



Effects of soil moisture deficits on the water relations of bambara groundnut (*Vigna subterranea* L. Verdc.)

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Abstract

The components of leaf water potential (Ψ_l) and relative water content (RWC) were measured for stands of bambara groundnut (*Vigna subterranea*) exposed to three soil moisture regimes in controlled-environment glasshouses at the Tropical Crops Research Unit, Sutton Bonington Campus. Treatments ranged from fully irrigated (wet) to no irrigation from 35 days after sowing (DAS) (dry). RWC values varied between 92–96% for the wet treatment, but declined from 93% to 83% in the dry treatment as the season progressed. Ψ_l at midday decreased in both the wet and dry treatments, but the seasonal decline was more pronounced in the latter: seasonal minimum values were -1.19 and -2.08 MPa, respectively. Plants in the wet treatment maintained turgor (Ψ_p) at about 0.5 MPa throughout the season, whereas values in the dry treatment approached zero towards the end of the season. There was a linear relationship between Ψ_p and Ψ_l , with Ψ_p approaching zero at a Ψ_l of -2.0 MPa. Mean daily leaf conductance was consistently higher in the wet treatment (0.46 – 0.79 cm s⁻¹) than in the intermediate and dry treatments (0.13 – 0.48 cm s⁻¹). Conductances in the intermediate and dry treatments were similar, and the lower evapotranspirational water losses in the latter were attributable to its consistently lower leaf area indices (L): L at final harvest was 3.3, 3.3 and 1.9 for the wet, intermediate and dry treatments. Bambara groundnut was apparently able to maintain turgor through a combination of osmotic adjustment, reductions in leaf area index and effective stomatal regulation of water loss.

Key words: *Vigna subterranea*, water relations, soil moisture.

Introduction

Bambara groundnut (*Vigna subterranea* L. Verdc.) is grown as a subsistence crop in semi-arid regions of Africa where the success of other legumes is uncertain because of poor soils, drought and disease (Vietmeyer, 1978; Haq, 1983). However, previous research on the crop has been limited, largely because its commercial value is restricted by a low lipid content (5–8%; Deshpande and Damodaran, 1990; Brough and Azam-Ali, 1992), even though it is an important source of protein at the subsistence level. Previous controlled environment experiments have shown that bambara groundnut is capable of producing a worthwhile yield under conditions where groundnut (*Arachis hypogaea* L.) may fail completely (Babekir, 1989). The mechanisms which enable bambara groundnut to produce at least some yield during severe drought are poorly understood, but may be linked with its relatively high root:shoot biomass ratio and small leaf area, which restricts transpirational loss of water (Collinson *et al.*, 1996).

Crops grown in drought-prone areas display varied responses to water stress which may be divided into three categories; escape, avoidance and tolerance (Turner, 1979). Drought escape is demonstrated by desert ephemerals and some short duration dryland crops which have a condensed growth cycle and reach maturity before drought occurs; their short life-cycle is often combined with developmental plasticity. Crop species displaying this type of adaptation are often photoperiod-sensitive so that flowering coincides with the average date of the end of the rainy season (Ludlow and Muchow, 1988). Drought-avoiding species, such as cowpea (*Vigna unguiculata* (L.) Walp.) and sorghum (*Sorghum bicolor* (L.) Moench), avoid water deficits by maximizing water uptake and minimizing water loss. This response is typi-

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fied by the tropical legume, *Siratro*, which has deep roots to maximize water uptake, stomata which are sensitive to decreased leaf water potential and increased leaf-to-air vapour pressure deficit, and exhibits paraheliotropic leaf movements to reduce interception of incident solar radiation (Ludlow, 1989). Other species, such as groundnut, pigeonpea (*Cajanus cajan* (L.) Millspaugh) and cotton (*Gossypium hirsutum*), have developed mechanisms to survive drought through dehydration tolerance. In these species, osmotic adjustment often assists in turgor maintenance, hence allowing stomatal opening, photosynthesis and leaf expansion to be maintained over a wider range of soil moisture stress than in more susceptible species.

Although bambara groundnut has clearly evolved mechanisms to withstand drought, the lack of quantitative evidence regarding the nature of its responses means that it has not yet been categorized into one of the three groups outlined above. Begemann (1988) examined 72 landraces of bambara groundnut grown under two water stress regimes in Ibadan, Nigeria. In the first, in which the plants received no water from 2 weeks after sowing, the highest yielding landraces were those which matured early, as they were able to escape drought by producing some yield before stress became intense. In the second regime, in which the plants received no water for the first 35 days after sowing (DAS), the highest-yielding landraces were those with extensive root systems capable of exploiting water held within deeper soil layers.

