

Physiological Analysis of Peanut Cultivar Response to Timing and Duration of Drought Stress

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Abstract

Pod yield response of two spanish (McCubbin and Red Spanish) and two virginia (Virginia Bunch and Q18801) cultivars were compared under a range of irrigation treatments applied at different growth stages on a Xanthozem soil in a subtropical environment in south-east Queensland. Detailed growth and soil water use measurements were taken on a fully irrigated treatment and a treatment which received no rainfall after 83 days after planting (DAP).

Soil water deficits occurring during the flowering to the start of pod growth phase (R/I) significantly reduced pod yields (range, 17-25%) relative to the well-watered control plots (I/I) for all cultivars. Where crops were irrigated until 83 DAP, then crop water deficits occurred throughout the pod growth phase (I/R), a significant cultivar by irrigation treatment interaction was observed for pod yield. The greatest reduction in yield occurred when severe stress occurred during the pod filling phase (Sh). Significant cultivar variation in pod yield was apparent. Differences in pod yield within this treatment were analysed in terms of a simple framework where pod yield is a function of transpired water (T), transpiration efficiency (TE) and harvest index (H). Estimates of TE derived from measurements of carbon isotope discrimination in leaves indicated only small variation in TE, and suggest this trait contributed little to pod yield variation in the cultivars used in this experiment. Variation in pod yield among the four cultivars was largely a result of differences in harvest index characteristics.

Introduction

Peanuts are grown as a summer crop utilizing natural rainfall throughout the tropics and subtropics. Drought periods of unpredictable timing and duration occurring throughout the season mean that water supply is one of the major environmental factors limiting yield (Virmani and Singh 1986).

The detrimental effects of drought can be modified to some extent through such management options as supplementary irrigation (Stansell and Pallas 1979; Nageswara Rao *et al.* 1985, 1988), manipulations of either maturity type or planting date (Huda *et al.* 1988) and intercropping of differing maturity cultivars (Nageswara Rao *et al.* 1990). Increases in pod yield, and stability of production under many different patterns of drought encountered are also possible through identification and selection of cultivars that are better able to resist such drought effects. However, selection for drought resistance has proved difficult in breeding programs because of the need to test large numbers of genotypes in multiple seasons and locations. The large cost in

terms of space, time and resources means that selection for characters other than yield at maturity is not feasible (Mathews *et al.* 1988a). More detailed understanding of the developmental and physiological adaptations enabling superior performance of genotypes under drought stress is therefore needed to identify reliable indices of drought resistance to complement conventional breeding programs.

In this paper we analyse pod yield performance in terms of a simple framework proposed by Passioura (1977), where pod yield in water limited environments can be considered as the product of three components: the amount of water transpired (T), the efficiency of use of transpired water in production of biomass (TE), and harvest index (H), the proportion of biomass harvested as pods. Ludlow and Muchow (1988) discussed the attributes that contribute to differences among cultivars in the components of the above framework. The framework has also been used recently to analyse and identify desirable drought resistance attributes in peanut (Mathews 1988a; Harris *et al.* 1988; Mathews *et al.* 1988b; Chapman 1989).

About 80% of the commercial crop in Queensland is planted with cv. Virginia Bunch, while the remaining 20% is sown with spanish types such as Red Spanish (Shorter and Simpson 1987). Recent introduction and breeding work has identified both virginia and spanish cultivars of substantial yield superiority, when compared to the older cultivars under a range of drought patterns. The study reported here was initiated to discover the physiological attributes contributing to the observed increases in yield potential under a range of drought patterns typical of dryland production areas in Queensland.

This paper investigates growth and yield performance, and soil water extraction and use of four peanut cultivars in response to a range of soil water regimes applied at different growth stages. The contribution of T , TE and H to cultivar yield superiority is considered in a severe end-of-season drought treatment.

Materials and Methods

The experiment was conducted on a Xanthozem soil (Uf6.4; Northcote 1971) during the 1986/87 summer at the Bjelke Petersen Research Station (26° 32'S., 151° 50'E) at Kingaroy, Qld.

Cultural Details and Experimental Design

Basal fertilizer containing 13% P and 13% K was applied before planting at a rate of 200 kg/ha. Weeds were controlled by a combination of the pre-plant herbicide trifluralin (2.0 L/ha) and hand-weeding. Seedling diseases were controlled by a seed dressing of captan applied at a rate of 250 g of product per 100 kg of seed. Foliage pathogens (*Cercospora* sp. and *Puccinia arachidis*) were controlled with the fungicide 'Bravo' on three occasions during the final three weeks of crop growth.

Peanuts (*Arachis hypogaea* L.) cvv. Virginia Bunch (VB), UF78114-1, known locally and referred to here as Q18801 (virginia types of c. 140 days maturity) and McCubbin and Red Spanish (spanish types of c. 125 days maturity), were sown on 6 November 1986 in rows 0.7 m apart, and emerged 10 days later. Plants were then thinned to achieve an intra-plant spacing of 0.17 m. Plot size was 8 rows by 6 m. The field was irrigated to field capacity after sowing. Irrigation was accomplished using trickle irrigation (T-tape with outlets every 20 cm) that distributed water uniformly in a given plot, with an application rate of 7.5 mm/h.

Irrigations were scheduled when the cumulative pan evaporation (less rainfall) deficit reached c. 40 mm, and generally occurred at weekly intervals where rainfall was negligible.

The experiment was set up as a split-plot design with four main treatments and four subtreatments (cultivars), each with three replications. Main treatments were the growth phases of the crop during which irrigation was varied:

- I/I: Continuous from emergence to maturity.
- R/I: Rainfed until the early seed growth stage (110 days after planting (DAP); irrigated until final harvest.
- I/R: Irrigated until late pod set (83 DAP), followed by rainfed conditions until final harvest.
- Sh: Rainfed until the late pod set (83 DAP), then rainfall excluded by rainout shelters until final harvest.

