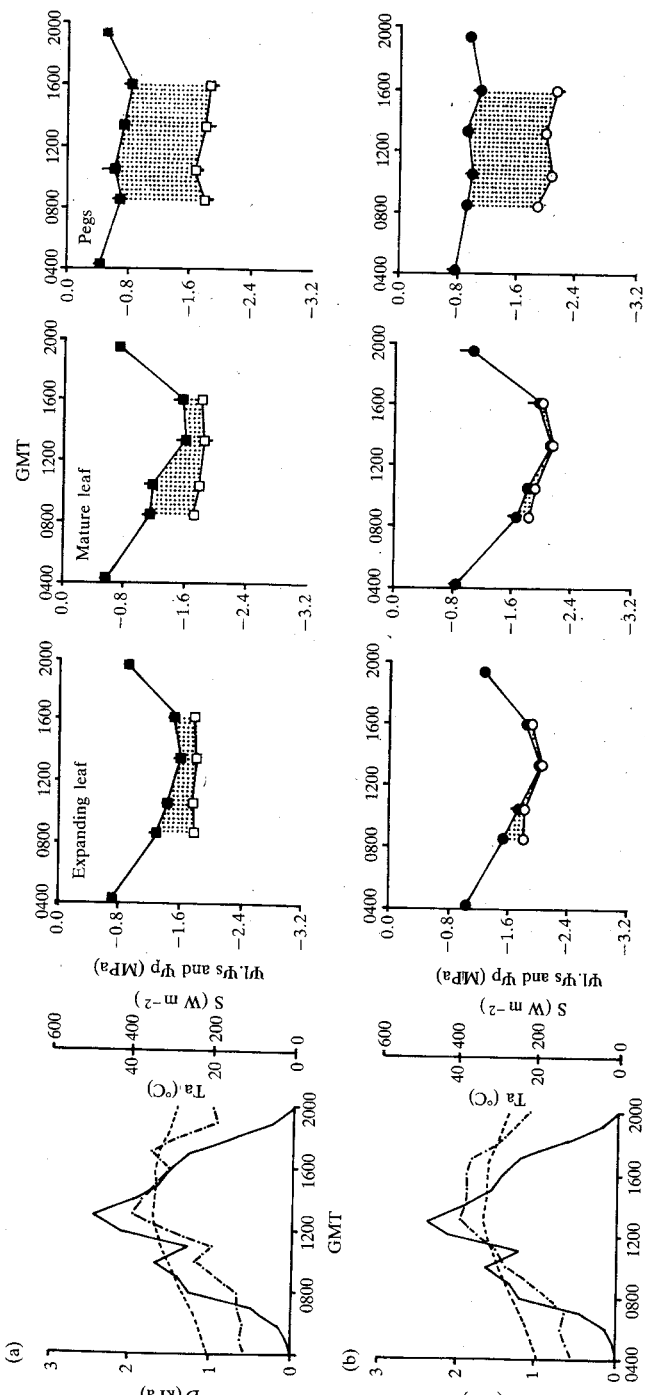

FIG. 3. Diurnal time-courses of air temperature (– – – –), irradiance (——), saturation deficit (–·–·–) and water status in the expanding and mature leaves and pegs on 65 DAS in the (a) 130/0 and (b) 0/160 treatments. Closed and open symbols refer to ψ_w and ψ_s, respectively, and ψ_p is represented by the stippled area.