Cell expansion is extremely sensitive to water stress, mainly due to reductions in the hydrostatic pressure or turgor potential necessary for expansion (Ong *et al.*, 1985). Growth is usually positively correlated with turgor above a threshold value which varies between species, for example, from 0.1 MPa in millet (*Pennisetum typhoides* S.&H.) (Squire *et al.*, 1983) to 0.25 MPa in sunflower (*Helianthus annuus* L.) (Mathews *et al.*, 1984), although this value may be modified by water stress. Plant water status is described here in terms of leaf water potential (Ψ_1) or relative water content (RWC), which may be used as indicators of drought susceptibility or tolerance. Species which exhibit restricted changes in relative water content per unit reduction in water potential are often considered to be more drought resistant. A detailed account of water potential and its components is given by Turner (1986).

In order to improve the yield of bambara groundnut in drought-prone areas, a more detailed understanding of its responses is required. This study aimed to establish the impact of drought on the components of leaf water potential in bambara groundnut and also examined the strategies underlying the effective water conservation mechanisms adopted by this species.

Materials and methods

The experiment was conducted in five controlled environment glasshouses located at the University of Nottingham Sutton

Bonington Campus, UK (52°50' N, 1°15' W, 50 m above sea level). The original design and control system of the glasshouses were described by Monteith *et al.* (1983) and improvements and alterations implemented in 1990 were reported by Clifford *et al.* (1993). The soil within each glasshouse was isolated from the external soil by heavy duty polythene installed to a depth of 1 m to prevent lateral and vertical infiltration of water. A similar lining subdivided every house into two plots, each approximately 16 m² in area.

Crop management

A basal fertilizer (NPK, 20:10:10) was incorporated into the soil at a rate equivalent to 40 kg N ha⁻¹. A cream landrace of bambara groundnut was supplied from farmers' fields in the Rusape region of Mashonaland, Zimbabwe by National Tested Seeds Ltd, Harare, Zimbabwe. The seeds were sown at 5 cm intervals in rows 35 cm apart on 25 May 1990, and the plants were thinned to an intra-row spacing of 10 cm at 23 DAS. Air temperature was maintained at a mean of 28°C with a sinusoidal amplitude of $\pm 5^\circ\text{C}$ using gas-fired heaters (Powmatic Ltd, UK) with an atmospheric flue to vent the fumes to the outside of the glasshouse. Spinning disc humidifiers (Mellor-Bromley Ltd, UK) were used to maintain the saturation vapour pressure deficit below a maximum of 2 kPa. Photoperiod was controlled manually at 12 h d⁻¹ from 39–112 DAS to prevent the inhibition of podding which had been observed under longer daylengths in previous experiments (Linnemann and Azam-Ali, 1993). This was achieved by drawing black polythene sheets over a frame suspended above the plants between 20.00 h and 08.00 h on consecutive days. Between 08.00 h and 20.00 h the crops received natural daylight with no supplementary lighting. Irrigation was supplied using PVC microporous tubing placed between the rows as described below.

Experimental treatments

The soil was maintained close to field capacity in all five glasshouses until 36 DAS to ensure successful germination and establishment. Volumetric soil water content was measured weekly using a 'Wallingford' neutron probe (Didcot Instruments, Wallingford, UK). Five irrigation regimes were imposed from 36 DAS (Table 1); these ranged from a fully irrigated control, which was irrigated weekly to replenish the amount of water lost during the previous week, to a dry treatment which received no irrigation from 36 DAS.

Crop evapotranspiration (*Et*) was estimated from weekly measurements of soil moisture content and soil evaporation. Soil moisture content was measured at 10 cm intervals to a depth of 1 m using a neutron probe and two access tubes permanently located within each plot. Soil surface evaporation was assessed following irrigation using two microlysimeters placed between the rows in each plot and reweighed after 6 d.

Incident radiation in each plot was measured using 1 m long tube solarimeters mounted above the canopy, and transmitted radiation was determined using paired solarimeters on the soil surface within the central harvest area (which was left untouched until final harvest). The fraction of total irradiance intercepted by the canopy (*f*) was calculated by subtracting the transmitted radiation from the incident radiation for each plot. Further experimental details are given by Collinson *et al.* (1996).

