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Water-Use Efficiency and Carbon Isotope Discrimination in Peanut under Water Deficit Conditions

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ABSTRACT

Because of its relationship with water-use efficiency (W), carbon isotope discrimination in leaves (Δ) was proposed to be useful for identifying genotypes with greater water-use efficiency. In this study we examined the relationship between W and Δ in four peanut (*Arachis hypogaea* L.) genotypes. The genotypes were grown in and around mini-lysimeters embedded in soil and were subjected to two drought regimes, intermittent and prolonged water deficit conditions, by varying the irrigation timing and amount. Automated rain-out shelters prevented any rain from reaching the experimental plots during the treatment period. The mini-lysimeters allowed accurate measurement of water use and total dry matter (including roots) in a canopy environment. Water-use efficiency, which ranged from 1.81 to 3.15 g kg $^{-1}$, was negatively correlated with Δ, which ranged from 19.1 to 21.8‰. Tifton-8 had the highest W (3.15 g kg $^{-1}$) and Chico the lowest (1.81 g kg $^{-1}$), representing a variation in W of 74% among genotypes. Variation in W arose mainly from genotypic differences in total dry matter production rather than from differences in water use. It is concluded that Δ is a useful trait for selecting genotypes of peanut with improved W under drought conditions in the field. A strong negative relationship existed between W and specific leaf area (SLA, cm^2 g $^{-1}$) and between Δ and SLA, indicating that genotypes with thicker leaves had greater W. SLA could therefore be used as a rapid and inexpensive selection index for high W in peanut where mass spectrometry facilities are not available.

IDENTIFICATION OF PHYSIOLOGICAL TRAITS contributing to superior performance of crop plants under drought conditions has been a long-term goal of plant scientists. Water-use efficiency is one such trait which can contribute to productivity when water resources are scarce. Reviews of the literature have suggested that intraspecific variations in W are small and are likely to be increased only by crop management (Fischer, 1979) or modifying the environment (Tanner and Sinclair, 1983). However, variation in W was shown to exist between and within species (Briggs and Shantz, 1914). More recently, variation in W was observed among genotypes of grass species (Farquhar and Richards, 1984, Frank et al., 1985), cotton (Hubick and Farquhar, 1987), and peanut (Wright et al., 1988, ICRISAT, 1990). While potentially useful, W cannot be easily exploited because of practical difficulties involved in measurement of transpiration and root biomass in the field. Spot measurements of transpiration ratio, i.e., CO_2 assimilation rate divided by transpiration rate, only give instantaneous estimates of transpiration efficiency, which may not necessarily correlate with long-term differences

Farquhar et al. (1982) predicted that at constant vapor pressure difference, discrimination against ^{13}C during CO_2 assimilation (Δ) will give an estimate of the ratio of the internal CO_2 concentration in the leaf (C_i) to ambient CO_2 concentration (C_a) in plants with the C_3 photosynthetic pathway. Lower Δ was associated with lower C_i/C_a and greater W (Farquhar et al., 1989). In agreement with the theory, Δ in leaf tissue was negatively correlated with W in wheat (Farquhar and Richards, 1984), peanut (Hubick et al., 1986, Wright et al., 1988), cotton (Hubick and Farquhar, 1987), barley (Hubick and Farquhar, 1989), and C_3 grasses (Johnson and Basset, 1991), suggesting that measurement of Δ could potentially be used to screen genotypes for greater W

Much of the research into genotypic variation in W has been conducted in pots under glasshouse conditions where accurate monitoring of water use and above and below ground biomass production could be made. Measurement of W in the field conditions is considerably more difficult. Problems in accurate measurement of water use and its apportionment into transpiration (T) and soil evaporation (Es) components, and difficulty in recovering roots for root mass determination can lead to erroneous estimates of W. In addition, the microclimate in field canopies can be considerably different from that of isolated plants in pots, leading to potential differences in stomatal control of transpiration and hence, a breakdown in the relationship between W and Δ (Cowan, 1988, Farquhar et al., 1988)

Wright et al. (1988) overcame some of the above mentioned difficulties by using a mini-lysimeter facility which enabled accurate measurement of transpiration and shoot and root mass in peanut genotypes grown in closed canopies. Under adequately watered conditions, substantial variation in W (range of 2.46–3.76 g kg $^{-1}$) among peanut genotypes, and a strong negative correlation between W and Δ was demonstrated ($r = 0.82$, $P < 0.01$). The situation under water-limited conditions is less clear. Wright et al. (1993) showed that severe plant water deficits can result in a break down in the relationship between W and Δ for peanut genotypes grown in small pots. Greater respiratory losses of carbon was suggested as a possible reason for this discrepancy (Masle et al., 1990)