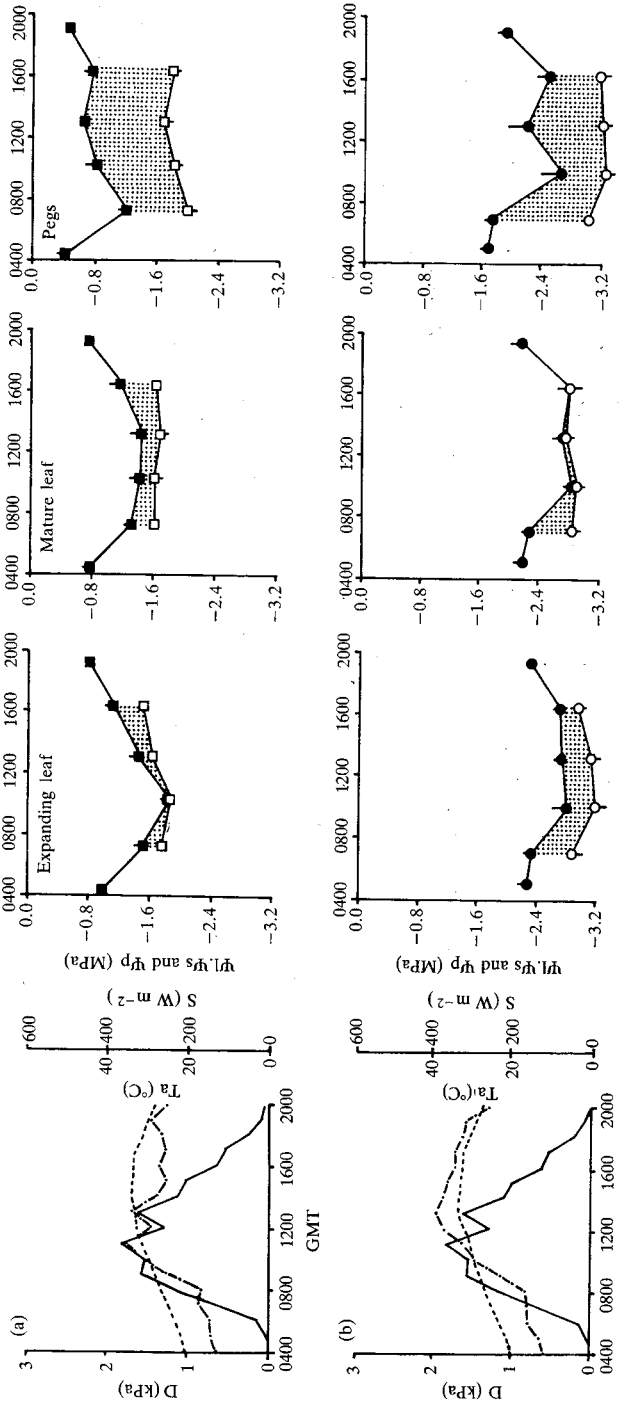

FIG. 4. Diurnal time-courses on 74 DAS in the (a) 130/0 and (b) 0/160 treatments. Symbols as in the legend for Fig. 3.