Plant water status

The components of leaf water potential (Ψ_1) and relative water content (RWC) were measured in the wet (A), intermediate (C) and dry (E) irrigation treatments at midday on 23 occasions

Table 1. Irrigation schedule between 36 and 118 DAS (mm applied)

DAS	Treatment A 'Wet'	Treatment B	Treatment C 'Intermediate'	Treatment D	Treatment E 'Dry'
36	20	20			
39	10	20			
41	10				
49	20	20	20		
56	40				
63	20	20			
70	30				
76	30	20	30	30	
83	20				
90	20	20			
97	20				
104	20	20	30		
111	20				
118	20	20			
Total	300	160	80	30	0

between 27 and 137 DAS. On each sampling date, Ψ_1 , osmotic potential (Ψ_π) and *RWC* were determined for the youngest fully expanded leaf of five plants selected at random from each treatment.

The trifoliolate leaf was enclosed in a humidified plastic bag to reduce water losses prior to excision. Leaf water potential was measured for the terminal leaflet using a portable pressure chamber (PMS Instrument Company, Oregon, USA). Water losses were further minimized by humidifying the air in the chamber. The excised terminal leaflet was then immediately placed in a screw-top glass vial (8 ml), frozen rapidly using a freezing aerosol (dichloro, difluoromethane) to destroy turgor and evacuate air within the vial to prevent condensation of moisture on the enclosed sample, and stored in a deep freeze. Ψ_π was measured on the following day after centrifuging the thawed leaflets using a Camlab microcentrifuge for 2 min to extract the sap. 25 μ l subsamples were then analysed using a Roebbling freezing point micro-osmometer calibrated with 0 and 300 mOsmol NaCl solutions, and Ψ_π was determined according to Wyn Jones and Gorham (1983). Turgor potential was calculated as the difference between Ψ_π and Ψ_1 . Observations that Ψ_π was occasionally less negative than Ψ_1 in severely stressed leaves, giving negative Ψ_p values, suggests the occurrence of some apoplastic dilution; this aspect is considered further below.

Relative water content was determined using 10 leaf discs (1 cm diameter) excised using a cork borer from the two lateral leaflets of the trifoliolate leaves used to measure Ψ_1 and Ψ_π . The discs were removed from the lateral leaflets immediately after excising the terminal leaflet for the measurement of leaf water potential. The discs were immediately placed in pre-weighed vials (8 ml), sealed and reweighed to derive their fresh weight (*FW*) before being placed in 1 cm diameter holes cut in blocks of foam rubber saturated with distilled water. These were sealed in plastic boxes to prevent evaporation and left overnight under a light source to allow the discs to rehydrate to their turgid weight (*TW*). Their dry weight (*DW*) was obtained after oven-drying at 80 °C for 48 h. *RWC* was calculated according to Turner (1986) as

$$RWC = \frac{FW - DW}{TW - DW} \times 100$$

Previous measurements on groundnut had shown that the values obtained for the water relations parameters did not depend on which leaflet within the leaf was sampled, provided

the leaflets were similarly exposed to incident radiation. For this reason, uniformly illuminated leaves were selected within the age-category being sampled. The lateral leaflets were chosen for the *RWC* measurements because they provided a greater combined sampling area than the terminal leaflet.

Leaf conductance (g_l) was measured using a diffusive resistance porometer (Delta-T Devices, Mark III) at 2–6 d intervals between 56–89 DAS. Measurements were made on both surfaces of the youngest fully expanded leaf of five plants in each treatment at 2 h intervals between 08.00 h and 16.00 h.

Results

Relative water content (RWC)

Leaf *RWC* values in the wet treatment were between 92–96% for most of the season (Fig. 1), in agreement with data reported by Muriuki (1990). In the dry treatment, *RWC* gradually declined from 93% at 60 DAS to 83% at 137 DAS (Fig. 1); the values were consistently lower than in the fully irrigated treatment after 45 DAS.