The objective of the present study was to examine the relationship between W and Δ in four peanut genotypes grown under intermittent and long-term water deficit conditions in the field. Such information is essential before large-scale use of this trait as a selection criterion in breeding programs can be recommended

MATERIALS AND METHODS

The field experiment was conducted on a deep red clay loam or oxisol (Soil Survey Staff, 1975) at the Bjelke Petersen Research Station, Kingaroy (151 °E, 26 °S), Queensland, during

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Abbreviations: W, water use efficiency, Δ, carbon isotope discrimination, T, transpiration, ET, evapotranspiration, Es, soil evaporation, RUE, radiation use efficiency, SLA, specific leaf area, C_i, internal CO_2 concentration in leaf, C_a, ambient CO_2 concentration, H_1 and H_2, initial and final harvests, respectively, I_i and I_c, intermittent and continuous water deficit, respectively, PAR, photosynthetically active radiation, VPD, air saturation vapor pressure deficit

Table 1 Schedule of irrigation followed in the two treatments

Date	Irrigation applied	
	I_1	I_2
	mm	
7 Jan 1991	70	70 0
11 Jan 1991	—	7 5
18 Jan 1991	—	12 0
25 Jan 1991	—	10 4
31 Jan 1991	100	10 0
9 Feb 1991	—	15 0
15 Feb 1991	—	15 0
22 Feb 1991	—	15 0

the 1990–1991 summer season (November–April) Four peanut genotypes, i e , Chico, McCubbin, Shulamit, and Tifton 8, were selected based on previously measured differences in W and Δ (Hubick et al., 1986, Wright et al , 1988) Each genotype was grown under two irrigation regimes (I_1 and I_2) in a split-plot design with genotypes as sub- and irrigation regimes as main treatments, replicated twice under each of two rain-out shelters (four replicates) Each rain-out shelter, covering an area of 6 by 19 m (Hatfield et al , 1989), prevented rain from reaching the experimental plots throughout the growing period. Staggered plantings were made to match the timing of imposition of treatments with the phenology of genotypes Planting dates were selected based on the thermal time requirement for flowering (Bell et al., 1991) Tifton-8 and Shulamit (long-duration types) were planted on 19 Nov 1990, and McCubbin (medium duration type) and Chico (short-duration type) were planted on 22 and 28 Nov 1990 respectively A basal fertilizer of P and K, each at a rate of 30 kg ha $^{-1}$ was incorporated into the top soil Seeds, treated with captan[1] [*N*-(trichloromethylthio)-4-cyclohexene 1,2-dicarboximide] at 3 g kg $^{-1}$ (to prevent seedling diseases) and ethephon [2 (chloro ethyl)phosphonic acid] (to ensure seed dormancy was broken), were hand-sown in excess and later thinned to the required population Each plot consisted of four rows each of 6 m length A density of 22 plants m $^{-2}$ was achieved with an interrow spacing of 30 cm and an intra plant spacing of 15 cm Main treatments were separated by planting two guard rows Plots were maintained weed free by hand weeding

About 3 wk before sowing, two intact soil cores 0 8 m deep and 0 3-m diam were excavated in each plot at a distance of 2 5 m from each other with a Proline coring machine (Evans Deakin Proline,[1] S A. Australia) Mini-lysimeters were prepared with PVC storm water pipe (0 3-m internal diam and 0 8 m deep) and the intact soil cores, as described by Wright et al (1988) Each plot consisted of two mini lysimeters, here after referred to as *pots*, to monitor transpiration and biomass production A basal fertilizer of P and K, each at a rate of 30 kg ha $^{-1}$ was mixed in the top soil of each pot before planting Five seeds of the appropriate genotype were planted and later thinned to two plants per pot

In addition to the two cores in each plot, three cores were similarly prepared in each shelter in the guard rows between the main treatments These pots were left unplanted (hereafter referred to as *bare pots*) and were used to monitor potential soil evaporation in the absence of plants