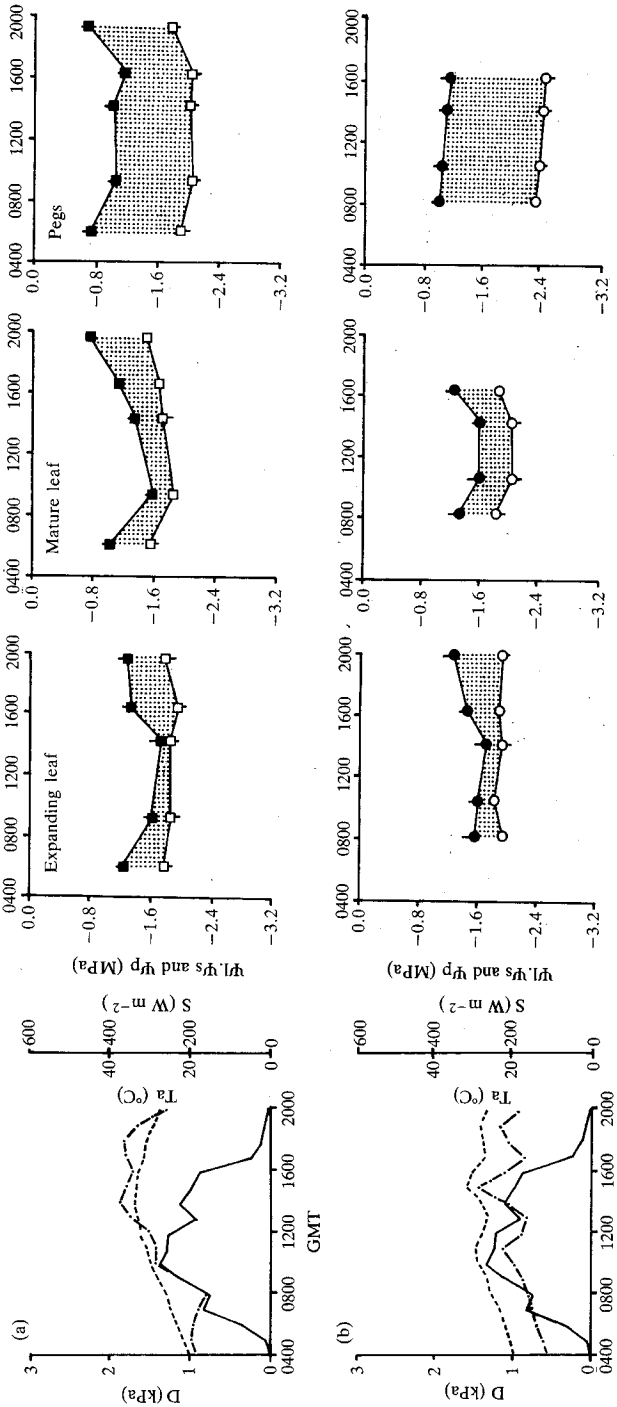

FIG. 5. Diurnal time-courses on 82 DAS in the (a) 130/0 and (b) 0/160 treatments. Symbols as in the legend for Fig. 3.

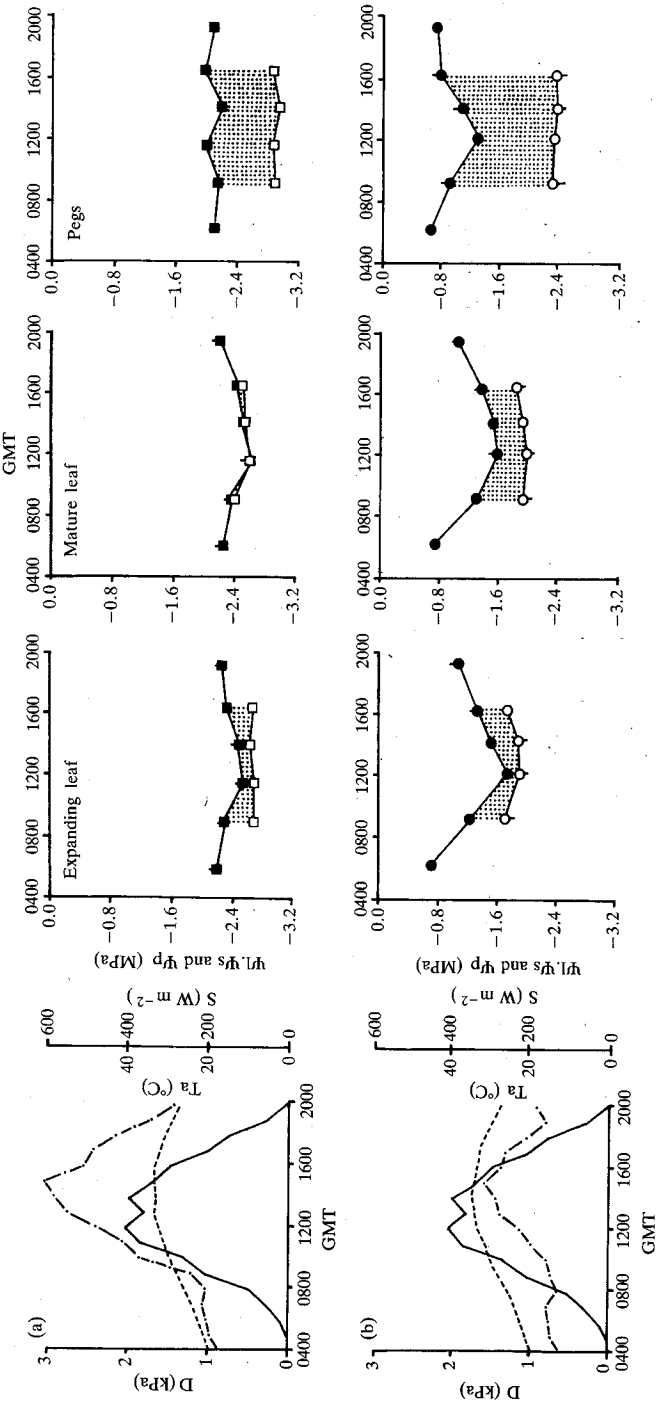

FIG. 6. Diurnal time-courses on 88 DAS in the (a) 130/0 and (b) 0/160 treatments. Symbols as in the legend for Fig. 3.

et al., 1989). Some leaf folding was observed in the assimilation chambers during periods of severe moisture stress in the late- and to a lesser extent, in the early-irrigated stands, which may have increased light penetration to the stems. Stems are capable of photosynthesis, providing a possibly important secondary site for CO_2 fixation when water conservation becomes a priority. Such responses may also explain the superior water use ratio of Kadiri-3 relative to other groundnut cultivars which exhibit less leaf folding during drought (Matthews, Harris, Williams, and Nageswara Rao, 1988).