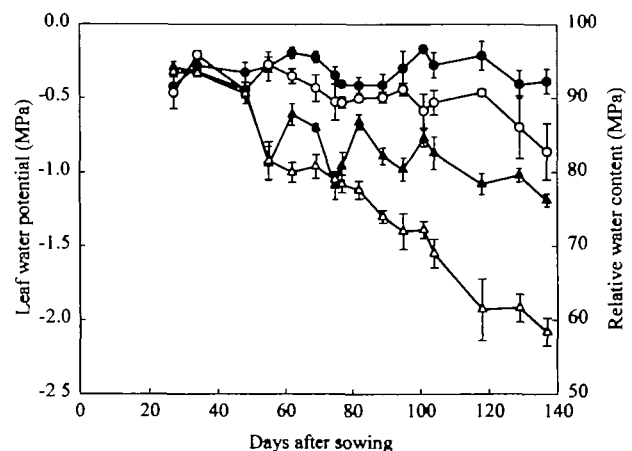


Fig. 1. Seasonal time-courses of leaf water potential (\blacktriangle , \triangle) and relative water content (\bullet , \circ) at midday. Closed and open symbols denote wet and dry treatments, respectively (Table 1). Bars indicate double standard errors of the mean.

Components of water potential

Leaf water potential at midday declined steadily throughout the season in both the wet and dry treatments, although the decrease was more pronounced in the latter (Fig. 1). In the dry treatment, Ψ_1 declined almost linearly after 45 DAS at an average rate of $16 \times 10^{-3} \text{ MPa d}^{-1}$ ($r^2=0.97$); the corresponding value for the wet treatment was $5.3 \times 10^{-3} \text{ MPa d}^{-1}$ ($r^2=0.66$). Substantial differences between treatments were observed later in the season, and seasonal minimum values for the wet and dry treatments were -1.19 and -2.08 MPa , respectively.

Osmotic potential (Ψ_π) declined steadily until about 90 and 110 DAS in the wet and dry treatments, respectively (Fig. 2a, c), and then remained relatively constant. Regression analysis revealed that Ψ_π declined at mean rates of $6.52 \times 10^{-3} \text{ MPa d}^{-1}$ ($r^2=0.64$) and $7.92 \times 10^{-3} \text{ MPa d}^{-1}$ ($r^2=0.90$) in the wet and dry treatments. Although Ψ_π clearly decreased as the season progressed, particularly in the dry treatment, the full extent of osmotic adjustment and its contribution to turgor maintenance could not be determined unequivocally since Ψ_π was not measured for fully hydrated tissue. An alternative approach was to divide Ψ_π by the corresponding *RWC* values to express Ψ_π in terms of tissue moisture content. The moisture-adjusted Ψ_π values decreased by 36% between 50–140 DAS in the wet treatment (from -1.4×10^{-2} to $-1.9 \times 10^{-2} \text{ MPa \%RWC}^{-1}$) and by 44% in the dry treatment (from -1.6×10^{-2} to $-2.3 \times 10^{-2} \text{ MPa \%RWC}^{-1}$).

Turgor (Ψ_p) proved to be the most variable water relations parameter examined (Fig. 2b, d). Plants in the

dry treatment generally maintained similar turgor potentials to the wet treatment until 80 DAS, after which Ψ_p decreased sharply to values close to zero towards the end of season. There was no equivalent decline in Ψ_p in the wet treatment, but rather a fluctuation around 0.5 MPa .

There was a linear relationship between Ψ_p and Ψ_1 (Fig. 3a), and Ψ_p approached zero at a Ψ_1 of about -2.0 MPa . The apparent negative Ψ_p values for severely stressed plants may have resulted from the dilution of intracellular solutes by extracellular water during freezing and thawing of the tissue (Squire *et al.*, 1981); apoplastic volume and hence apoplastic dilution may be greater in tissues produced during water stress. Negative turgor values have been reported previously by Maxwell and Redmann (1978) for the xeric grass, *Agropyron dasystachyum* (Hook.) Scribn. The relationship between Ψ_1 and *RWC* (Fig. 3b) indicates that zero Ψ_p was approached at a *RWC* of about 85%, above which Ψ_p increased linearly to a predicted maximum of 1.25 MPa at 100% *RWC*.

Conductance

Mean daily g_1 values declined gradually in all treatments (Fig. 4a), but were consistently higher in the wet treatment ($0.46\text{--}0.79 \text{ cm s}^{-1}$) than in the intermediate and dry treatments ($0.13\text{--}0.48 \text{ cm s}^{-1}$). The transient increase in g_1 in the intermediate treatment at 80 DAS reflects the irrigation applied at 76 DAS (Table 1). Leaf area index (*L*) values for the three growth analyses carried out during the period 55–90 DAS are presented in Fig. 4b; *L* was invariably much higher (4.1–5.4) in the wet and intermediate treatments than in the dry treatment (1.8–2.5).