Details of irrigation timing and amounts for each treatment as well as rainfall and mean weekly pan evaporation throughout the experimental period are shown in Fig. 1. Rainout shelters (dimensions 25 m by 7.5 m (Hatfield *et al.* 1990)) were used to exclude rainfall in the Sh treatment. Water captured by the rainout shelters during rainfall events was diverted into drains (0.4 m depth) dug around and which led away from the rainout shelter area.

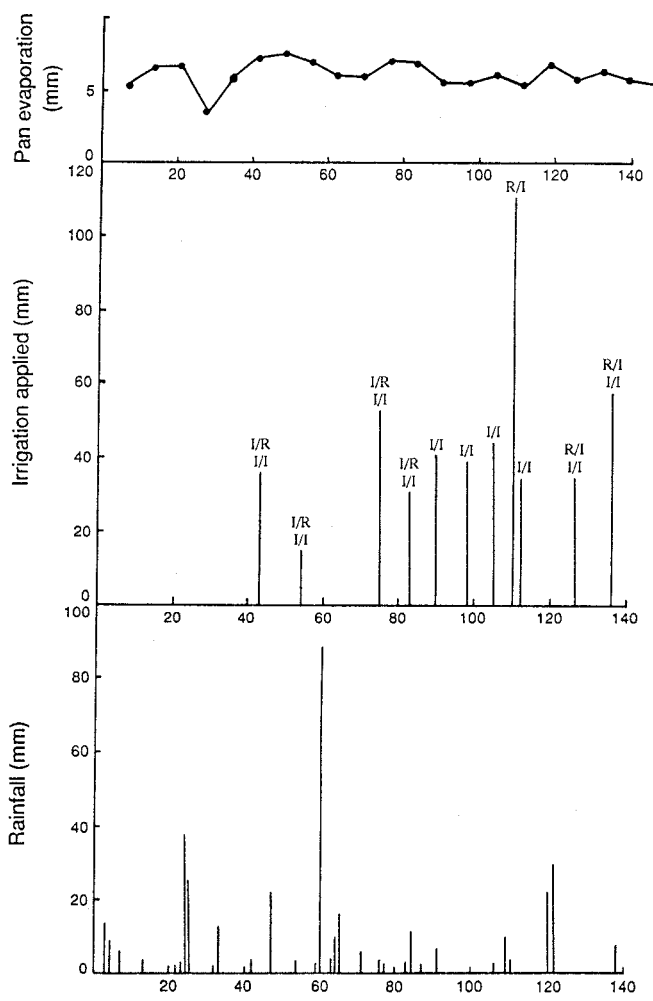


Fig. 1. Daily pan evaporation, rainfall and irrigation timing and amounts during the experiment.

Soil Water Measurements

Volumetric water content of the soil was measured at regular intervals during crop growth using a neutron probe (Campbell Pacific, California, U.S.A.) calibrated against gravimetric soil water and bulk density measurements made in the same field. Readings were taken at 0.2, 0.3, 0.4, 0.5, 0.65, 0.8, 1.0, 1.2, 1.4, 1.6, and 1.8 m depths in a single aluminium access tube installed in the central row of each plot in the I/I and Sh treatments only. At each sampling time, three composite gravimetric samples were taken at the 0 to 0.1 m depth from each plot along with neutron probe measurements to determine the profile volumetric water content.

Cumulative seasonal evapotranspiration were estimated using the water balance equations:

$$E_t = R + I + (S_1 - S_2) \quad (1)$$

where E_t is the evapotranspiration, R is rainfall, I is irrigation water applied and S_1 and S_2 were the initial and final soil water contents for the calculation period. Deep drainage below 1.8 m and surface run-off during the experiment were assumed to be negligible.

Plant Measurements

From 42 DAP onwards six consecutive plants (0.7 m^2) were removed at 2-weekly intervals until maturity from a previously undisturbed row in each plot of the I/I and Sh treatments. Plants were separated into vegetative (leaf, stems including pegs) and pod components, and dry weights were measured after drying for 48 h at 85°C .

At maturity (determined by regular destructive sampling and use of internal pericarp colour to assess maximum percentage of mature pods (Sanders *et al.* 1982)), plots were dug by hand to determine total above-ground biological and commercial yields. Maturity was assessed to have occurred at 131 DAP for McCubbin and Red Spanish for each irrigation treatment, and at 142 DAP for VB and Q18801 for treatments I/I, R/I and I/R. Severe end of season drought in the Sh treatment hastened maturity of VB and Q18801 by 11 days. Total biological yield was assessed by the destructive sampling techniques used during the season. Commercial yield was assessed in all plots by harvesting two 3.0 m lengths of row by hand, and field-drying until pods reached about 12% moisture content. Plants were then machine-threshed, pod yields were recorded, and 500 g representative subsamples of pods were mechanically shelled to determine kernel yields and shelling percentages. The percentage of kernels classes as sound and mature (SMK) was determined (kernels riding a round-holed screen with holes of 7.9 mm diameter for VB and Q18801, and 7.1 mm for McCubbin and Red Spanish). The percentage oil grade (kernels passing through the above screens) was also determined. Mean individual kernel weights (MIKW) were determined from 200 kernels selected from the total sample, and the number of kernels per m^2 was calculated by dividing MIKW into seed yield. Harvest indices were calculated as total pod yield : biological yield.

At 89, 103, 117 and 131 DAP, the incident photosynthetically active radiation (PAR) above each plot in the I/I and Sh treatments, and PAR transmitted at ground level below each crop canopy were measured around solar noon. These measurements were performed on cloudless days, using a 1.0 m line sensor (LI-191S, Li-Cor Inc., Lincoln, Neb., U.S.A.) which was inserted five times across the inner rows of each plot on each occasion. The fraction of PAR intercepted (f) was then calculated.