There was close agreement between the patterns of ^{14}C-partitioning and growth and development. For example, the restricted ^{14}C-assimilate supplies to vegetative and reproductive meristems late in the season in the 130/0 stand (Fig. 2a) were associated with a slowing of canopy expansion and reproductive development (Stirling *et al.*, 1989). The continued assimilate allocation to stems during reproductive development in this stand may have originated from inadequate sink capacity elsewhere in the plant for current assimilates, as has been reported previously, for a range of species (Biddulph and Cory, 1965; Adams, Wiersma, and Salazar, 1978). This view is supported by the concurrent virtual cessation of pod production in the 130/0 stand (Stirling *et al.*, 1989). In contrast, early water stress limited initial shoot growth and development but this was followed by the synchronous renewal of vegetative and reproductive development after irrigation, which reflected the more balanced ^{14}C-partitioning between stem apices and pods at the expense of stems in the 0/160, and to a lesser extent, in the 40/120 stands (Fig. 2c, b). The marked recovery of growth and development following irrigation in the 0/160 stand was reflected by continued apical sink activity, whereas apical sink activity was almost entirely lost after 74 DAS in the late-stressed 130/0 stand (Fig. 2a). This decline in apical sink activity may have been caused either by the inability of apices to compete effectively for current assimilates or by increased respiratory losses. The former appears more probable since the concurrent decline in vegetative development (Stirling *et al.*, 1989) implies an overall reduction in meristematic activity.

The subtle competitive balance between vegetative and reproductive sinks is illustrated by the intermediate 40/120 treatment. For example, while early drought reduced net ^{14}C-import by stems during reproductive development (Fig. 2b, c), the limited irrigation of the 40/120 stand before 56 DAS appeared to favour pod sink activity at the expense of apices late in the season (Fig. 2b), an effect which was much less pronounced in the 0/160 stand (Fig. 2c). This decline in the partitioning of assimilates to stem apices in 40/120 stand may explain the incomplete recovery of vegetative development after irrigation at 79 DAS (Stirling *et al.*, 1989).

There was apparently no simple interrelationship between ^{14}C-partitioning and plant water status, and there was particular anomalies with respect to the timing of events. For example, the decline in ^{14}C-partitioning to reproductive structures after 74 DAS in the 130/0 stand (Fig. 2a) preceded any major reduction in peg turgor (Figs 4a, 5a, 6a). Similarly, while the reduced ^{14}C-assimilate supply to stem apices in the 0/160 stand at 77 and 84 DAS (Fig. 2c) was correlated with decreased rates of main stem leaf appearance and canopy expansion (Stirling, 1988; Stirling *et al.*, 1989), there was no loss of turgor within the expanding leaf, owing to the concurrent reduction in ψ_s (Fig. 4b). Thus, changes in ^{14}C-assimilate partitioning to stem apices and reproductive structures preceded any detectable reduction in bulk turgor levels.

A similar lack of correlation between growth and turgor was reported by Van Volkenburgh and Boyer (1985), who observed marked reductions in leaf extension in maize as soil moisture deficits increased despite complete turgor maintenance in the growing region. More recent work suggests that factors other than cell turgor, such as cell wall extensibility (Van Volkenburgh and Cleland, 1986; Barlow, 1986) and plant growth substances (Davies, Metcalfe, Lodge, and da Costa, 1986; Turner, 1986), may mediate the responses of developmental processes to increasing moisture deficits.

Water status

While expanding leaves maintained positive turgor values during periods of severe stress in both the 0/160 and 130/0 stands (Figs 4b, 6a), the mature leaves frequently lost turgor around midday in both early-and late-irrigated stands (Figs 6a, 4b). Unlike leaves, pegs lose little water directly to the atmosphere because of their shaded position within the canopy, and retained high levels of turgor during periods of drought in both the 130/0 and 0/160 stands (Figs 6a, 4b). Turgor maintenance by pegs was facilitated by their substantially lower ψ_s levels than in leaves.