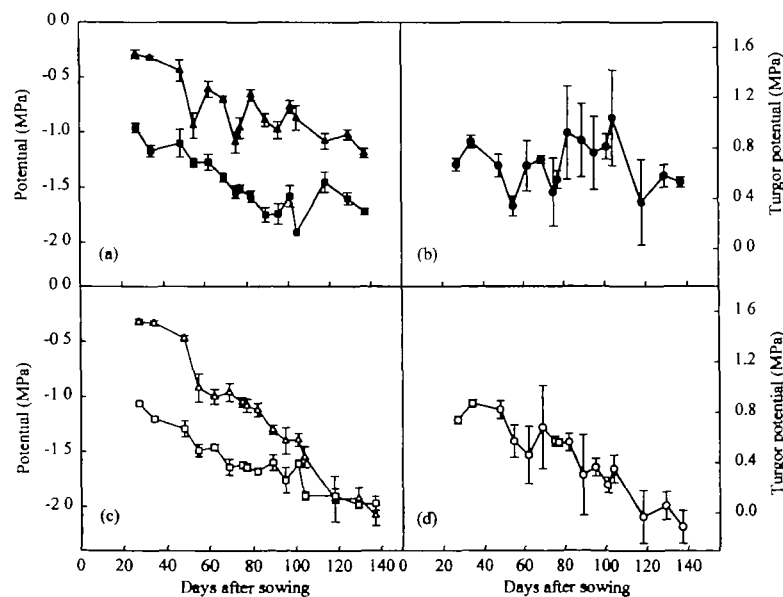


Fig. 2. Seasonal time-courses of (a, c) water (▲, △) and osmotic (■, □) potentials in the wet and dry treatments, and (b, d) turgor potential (●, ○) in the wet and dry treatments. Closed and open symbols denote wet and dry treatments, respectively. Bars indicate double standard errors of the mean.

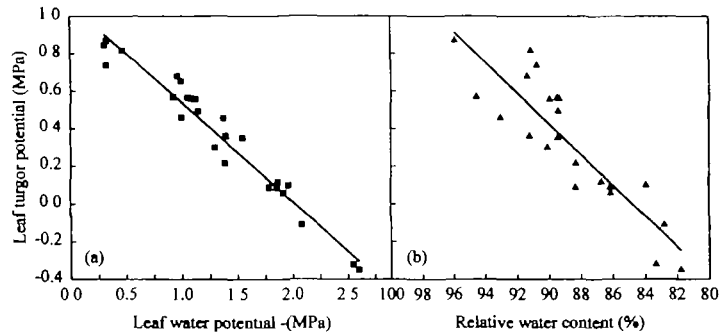


Fig. 3. Relationships between (a) leaf turgor potential and leaf water potential ($\Psi_p = 1.0672 - 0.5272 \Psi_1$, $r^2 = 0.95$, 24 d.f.) and (b) leaf turgor potential and relative water content ($\Psi_p = 0.0819 RWC - 6.94$; $r^2 = 0.78$, 20 d.f.).

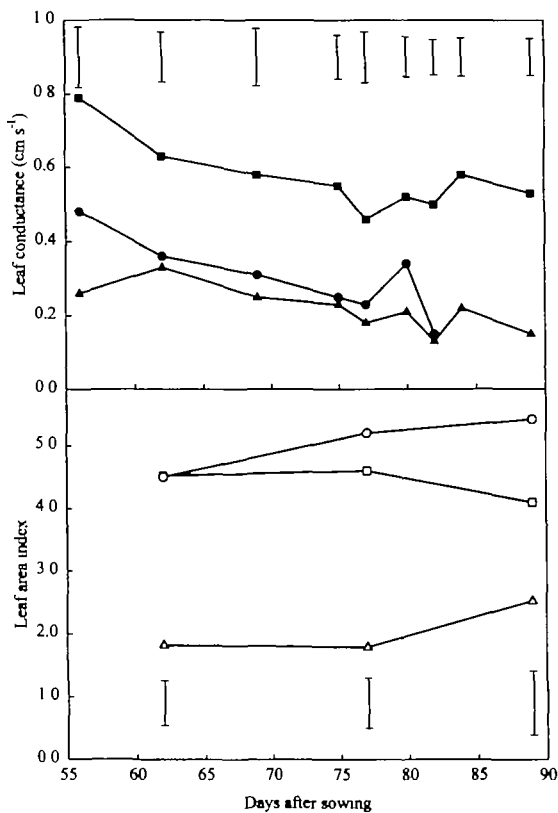


Fig. 4. Time-courses of (a) leaf conductance and (b) leaf area index between 55–90 DAS for the wet (■, □), intermediate (●, ○) and dry (▲, △) treatments. Bars indicate mean double standard errors for leaf conductance and leaf area index on specific days (all treatments).