After planting, irrigation of the bulk crop area was accomplished with trickle-irrigation (T tape with outlets every 20 cm), and irrigation input into each main treatment was measured by water meters (having an accuracy of + 2%)

Plants in pots were irrigated at a depth of 20 cm to minimize soil evaporation Before sowing in pots, a perforated plastic pipe (25-mm diam) was made into a circular shape by connecting each end to a T junction Another plastic feeder pipe of 50 cm length (25 mm diam) was connected to the other end of the T junction The ring was buried at a depth of 20 cm in the pot allowing the feeder pipe to reach about 30 cm above the soil surface through which desired amounts of water were added by hand The bulk crop, as well as plants in the pots, were kept well watered until the imposition of treatments

Two treatments, an intermittent (I_1) and a continuous water deficit (I_2), of 50-d duration (7 January–25 February) were imposed after flowering by varying the timing and amount of irrigation (Table 1) In I_1, two drought episodes of 25-d duration each, were imposed, with a single release from drought on 31 January For I_2, plants were subjected to continuous water deficit by irrigating weekly, with an amount equal to 25% of weekly cumulative pan evaporation during the treatment period One of the three bare pots in each shelter received irrigation similar to I_1, while the other two received irrigation similar to I_1, while the other two received irrigation similar to I_2 The experiment was terminated on 25 February to avoid any confounding effects from maturity differences among genotypes

An initial harvest (H_1) was performed on 6 Jan 1991 in which ten uniform plants from each plot and one plant from each pot were harvested to provide dry matter estimates at the beginning of the treatments Plants from the bulk crop were harvested at ground level while one of the two plants from each pot was harvested, with care in order to recover as much of the root system as possible The final harvest (H_2) was made on 25 February in which plants in the two middle rows of the bulk crop (2 m length) were harvested, and the remaining plant in each pot was harvested separately

Plants from each pot and a sub-sample of three plants from the bulk crop were partitioned into leaf, stem, pods, and roots prior to drying (at 80 °C for 48 h) and weighing Specific leaf area (SLA) was determined as the ratio of the leaf area of a leaf sub sample (about 40 leaflets) to the oven-dry weight of the leaf sub sample At H_2, total root biomass was measured, following recovery of roots from the soil cores as described by Wright et al (1988)

Water loss from pots was estimated by weighing them at weekly intervals An electronic load cell (accuracy of ± 0 1 kg) mounted on a tractor driven gantry was used to weigh pots by lifting them approximately 10 cm above the ground Transpiration (T), during the treatment period was then determined as

$$T = I + (Wt_1 - Wt_2) - Es,$$

where I was irrigation (in kilograms), Wt_1 and Wt_2 were the weights of each pot at the beginning and end of the week, respectively, and Es was soil evaporation during the period of measurement The value of Es was estimated as $e(1 - f)$, where e was the potential soil evaporation determined from the changes in water content in bare pots and f was the fractional radiation interception by the foliage (Cooper et al , 1983) The value of W was then estimated as the ratio of total dry matter production (leaf + stem + pod + roots) and transpiration between H_1 and H_2

Fractional photosynthetically active radiation (PAR) intercepted by the crop (f) was measured at 1400 h AST at H_1, and at both 0900 and 1400 h at H_2 with a line quantum sensor (LI 1915, LI COR, Lincoln, NE). Radiation use efficiency (RUE) of the crop was estimated as the ratio of dry matter produced and the cumulative PAR intercepted by the crop between H_1 and H_2 Leaf temperature was measured at weekly intervals at 1400 h on fully expanded leaves (third or fourth leaf on main axis) with a copper-constantan thermocouple fixed to a leaf clip In each plot, measurements were made on two plants in the bulk crop and on one plant in each pot

Dried leaf samples used for SLA measurements at H_1 and H_2 were ground to pass through a 100 μm sieve The Δ of these samples were measured by ratio mass spectrometry using

[1] Mention of commercial products or companies does not imply endorsement or recommendation by ICRISAT over others of similar nature