At the 89, 103, 117 and 131 DAP harvests, the dried leaf material was ground to pass through a $100 \mu\text{m}$ sieve. The carbon isotope discrimination for each cultivar under the I/I and Sh treatments was calculated from measurements of the difference in carbon isotope ratios of the air and of the leaf material. Isotopic composition was measured by ratio mass spectrometry. Briefly, subsamples of approximately 10 mg were combusted in an elemental analyser (Carlo Erba Instrumazione, Italy). The combustion products were moved in a stream of helium, and CO_2 in the effluent gas was separated from impurities chromatographically. CO_2 was concentrated in a trap cooled with liquid N_2 and the helium was pumped away. The trap was warmed and the CO_2 allowed to enter the inlet of the ratio mass spectrometer (VG SIRA 24) for measurement of isotopic ratio. The isotope ratio of samples were estimated by comparison with a working standard of CO_2 with an isotope ratio of -35.08% relative to PDB. The isotope composition of the air was taken to be -7.6% on the PDB scale, and

the carbon isotope discrimination in plant material was calculated according to Hubick *et al.* (1986).

Meteorological Data

Monthly means of daily maximum and minimum temperatures and incident shortwave radiation for the duration of the experiment were obtained from a meteorological station located 200 m from the experimental site, and are shown in Table 1.

Table 1. Monthly means of daily maximum and minimum temperatures, and daily incident shortwave radiation during the experiment

	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
Maximum temp. (°C)	27.0	29.7	31.7	30.4	29.5	26.1
Minimum temp. (°C)	12.8	15.6	20.0	17.3	14.7	13.0
Shortwave radn. (MJ m ⁻² day ⁻¹)	24.7	26.3	25.5	24.1	23.3	17.4

Results

Phenology

The actual dates of first flower were not recorded; however, visual observations indicated the flowering occurred at c. 36 and 46 DAP for spanish and virginia types respectively. Maturity was assessed to have occurred at 131 DAP for the spanish types for each irrigation treatment, and at 142 DAP for virginia types for treatments I/I, R/I and I/R. Severe end of season drought in the Sh treatment hastened maturity of VB and Q18801 by 11 days.

Yield at Maturity

Yields of pods and kernels at maturity, along with selected yield attributes for the four cultivars under each treatment are shown in Table 2. Under full irrigation (I/I) Q18801 had significantly higher ($P < 0.05$) pod yield than the other cultivars. The decrease in pod yield in the R/I treatment for VB, Q18801, McCubbin and Red Spanish compared with the fully irrigated treatment was 17, 24, 17 and 28%. Under the I/R treatment which resulted in late stress, pod yield was affected more substantially in the virginia cultivars. Pod yield relative to the fully irrigated treatment decreasing by 38 and 30% for VB and Q18801, compared with only 5 and 7% for McCubbin and Red Spanish.

The greatest reduction in yields occurred in the Sh treatment, with the decrease in pod and kernel yield relative to the fully irrigated treatment being 71, 59, 35 and 42% for VB, Q18801, McCubbin and Red Spanish respectively. It should be recalled that the severe end of season drought hastened maturity by c. 11 days in the virginia types, resulting in similar maturity dates for all cultivars. Pod and seed yield of VB was significantly less ($P < 0.05$) than the other cultivars under this severely stressed treatment.

Dry Matter Accumulation, Harvest Index and Canopy Light Interception

In an attempt to explain cultivar pod yield responses to the most severe soil moisture treatment, a detailed examination of vegetative and pod dry matter

accumulation, dry matter partitioning and canopy light interception was made on the I/I and Sh treatments.

Vegetative (leaf plus stem and pegs) and pod dry matter accumulation over the growing season are shown in Fig. 2. Under both I/I and Sh treatments, vegetative dry matter accumulation of VB was significantly greater ($P < 0.05$) than the other cultivars from about 70 DAP to maturity. In contrast the rate of pod yield accumulation of VB was slower than the other cultivars under both treatments. These cultivar differences in dry matter partitioning are reflected

Table 2. Commercial pod yield and yield components for the four cultivars under I/I, R/I, I/R and Sh treatments

Cultivar	Treatment	Pod yield (kg/ha)	Kernel yield (kg/ha)	Total kernel percentage (%)	Percentage oils (%)	Mean individual kernel weight (mg)	Kernels/m ²
VB	I/I	3810	2730	71.7	3.9	0.82	292
Q18801	I/I	4370	3160	72.2	3.0	1.02	309
McCubbin	I/I	3450	2640	76.6	4.0	0.59	448
Red Spanish	I/I	3520	2790	79.1	5.2	0.44	633
VB	R/I	3170	2100	66.3	10.5	0.66	319
Q18801	R/I	3310	2370	71.5	4.3	1.05	225
McCubbin	R/I	2880	2100	72.8	11.4	0.55	381
Red Spanish	R/I	2520	1860	73.7	20.1	0.38	489
VB	I/R	2380	1670	69.9	7.0	0.73	230
Q18801	I/R	3040	2180	71.5	3.0	0.94	231
McCubbin	I/R	3274	2540	77.5	2.1	0.54	465
Red Spanish	I/R	3260	2620	80.3	2.5	0.44	593
VB	Sh	1160	770	66.7	5.9	0.71	109
Q18801	Sh	1824	1280	69.9	3.6	0.84	152
McCubbin	Sh	2220	1740	78.4	2.7	0.53	344
Red Spanish	Sh	2041	1620	79.3	3.5	0.41	396
I.s.d. ($P < 0.05$)							
Cultivar × irrigation		460	340	2.5	1.8	0.05	69