The maintenance of positive turgor values within expanding but not in mature leaves, at low water potentials (Figs 4b, 6a) accords with previous studies on wheat (Munns, Brady, and Barlow, 1979) and was associated with their lower solute potential during periods of severe drought. Estimates of osmotic adjustment were obtained for leaves by comparing ψ_s values at zero turgor in irrigated and stressed plants. No solute adjustment occurred in mature leaves during periods of stress since ψ_s at zero turgor remained virtually constant ($-1{\cdot}84 \pm 0{\cdot}08$ MPa) in both stands throughout the measurement period. However, expanding leaves exhibited lower ψ_s values at zero turgor during periods of stress giving estimated maximum osmotic adjustments of 1·58 and 0·84 MPa in the 0/160 and 130/0 stands. Solute potentials were measured between 41 and 88 DAS, at which time plants in the 130/0 treatment had experienced a much shorter period of stress

than those in the late-irrigated 0/160 stand. Since progressive moisture deficits are known to promote solute accumulation (Turner and Jones, 1980), water stress may not have been sufficiently sustained to promote the same degree of osmotic adjustment in the 130/0 as in the 0/160 stand.

The osmotic adjustment observed in expanding leaves during periods of moisture deficits may have arisen partly from the inhibitory influence of water stress on leaf expansion, acting primarily through decreases in cell size (Cutler, Rains, and Loomis, 1977). However, osmotic adjustment was not permanent since ψ_s increased sharply between 72 and 82 DAS following the release of water stress in the 0/160 stand (Figs 4b, 5b). A reversal of leaf water status also occurred, whereby turgor became lower in expanding leaves than in mature leaves in both treatments during the central hours of the day (Figs 4a, 5b, 6b). Similar responses occur in other species (Michelena and Boyer, 1982; Barlow, 1986) and it has been suggested that cell wall extension in rapidly growing leaves may prevent turgor from being maintained at the same level as in fully expanded tissue (Barlow, 1986).

While the absence of osmotic adjustment in mature leaves of groundnut agrees with earlier glasshouse studies (Black, Tang, Ong, Solon, and Simmonds, 1985; Ong, Black, Simmonds, and Saffell, 1985), its occurrence in expanding leaves contrasts with the findings of Ong *et al.* (1985). This variability in response may reflect differences in the severity of the water stress imposed, since a rising water table following heavy rain replenished the soil moisture reserves at 63 DAS in the previous study (Simmonds and Ong, 1987), with the result that ψ_w in expanding leaves never exceeded $-2{\cdot}0$ MPa (Ong *et al.*, 1985), as compared with $-2{\cdot}77$ MPa in the present experiment (Fig. 4b).

Although partial turgor maintenance in expanding leaves during periods of drought in the late-irrigated 0/160 stand (Fig. 4b) failed to maintain developmental rates at the pre-stressed levels in the early-irrigated stands (Stirling *et al.*, 1989), it may have been important in ensuring the survival of the meristematic regions, thereby allowing the remarkable recovery of development once water stress was released at 79 DAS (Stirling *et al.*, 1989). Indeed, previous studies have shown that developmental rates are more closely correlated to the water status of mature leaves, rather than expanding leaves, although it is not known if this relationship is causal or consequential (Barlow, 1986; Davies *et al.*, 1986).

CONCLUSIONS

This study has provided an insight into the mechanisms responsible for the relative insensitivity of pod yield in groundnut to early moisture deficits. While early moisture deficits slowed both vegetative and reproductive development, the maintenance of apical sink activity and turgor within the expanding leaves was associated with a rapid recovery of these processes when stress was released. Early drought had no marked effect on peg turgor, allowing all stands to enter the reproductive phase almost simultaneously (Stirling *et al.*, 1989). This has important implications for the development of improved irrigation scheduling in semi-arid regions where it is important for pods to be set sufficiently early to ensure that at least some are filled prior to harvest, because of the short growing season. Thus, management practices should aim to optimize water availability at the time of pegging in order to minimize the delay in pod initiation and consequent yield losses.

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