The diurnal trend in g_1 on the three sampling dates generally followed the daily time-course of irradiance in the irrigated and, to a lesser extent, the intermediate treatment, but the values remained relatively constant in the dry treatment (Fig. 5a, b, c).

Transpiration per unit of fractional interception ($E1/f$) declined rapidly from 3.0 to 0.5 in the dry treatment, but remained around 2.5 throughout the season in the wet treatment (Fig. 6).

Discussion

Water stress is generally characterized by decreases in RWC and Ψ_p , resulting in wilting, stomatal closure and reduced growth (Kramer and Boyer, 1995). Reductions in leaf growth resulting from decreased turgor within expanding cells may indirectly help to maintain water status during drought. Thus, drought-induced reductions in leaf area index (L) are common and may improve foliar water status, resulting in higher leaf conductances and water potentials because of the consequent restrictions imposed on light interception and transpiration (Ong *et al.*, 1996). For example, leaf expansion rate in groundnut is extremely sensitive to foliar water status, declining by approximately 10% for every 0.1 MPa reduction in Ψ_p (Ong *et al.*, 1985). In the present study, reductions in leaf area (Fig. 4b) helped to restrict water loss in the dry treatment, thus enabling the crop to survive severe soil moisture stress.

The seasonal decline in Ψ_1 , Ψ_x and RWC was invariably greater in the dry treatment than in the wet treatment (Figs 1, 2). Ψ_p remained relatively constant at around 0.5 MPa in all treatments until about 80 DAS, but thereafter decreased to values close to zero in the dry treatment (Fig. 2). Ψ_p is widely believed to be an important sensory mechanism responsible for initiating a chain of physiological and biochemical responses which affect photosynthetic activity (Hsiao and Acevedo, 1974). Many aspects of plant metabolism, growth and development are adversely affected by water deficits, including stomatal control (Black *et al.*, 1985), leaf and flower growth (Ong *et al.*, 1985; Kramer and Boyer, 1995) and root development (Ong *et al.*, 1985). However, there is also evidence that Ψ_p is not the universal transducer of water deficits in cells; for example, Gollan *et al.* (1986) found no correlation between leaf turgor and stomatal conductance in wheat and sunflower. There is substantial evidence that the roots may be the primary sensor of soil water status and that abscisic acid (ABA) may act as a root-sourced chemical messenger involved in mediating plant responses to soil drying and other stress factors (Hartung and