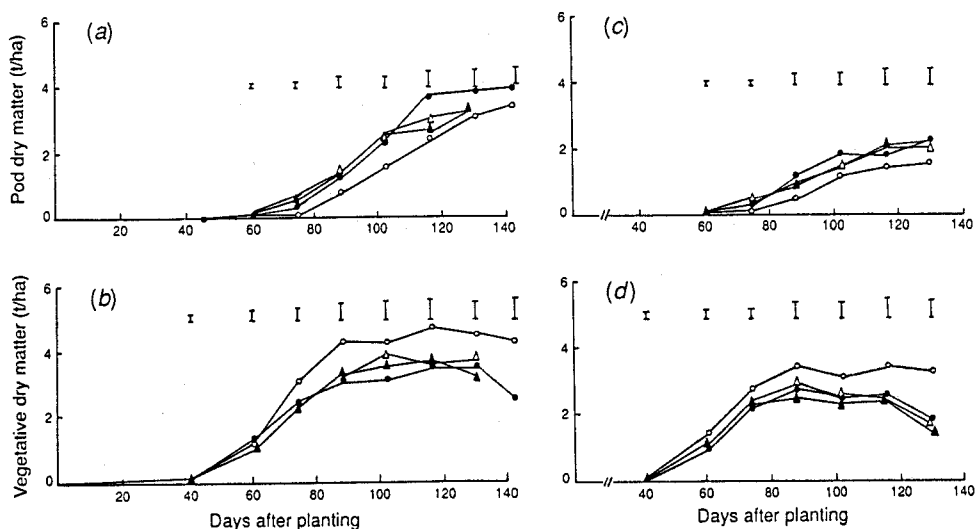


Fig. 2. Changes in pod dry matter with time under I/I (a) and Sh (c) treatments, and vegetative dry matter with time under I/I (b) and Sh (d) treatments for VB (O), Q18801 (●), McCubbin (Δ) and Red Spanish (▲). Vertical bars denote l.s.d. at $P < 0.05$.

in the harvest index data (Fig. 3), where both the rate of increase, and final value of harvest index of VB, were below that of the other cultivars. This response was particularly evident under the Sh treatment where harvest index of VB was significantly lower ($P < 0.05$) than the other three cultivars from 70 DAP until maturity.

Changes in fractional canopy light interception (f) at intervals from 89 to 131 DAP for the I/I and Sh treatments are shown in Table 3. Differences between the cultivars under the I/I throughout this period were small, and interception averaged *c.* 90%. Drought resulting from the shelter treatment had a large effect on f for all cultivars, with maximum values of only *c.* 65% being achieved.

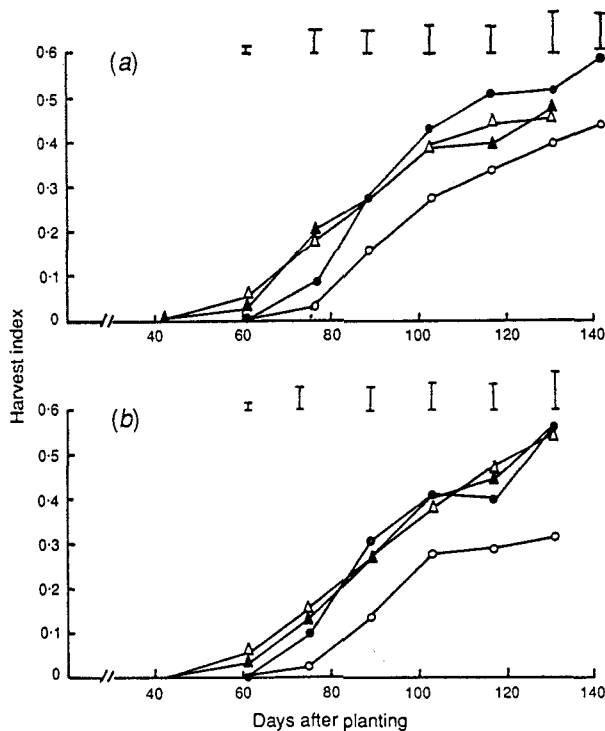


Fig. 3. Change in harvest index with time for I/I (a) and Sh (b) treatments. Symbols as in Fig. 2.

Table 3. The fractional canopy light interception at 89, 103, 117 and 131 days after sowing for each cultivar under the Sh treatment

Cultivar	Days after sowing:							
	89		103		117		131	
	I/I	Sh	I/I	Sh	I/I	Sh	I/I	Sh
VB	0.96	0.61	0.89	0.65	0.94	0.67	0.94	0.65
Q18801	0.93	0.58	0.86	0.50	0.90	0.50	0.89	0.31
McCubbin	0.94	0.66	0.86	0.60	0.90	0.47	0.92	0.33
Red Spanish	0.93	0.64	0.87	0.57	0.83	0.43	0.85	0.28
<i>l.s.d.</i> ($P < 0.05$)	0.09		0.08		0.07		0.09	

Late in the season (117 and 131 DAP samplings), a significant interaction between irrigation and cultivars ($P < 0.05$) resulted, with f of VB under the Sh treatment being maintained at *c.* 65%, while in the other three cultivars it declined dramatically because of increased leaf senescence. It should be noted that, although there was substantial leaf mortality, there was negligible leaf loss from plants of affected cultivars. Thus, increased penetration of light to the ground was associated with shrivelled leaves left remaining on stems, rather than due to direct leaf fall.

Carbon isotope discrimination (Δ) in leaves of the four cultivars averaged over sampling intervals from 89 to 131 DAP in I/I and Sh treatments are shown in Table 4. There were significant ($P < 0.05$) cultivar and irrigation treatment effects on Δ , although there were no significant interactions between cultivar, irrigation treatment and time of sampling. When averaged over irrigation treatments, Δ in leaves of Virginia cultivars (VB and Q18801) were significantly ($P < 0.05$) less than for the Spanish types.