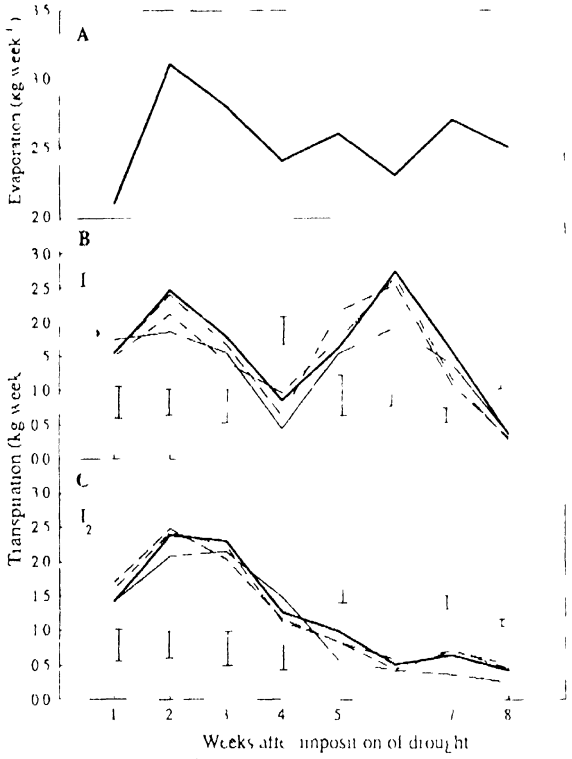

Fig. 1. Pan evaporation (E,1A), and transpiration (T) of Chico ( ), McCubbin (—), Shulamit (– – –) and Tifton-8 (– – –) grown in pots under (1B) and intermittent (I_1) and (1C) continuous drought (I_2) treatments. Vertical bars indicate LSD ($P < 0.05$) to compare means within a given sampling time.

techniques as described by Hubick et al. (1986). The Δ, which occurred between H_1 and H_2, was derived as follows. If at H_1, plant dry weight was M_1, and the associated discrimination in fixing the carbon to that point was Δ_1, and there followed a period where dry weight increased to M_2, during which the carbon was fixed with discrimination Δ, then the average discrimination for the total mass, Δ_2, would be,

$$\Delta_2 = [M_1 \Delta_1 + (M_2 - M_1)\Delta] / M_2$$

Solving the above equation for Δ would be

$$\Delta = (\Delta_2 M_2 - \Delta_1 M_1) / (M_2 - M_1)$$

where Δ_1 and Δ are the isotope discrimination, and M_1 and M_2 are total plant dry weights, at H_1 and H_2, respectively.

Maximum and minimum temperatures, relative humidity, incident solar radiation and Class A pan evaporation were collected daily from an automatic weather station located adjacent to the experimental site. Air saturation vapor pressure deficit (VPD) was calculated with air temperature and RH.

RESULTS

Mean maximum and minimum air temperatures during the growing season were 30 ± 4 °C and 15 ± 3 °C respectively while incident solar radiation ranged from 20 to 35 MG m^{-2} d^{-1}, and VPD ranged from 1.7 to 2.2 kPa during the treatment period.

There was an initial increase in transpiration, T in response to higher evaporative demand in both treatments at 2 wk following the start of irrigation treatments (Fig. 1). This was followed by a steady decline in T as drought progressed. In general, seasonal T of Chico was lower compared to other genotypes in both treatments. However, genotype differences in T were only significant ($P < 0.05$) at 2 and 6 wk after imposition of I_1, with Chico having significantly lower T compared to the other genotypes. These differences were also associated with higher soil evaporation (Es) losses in Chico due to relatively smaller ground cover compared to other genotypes. In I_2, T was not significantly different among genotypes, and declined gradually as drought progressed until it reached a stable rate of 0.5 kg wk^{-1}, on a pot basis (Fig. 1). Evapotranspiration (ET) was generally lower in I_2 compared to I_1.

Total dry matter (TDM, including roots) which accumulated during the treatment period varied significantly ($P < 0.05$) among genotypes and ranged from 20 to 37 and 18 to 31 g plant^{-1} in I_1 and I_2, respectively (Table 2). In both treatments, Chico produced the least, and Tifton-8 the greatest TDM during the treatment period. The difference in TDM between McCubbin, Shulamit, and Tifton-8 were not significant.

Significant ($P < 0.01$) genotypic variation in root weight of the order of 250% was evident in both irrigation treatments. These differences in root weight and root shoot ratios were associated with relatively small variation in T between genotypes (Table 2).