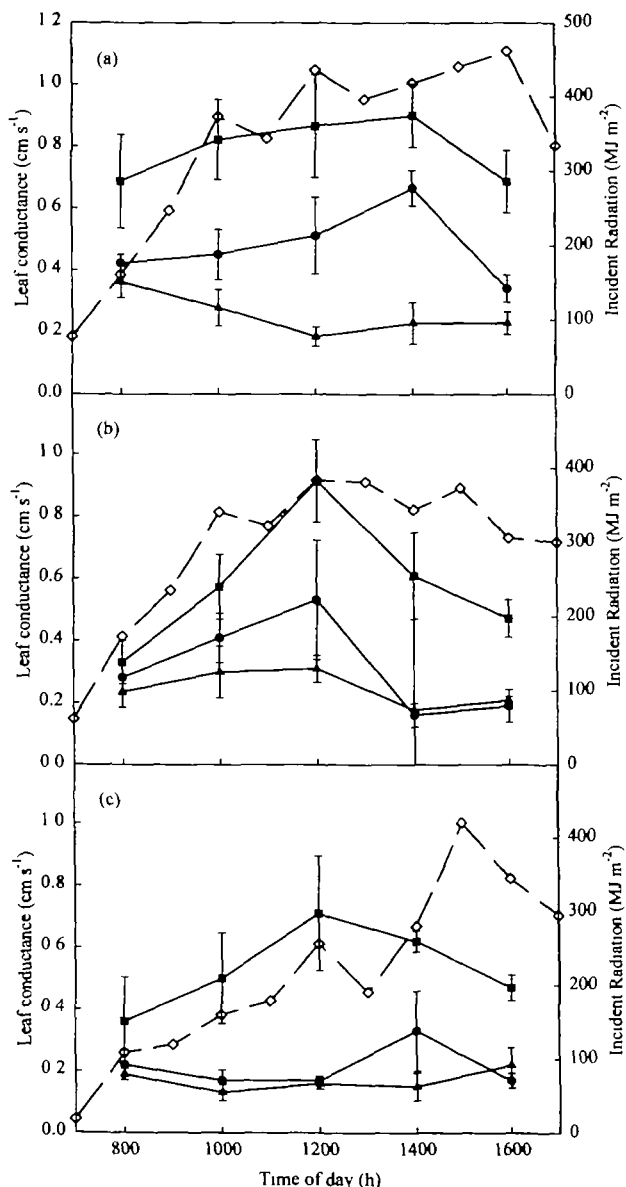


Fig. 5. Diurnal time-courses of solar radiation (\diamond) and leaf conductance for the wet (\blacksquare), intermediate (\bullet) and dry (\blacktriangle) treatments on (a) 56 DAS, (b) 69 DAS and (c) 89 DAS. Bars indicate double standard errors of the mean.

Heilmeier, 1993; Davies *et al.*, 1993). The important regulatory influence of ABA on root and shoot growth, stomatal conductance, photosynthetic activity and other drought resistance traits is now well-established (Davies *et al.*, 1994). However, it is clear that sensitivity to ABA may be modified by the pH, ionic status and concentrations of other plant growth regulators within the xylem sap (Munns and King, 1988; Hartung and Heilmeier, 1993).

Mechanisms which promote turgor maintenance or sustain high tissue hydration may be vital for survival during periods of limited water availability (Turner and Jones, 1980). Extraction of water from cells reduces their

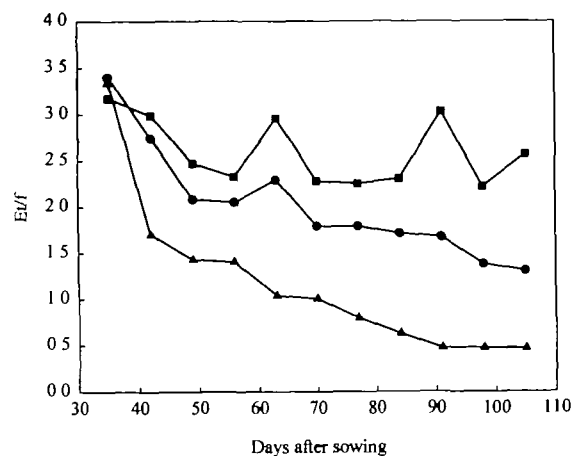


Fig. 6. Seasonal time-courses of evapotranspiration (E_t) per unit of fractional interception (f) for the wet (\blacksquare), intermediate (\bullet) and dry (\blacktriangle) treatments.

volume to an extent dependent on cell wall elasticity (Turner, 1986); cellular elasticity, therefore, has a significant influence on the relationship between Ψ_1 and RWC . Thus sorghum leaves have been reported to undergo larger changes in Ψ_p but smaller changes in hydration during the development of water stress than the less drought-resistant maize because of the lower cell wall elasticity of the former (Sanchez-Diaz and Kramer, 1973). The maintenance of relatively high RWC values despite the development of low leaf water potentials exhibited by bambara groundnut (Fig. 1) appears to be a common trait in drought-resistant species.

The mature leaves of bambara groundnut were 28% thinner in the dry treatment than in the wet treatment because of consistent decreases in cell size; the mean cross-sectional areas of the adaxial epidermal, palisade and mesophyll cells were 1925, 576 and 361 μm^2 in the wet treatment, as compared to 759, 364 and 270 μm^2 in the dry treatment (Brown, 1991). Similar results were obtained by Nobel (1982), who found that soil drying promoted an increased number of layers of smaller mesophyll cells, but reduced leaf thickness. In such cells, symplastic volume is reduced and Ψ_x at full hydration is increased (Cutler *et al.*, 1977), with the result that a small decrease in RWC produces more negative values of Ψ_x , resulting in turgor maintenance to lower Ψ_1 values.