Table 4. Effects of irrigation treatment and cultivar on carbon isotope discrimination ($10^3 \times \Delta$) when averaged over four times of sampling (89, 103, 117, 131 DAP)

Cultivar	Irrigation treatment		Cultivar mean (l.s.d. $P = 0.05$: 0.30)
	I/I	Sh	
VB	21.00	20.67	20.84
Q18801	21.31	20.86	21.09
McCubbin	21.48	21.15	21.32
Red Spanish	21.66	21.20	21.43
Irrigation mean (l.s.d. $P < 0.05$: 0.24)	21.36	20.97	

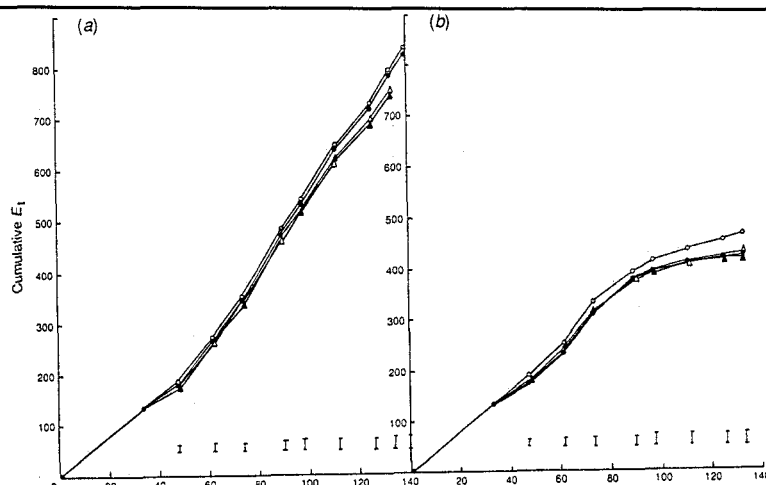


Fig. 4. Change in cumulative E_t for I/I (a) and Sh (b) treatments. Symbols as in Fig. 2.

Seasonal Water Use and Crop Water Extraction

Cumulative evapotranspiration (E_t) and total evapotranspiration (and its components) estimates for all cultivars under I/I and Sh treatments are shown

in Fig. 4 and Table 5 respectively. Under the I/I treatment, total water use of the virginia cultivars (VB and Q18801) was significantly greater ($P < 0.05$) than the spanish cultivars (McCubbin and Red Spanish) partly as a result of longer maturity and hence greater irrigation and rainfall inputs. Under the Sh treatment, total E_t of VB was *c.* 40 mm more than the other cultivars (significant at $P < 0.05$). The difference was a function of greater end of season soil water extraction. Fig. 5 illustrates that VB was able to extract substantial quantities of soil water at depths from 0.8 to 1.4 m compared to the three other cultivars.

Table 5. The change in soil water storage between sowing and maturity, rainfall, irrigation and total evapotranspiration for each cultivar under the I/I and Sh treatments

Cultivar	Treatment	Change in soil water storage (mm)	Rainfall (mm)	Irrigation (mm)	Total evapotranspiration (mm)
VB	I/I	71	382	379	832
Q18801	I/I	60	382	379	821
McCubbin	I/I	59	376	322	757
Red Spanish	I/I	39	376	322	737
VB	Sh	179	287	0	466
Q18801	Sh	139	287	0	426
McCubbin	Sh	143	287	0	430
Red Spanish	Sh	139	287	0	426
l.s.d. ($P < 0.05$)					31*

* Irrigationxcultivar interaction significant at $P < 0.01$.

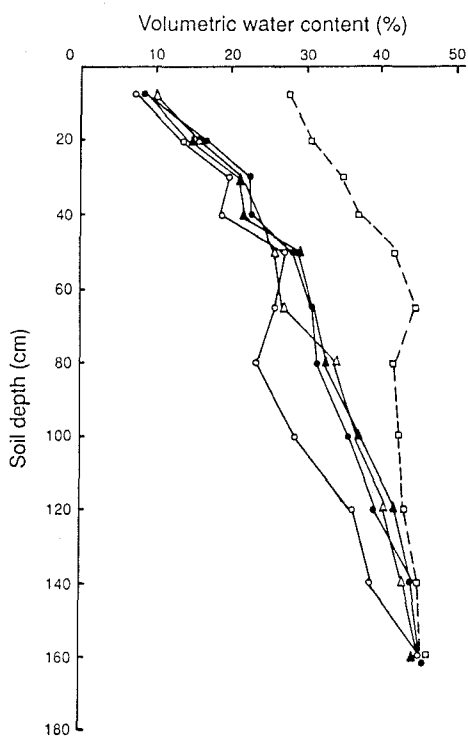


Fig. 5. End of season volumetric water content profiles for the Sh treatment. Symbols as in Fig. 2. The initial volumetric soil water content profile measured 2 weeks after sowing is also shown (\square - \square).

Discussion

Fully Irrigated (I/I)

Pod yields of the four cultivars used in this study under full irrigation ranged from 3.5 to 4.4 t ha⁻¹. Both total biomass and pod yield performance under water non-limiting conditions are expected to be lower in the spanish types as a direct function of their shorter growth cycle, and lower total intercepted radiation receipt, in agreement with other reports (Boote *et al.* 1982). Within the virginia types, however, Q18801 significantly outyielded VB by c. 0.5 t ha⁻¹. The higher partitioning of biomass produced during reproductive growth to the pod component relative to the vegetative parts, and resultant higher harvest index, was largely responsible for this increase (Figs 2 and 3). Duncan *et al.* (1978) suggested that peanut yield improvement in the U.S.A. has occurred through selection of cultivars that partition more of their daily assimilate to fruit. Similar physiological changes in the recently introduced Q18801 line are no doubt responsible for the observed yield improvement under non-limiting water conditions.

Cumulative E_t for the four cultivars ranged from c. 740 to 830 mm. Pod yields achieved for this amount of water use agree well with other data relating yield to water use in peanut (Lenka and Misra 1973; Narasimham *et al.* 1977).

Rainfall until Beginning of Podfilling, then Irrigated to Maturity (R/I)

Soil water deficit occurring during the flowering to the start of pod growth phase (treatment R/I) significantly reduced pod yields (range, 17–25%, Table 2) relative to the well-watered control plots (I/I) for all cultivars. Similar reductions in pod yield (18–29%) for a virginia cultivar were recorded in a nearly identical stress treatment applied over two years by Nageswara Rao *et al.* (1985, their treatment T3,A). Pod yields for Q18801, McCubbin and Red Spanish appeared to be reduced by water stress effects on pod, and hence kernel loading, as kernel number per m² was significantly lower than the well-watered controls. Interestingly though, MIKW was unaffected, so yield reduction was solely due to effects on pod and kernel numbers per m² (Table 2). Reduced pod set during the pegging phase may have been associated with low soil moisture in the podding zone affecting peg penetration and pod formation (Underwood *et al.* 1971; Wright 1989). Alternatively, water stress can severely reduce photosynthesis in peanut (Bhagsari *et al.* 1976), and thereby reduce assimilate availability for normal pod and kernel formation.

The influence of the R/I soil water treatment on VB was different from the other cultivars, with MIKW being the major yield component affected, compared to kernel number in the other cultivars. This response may be associated with the tendency of this cultivar to initiate a flush of pegs and pods following the relief from the water stress period. Shorter and Simpson (1987) presented data for VB which showed that peg and pod numbers did not increase significantly over a drying cycle between 75 and 103 days after planting. However, peg and pod numbers increased by over 50% within 7 and 20 days respectively, upon relief from the stress period. The present observation, combined with other work, demonstrates that the more indeterminate peanut cultivars, such as VB, can partially compensate for an early drought period by initiating new

reproductive structures when moisture becomes adequate. This response may however, lead to delayed harvesting until later fruits mature. In the south-east Queensland environment, however, full yield compensation through delayed harvesting may be difficult, as overmature pods may remain in the soil, and low temperatures late in the season may slow the rate of podfilling. Thus in most seasons harvesting would not be able to be delayed, and weight per pod and kernel, and quality may be lower because the late fruits would lack time to fill. With cultivars such as Q18801, and most spanish types, pegging and podding patterns are more synchronous, and pod loads tend to increase over time, despite the occurrence of soil water deficits. Thus, overmaturity and poor kernel size are less of a problem under these conditions when water stress occurs during the peg and pod development phase.

Irrigated to Beginning of Podfilling, then Rainfed until Maturity (I/R)

A significant cultivar by irrigation treatment interaction was apparent for pod and kernel yield in the I/R treatment, where plots were irrigated until 83 DAP, then rainfed through the podfilling period. This occurred because, while pod yields of the spanish types were not significantly different from the well-watered controls, pod yields of the virginia types were reduced by 30 and 38% for Q18801 and VB respectively. It was apparent that the earlier flowering, pegging and podding habit of the spanish types enabled the attainment of a full pod load prior to 83 DAP, with crop water deficits occurring after this time having only small and non-significant effects on MIKW compared to control plants. Boote *et al.* (1982) suggest that water deficits occurring during the latter part of podfilling can be somewhat less critical than earlier stresses, because pods have been formed and water use and evapotranspiration tend to decline as leaves senesce.

Late-season drought in the longer season virginia types reduced pod yields more severely than in the spanish types, largely through significant reductions in both kernel number per m² and MIKW relative to the controls. Presumably pod initiation and development, which continue after the start of kernel growth in longer season and more indeterminate types, were more severely reduced by soil water deficits during the pod-filling stage. Similar yield depressions in response to late season drought in peanut have also been observed elsewhere (Boote *et al.* 1976; Pallas *et al.* 1979; Nageswara Rao *et al.* 1985).

Rainfed until Late Pod Set, then Rainfall Excluded until Maturity (Sh)

This treatment resulted in severe crop water deficits during the pod filling phase. For the purposes of the following discussion, the physiological analysis of seed or pod yield under water-limiting conditions described earlier will be used. Pod yield (Y) can be described in terms of water transpired (T), the ratio of total dry matter production to transpiration (TE) and the ratio of pod yield to total biomass at maturity, harvest index (H) (Passioura 1977), to give the following identity:

$$Y = T \times TE \times H. \quad (2)$$

This description assists in identifying where differences among cultivars exist, and what mechanisms may be operating to affect pod yield at maturity.

Water Used

Soil evaporation was not measured in this study, so it is difficult to estimate actual crop transpiration. There no doubt would have been large soil evaporative losses early in the season. Later in the season (after 83 DAP) soil evaporation would have been negligible as rainfall was excluded by rainout shelters. For the purposes of the following comparative analysis we assume that our estimates of E_t provide a measure of relative variation in transpiration.

There were large cultivar differences in the amount of water used by the end of the season, which were largely associated with differences in water extraction at depth. VB was able to extract *c.* 40 mm more soil water at depths predominately below 70 cm compared to the other three cultivars (Fig. 5, Table 5). Chapman (1989) studied soil water extraction and root growth in four peanut cultivars including VB. During a stress applied between 56 and 76 days after sowing, VB extracted significantly greater amounts of soil water (up to 30 mm) than the other cultivars, particularly at depths between 80 and 150 cm. Limited root length density data measured in the surface 90 cm prior to and after the stress period, however, indicated root length density in VB tended to be less than other cultivars. Presumably in Chapman's and the present study, higher root length densities in VB at depths below about 1 m in the soil profile may have lowered the soil and root resistances to water uptake (Taylor and Klepper 1975; Burch 1979) and permitted higher flow rates until late in the season. Willatt and Taylor (1978) have found that a few deep roots can account for a disproportionately large proportion of total water uptake, through their capacity for exceptionally high rates of water uptake.