Turgor maintenance may also be achieved by osmotic adjustment, which involves the accumulation of solutes and reductions in Ψ_x (Turner and Jones, 1980). Drought-induced reductions in Ψ_x may result either from passive concentration of existing solutes as water is withdrawn from the vacuole or cell expansion is reduced, or active accumulation of solutes, i.e. osmotic adjustment, as defined by Turner and Jones (1980). The capacity for osmotic adjustment depends on the species involved and the nature of the stress imposed, since mild or rapidly

imposed stress induces little or no active adjustment, while progressive severe stress may stimulate substantial solute accumulation (Ong *et al.*, 1985). Drought-induced osmotic adjustment has been reported for a range of crop species including sorghum and pearl millet (Jones and Turner, 1978; Shackel and Hall, 1983).

Stomatal closure is important in protecting against severe dehydration during water stress since the guard and subsidiary cells control over 95% of the gaseous exchange between leaves and the atmosphere (Willmer and Fricker, 1996). Stress-induced stomatal closure therefore greatly reduces transpiration, thereby improving water status or arresting its decline. Crop plants exhibit extensive variation in stomatal sensitivity to water stress, although closure normally occurs once a threshold value of Ψ_1 or Ψ_p is reached (Begg and Turner, 1976). However, Turner (1986) demonstrated that, although rapid soil drying induced a threshold response in two sunflower cultivars, a slower rate of soil drying produced an almost linear response. g_1 values for both leaf surfaces were consistently higher in the wet treatment than in the dry treatment (Fig. 4a), although the latter maintained stomatal opening at lower leaf potentials; this is a common adaptive response to drought usually attributed to turgor maintenance by osmotic adjustment. For example, groundnut maintains high stomatal conductances even in wilted leaves (Black *et al.*, 1985), possibly to maintain transpirational cooling at the expense of continued water losses. Although g_1 values were similar in the intermediate and dry treatments, evapotranspiration was consistently lower in the latter because of its lower L (Fig. 4b). Thus, water loss was regulated primarily by decreased leaf conductance in the intermediate treatment, but by a combination of reductions in leaf area and conductance in the most severely stressed plants (Fig. 4a), thereby decreasing evapotranspiration per unit of fractional interception (Fig. 6).

Although stomatal conductance provides some indication of potential transpiration, the relationship is not straightforward. For instance, stomatal closure may be accompanied by increases in leaf temperature of up to 6°C under conditions of high irradiance which, in turn, increase the leaf-to-air vapour pressure gradient driving transpiration, thereby partially offsetting the conservative influence of stomatal closure (Rawson *et al.*, 1978; Black *et al.*, 1985). Indeed, Black *et al.* (1985) reported that the lower daily water use of droughted groundnut was entirely attributable to its smaller L rather than decreased stomatal conductance, due to the opposing influence of concurrent increases in the vapour pressure gradient. This illustrates the danger of predicting transpirational water losses from stomatal conductance data in the absence of a full knowledge of other environmental and biological variables which influence transpiration, canopy development and water use. Nevertheless, it is worth noting that

in previous experiments at Nottingham, the leaf conductance values recorded for bambara groundnut were substantially lower than those for groundnut stands growing under identical conditions even when water was not limiting. For example, in 1989 the seasonal mean leaf conductance values for bambara groundnut and groundnut were 0.49 and 0.77 cm s⁻¹, respectively (unpublished data).

The leaves approached zero turgor at a Ψ_1 of about -2.0 MPa (Fig. 3a), considerably lower than the values of -1.2 to -1.6 MPa reported for groundnut (Bennett *et al.*, 1981), indicating that bambara groundnut can maintain turgor to lower values of Ψ_1 . Zero turgor was approached at a RWC of 85% (Fig. 3b), above which Ψ_p increased to a predicted value of 1.25 MPa at 100%. The former value corresponds to previous reports of 82–83% for soybean (Turner *et al.*, 1978), 90–94% for sorghum and maize (Jones and Turner, 1978) and 87% for groundnut (Bennett *et al.*, 1981).

In conclusion, the maintenance of Ψ_p despite declining water availability is believed to be vital to the survival of bambara groundnut during severe drought, and is apparently achieved primarily by a combination of osmotic adjustment, reductions in leaf area index and effective stomatal regulation of water loss. Previous research (Collinson *et al.*, 1996) has shown that increased partitioning of dry matter to the roots and increases in rooting density were important in maintaining water supplies in drying soil. Thus bambara groundnut depends on a range of complementary physiological and morphological attributes for its drought resistance.

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