The superior soil water extraction capability of VB under severe drought conditions late in the season was associated with greater leaf area longevity, as evidenced by the significantly higher f values compared to the other cultivars (Table 3). An increased rate of leaf senescence in these cultivars was responsible for lower f relative to VB. Fischer and Kohn (1966*a*, 1966*b*) have shown that leaf senescence was highly correlated with the degree of leaf tissue dehydration in wheat; thus it appears that the superior soil water extraction capability of VB enabled maintenance of leaf water status and leaf function despite lowered water availability. In grain sorghum, similar cultivar responses to declining soil water availability have also been reported (Wright *et al.* 1983). Unfortunately the longer duration of photosynthetic tissue in VB relative to the other cultivars did not result in higher pod yield. This was because most of the extra assimilate produced was partitioned into vegetative parts. It could be hypothesized that the greater apparent root growth at depth of VB may be at the expense of poorer partitioning of assimilate to pods. If this were the case, it seems possible that selection for greater water extraction could be linked to the poor partitioning syndrome of VB, in which relatively less dry matter is partitioned to reproductive structures during podfilling and more to vegetative parts of the plant. Further research is needed to verify this hypothesis across a wider range of peanut germplasm.

Mathews *et al.* (1988*a*) observed only minor differences in patterns of water extraction and total water use among four peanut cultivars grown under a severe end of season drought. Based on their limited cultivar range, they suggested that the extent to which root characteristics and water extraction

patterns contribute to variation in yield was small, and did not warrant major research effort in the light of the expensive and tedious nature of root measurement. Our results, in combination with the considerable variation found in peanut genotypes in the depth and length of root systems (Ketring 1984; Wright, unpublished data), suggest that the effort required to develop large-scale screening methods for breeding programs may well be justified. Deep-rootedness and water extraction may be very appropriate in tropical environments where peanut is grown solely on stored moisture in the dry season (often following rice) on deep and high water-holding capacity soils.

Transpiration Efficiency

The accurate measurement of transpiration efficiency, TE, in field studies is difficult owing to problems in the estimation and/or measurement of total biomass and water transpired by the crop. For instance, there are difficulties in separating soil evaporation and transpiration from crop water use measurements, as well as inaccuracies in the measurement of soil water by neutron scattering techniques. Similarly, root biomass is difficult to measure, and may become a significant component of the total biomass under water-limited conditions. These difficulties probably explain the lack of reports in the literature of variation in TE among field-grown cultivars of peanut or other species.

An alternative approach to assess genetic variation in TE in this experiment was to use leaf carbon isotope discrimination (Δ) to derive theoretical estimates of TE, based on theoretical arguments presented previously (Farquhar and Richards 1984; Hubick *et al.* 1986; Hubick and Farquhar 1989).

From simple theory for a well-stirred leaf, the ratio of assimilation and transpiration rates (A/E) (which is a component of TE) is proportional to p_i/p_a , the ratio of atmospheric and intercellular partial pressures of carbon dioxide (CO_2) according to the following equation

$$A/E = p_a(1 - p_i/p_a)/(1.6V), \quad (3)$$

where V is the water vapour pressure difference between the intercellular spaces and the atmosphere. Conveniently, and quite independently for C_3 species, carbon isotope discrimination, Δ , by leaves is approximately linearly and negatively related to p_i/p_a by the following simplified equation (Farquhar and Richards 1984)

$$\Delta = 4.4 + 22 \cdot 6 p_i/p_a. \quad (4)$$

The extremes of leaf Δ measured among the cultivars of the Sh treatment in this experiment were 20.84 and 21.43 for VB and Red Spanish respectively (Table 4). From equation (4) these are equivalent to values of p_i/p_a of 0.727 and 0.754, giving values of $(1 - p_i/p_a)$ of 0.273 and 0.246 for VB and Red Spanish respectively. Based on these estimates, which represent ideal non-canopy conditions, variation in TE among these cultivars would be expected to be of the order of only 11%. Thus it could be hypothesized that variation in TE among the cultivars used in this experiment contributed little to the observed pod yield variation.

There have, however, been recent reports of peanut cultivar variation in W measured in the field. Mathews *et al.* (1988a) reported variation of 27% in peanut cultivars subjected to three cycles of drying between emergence and maturity. In a more controlled field experiment, where water application and plant transpiration, and shoot and root biomass, were accurately measured in mini-lysimeters located in small field canopies, variation in W of greater than 50% was demonstrated among eight peanut cultivars (Wright *et al.* 1988). Transpiration efficiency (TE) was shown to be strongly negatively correlated with leaf Δ which along with other studies (Hubick *et al.* 1986, 1988) suggests leaf Δ could be used to effectively select for TE in large scale peanut breeding programs. Other work in peanut has suggested that Δ has moderately high heritability, and that effective selection for Δ , and hence TE, could be conducted in a limited number of environments under either well-watered or rainfed conditions (Hubick *et al.* 1988). The lack of interaction between cultivars or irrigation treatment and time of sampling between 89 and 131 DAP for Δ in the current study further indicates that this selection could take place well before maturity (e.g. 89 DAP), and possibly even earlier. Selection for this trait early in a plant's life cycle would facilitate rapid generation time in a breeding program, and hence maximize the potential for genetic gain.

Harvest Index

Harvest index (H) is a function of the crop growth rate (CGR), partitioning of assimilate to pods (p), and the effective duration of the podfilling phase (Duncan *et al.* 1978). Mathews *et al.* (1988a) showed that H can be expressed as the mean value over the season of p weighted by CGR. The following expressions can be used to describe these variables:

$$P = \frac{\text{PGR}}{\text{PCF}} \times \frac{1}{\text{CGR}}, \quad (5)$$

where pod growth rate (PGR) and CGR are calculated over a specific period during podfilling, and PCF is the pod composition adjustment factor to account for the higher energy costs required for oil and protein synthesis in pods. A value of 0.606 for PCF has been used in previous studies (Duncan *et al.* 1978; Freyer 1982). This factor assumes similar oil and protein contents exist among cultivars. Although these were not explicitly measured for each cultivar in this study, other data of Chapman (1989) and Bell and Wright (unpublished) indicate that kernel oil and protein contents of the cultivars used in this study vary by less than 3–4%. We therefore consider that the PCF used here is valid for comparing partitioning characters among cultivars. Then,

$$H = \frac{(p \cdot \text{CGR} \cdot t)}{W}$$

where t is the specific time period during podfilling, and W is total biomass (adjusted for energy content in pods using a PCF of 0.606) at maturity. This simple analysis therefore allows us to investigate which variables were responsible for cultivar differences in H in response to the drought treatment imposed in this study. For simplicity, CGR, PGR and p were calculated from the

beginning of pod fill to maturity for each cultivar under the shelter treatment, and are shown in Table 6.

Table 6. Crop growth rates (CGR), pod growth rates (PGR) and partitioning factors (p) for each cultivar under the Sh treatment

The time interval (t) for calculation was from 75–131 days after sowing for VB and Q18801, and from 61–131 days after sowing for McCubbin and Red Spanish

Cultivar	t (days)	CGR (kg ha ⁻¹ day ⁻¹)	PGR (kg ha ⁻¹ day ⁻¹)	p
VB	56	55.6	45.4	0.82
Q18801	56	60.2	66.0	1.10
McCubbin	70	58.7	51.6	0.88
Red Spanish	70	56.4	49.4	0.88

There were only minor cultivar differences in the energy adjusted CGR during podfilling (range of 56–60 kg ha⁻¹ day⁻¹), suggesting that this type of drought and associated plant water deficits, affected assimilatory capacity in a similar fashion among cultivars. Duncan *et al.* (1978) concluded that CGR's in a range of peanut cultivars grown under well-watered conditions did not differ significantly, and therefore had only small effects on the large cultivar differences observed in H and pod yield.

Differences in both p and t were largely responsible for cultivar variation in H in response to the severe end of season drought applied in this study. Drought-hastened maturity in the virginia cultivars (by *c.* 10 days relative to the well-watered controls) such that crop duration of both virginia and spanish types was similar (*c.* 121 days from emergence to maturity). Earlier flowering, pegging and pod development in the spanish types therefore meant the effective pod-filling phase was longer (70 days), and in combination with high p , resulted in high H observed in the spanish cultivars. Also, earlier reproductive development would have enabled subsequent filling of pods to be carried out under less severe levels of crop water deficit compared to the later flowering and podding virginia types. This response highlights the fact that improved H under severe end of season droughts could most easily be improved by manipulating phenology, as demonstrated elsewhere (Passioura 1972; Harris *et al.* 1988; Mathews *et al.* 1988a; Chapman 1989).

Among the virginia types, variation in H was large (Fig. 3) and resulted largely from differences in p (0.82 compared to 1.10 for VB and Q18801 respectively). Variation in p could arise from cultivar differences in the timing of establishment of reproductive sinks, the rate of addition of sinks and the filling of sinks in response to the end of season drought. The fact that H of Q18801 was significantly greater than VB under I/I conditions (Fig. 3a), however, indicates that the difference in p may well be genetic rather than a response to drought. Lack of peg and pod number data throughout the reproductive phase precludes any detailed analysis of which processes may have been operating to influence H . The fact that the number of kernels per m² in VB was reduced by 268% compared to 204% for Q18801 (Table 2) suggests however that pod addition rate in VB was more sensitive to declining soil and plant water status. Shorter and Simpson (1987) found peg and pod addition rates of VB almost ceased in response to mid-season drought. Also, partitioning ratios in excess

of 1.0 for Q18801 suggest that assimilate from storage elsewhere in the plant prior to podfilling may have been retranslocated, and thereby increased pod growth rates. Partitioning ratios in excess of 1.0 have also been recorded in irrigated peanuts grown in a tropical environment (Bell 1986) and peanuts subjected to water stress during the pod filling phase (Chapman 1989). The extent of cultivar variation in the degree of remobilization during podfilling is unknown in peanut. Based on the results presented here, more research into its role in improving *H* and pod yield under drought conditions seems warranted.

Concluding Discussion

Crop water deficits occurring during early crop growth reduced pod yields in all cultivars by between 17 to 25% relative to the I/I treatment for all cultivars. In Q18801, McCubbin and Red Spanish pod, yield reductions were largely due to drought effects on pod numbers per m², with only minor effects on kernel size and quality. In contrast VB appeared to produce fewer pods during the drought period, but following rewatering initiated numerous pegs and pods which failed to mature late in the season. As a result weight per pod and kernel (and hence quality) were reduced relative to the I/I treatment.

Late season drought in the longer season virginia types reduced pod yields more severely than in the spanish types, through reduction in both pod numbers per m² and kernel size relative to fully irrigated crops.

The greater pod yields of Q18801, McCubbin and Red Spanish compared to VB were largely a result of superior harvest index characteristics (>70% higher). Duncan *et al.* (1978) concluded that unintended selection for higher *H* had largely been responsible for cultivar pod yield improvement in the USA over the past 40 years. Similarly, Mathews *et al.* (1988) concluded that variation in *H* was largely responsible for pod yield superiority among four peanut cultivars grown under severe drought stress. Clearly, it is apparent that continued improvement in peanut pod yield in response to drought stress should be possible via continued selection for this relatively easily measured parameter.

VB was able to extract significantly greater amounts of soil water at depth (c. 40 mm) and hence had greater *T* compared to the other cultivars. However, greater *T* resulted in greater vegetative biomass accumulation, due to this cultivar's poor partitioning characteristics. The fact that there is substantial variation in the character should, however, provide considerable scope for selection in breeding programs, provided suitable selection methods can be identified, and negative correlations between water extraction and partitioning of biomass to pods do not exist.

The variation in TE appeared to be relatively small among cultivars, indicating that TE contributed little to the observed pod yield variation among the limited range of cultivars used in this study. Other studies have, however, demonstrated that considerable variation in TE does exist among peanut cultivars, and could potentially improve pod yield performance under drought conditions (Hubick *et al.* 1986, 1988; Wright *et al.* 1988).

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