It was interesting to note that while differences in TDM between genotypes were of the order of 72 to 85%, corresponding differences in T were only 12 to 19%. Thus, variation in TDM seems to dominate, although

Table 2. Total dry weight (TDM, including roots), root weight, transpiration (T), water-use efficiency (W), root shoot ratio (RS), radiation-use efficiency (RUE), and carbon isotope discrimination in leaf (Δ × 10^3) for four peanut genotypes grown under two drought treatments

Trt	Genotype	TDM	Root	I	W	RS	RUE	Δ pot	Δ crop
		g plant^{-1}		mm	g Kg^{-1}	g g^{-1}	g MJ^{-1}		
I_1	Chico	20 5	3 3	11 3	1 81	0 15	0 66	21 1	21 1
	McCubbin	36 3	5 7	13 4	2 72	0 15	0 80	20 2	20 7
	Shulamit	35 7	7 2	12 8	2 78	0 21	0 79	19 1	19 9
	Tifton-8	37 5	6 8	12 2	3 05	0 19	0 86	19 3	19 4
I_2	Chico	17 8	2 3	8 9	2 02	0 11	0 62	21 8	20 9
	McCubbin	26 8	4 6	10 0	2 68	0 16	0 64	20 2	19 4
	Shulamit	29 0	5 9	9 9	2 93	0 20	0 66	19 5	18 8
	Tifton-8	31 3	6 4	10 0	3 15	0 21	0 75	18 6	18 6
	LSD 5%	5 5	1 2	1 1	0 38	0 033	0 09	0 41	0 93

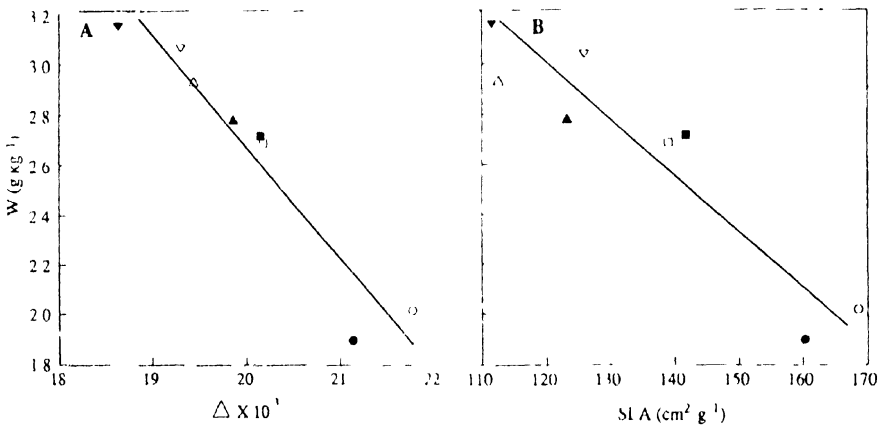

Fig. 2. Relationship between W and Δ (A) and W and SLA (B) in leaves of Chico (○), McCubbin (□), Shulamit (△) and Tifton-8 (▽) under intermittent (closed symbols) and continuous (open symbols) drought treatments. W = 11.31 − 0.43 Δ, (r^2 = 0.89, P < 0.01); W = 5.4 − 0.2 SLA, (r^2 = 0.84, P < 0.01).

considerable variation exists for T among peanut genotypes.

Genotypic differences in W ranged from 1.81 to 3.05 g kg^{-1} in I_1 and from 2.02 to 3.15 g kg^{-1} in I_2, representing variation in W of the order of 56 to 69% (Table 2). Differences in TDM among genotypes accounted for up to 80 and 90% of the variation in W measured in I_1 and I_2, respectively. Genotype × treatment interaction for W was not significant, and the ranking of genotypes for W was similar in the two drought treatments. Radiation-use efficiency (RUE) ranged from 0.66 to 0.86 g MJ^{-1} in I_1 and was lower in I_2 (0.62–0.75 g MJ^{-1}), with Tifton-8 and Chico having the maximum and minimum RUE, respectively, in both treatments (Table 2). There was a strong positive relationship between W and RUE in both I_1 (r^2 = 0.99, P < 0.01) and I_2 (r^2 = 0.66, P < 0.05) treatments (not shown). Although RUE of all genotypes declined in I_2, ranking of genotypes for W and RUE was consistent in both treatments.

The Δ varied significantly among genotypes (Table 2) with Tifton-8 and Chico having the least (19.0 ± 0.17%) and the greatest (21.5 ± 0.17%) values, respectively (when averaged over both treatments). There was a strong negative relationship between Δ and W (r^2 = 0.89, P < 0.01, Fig. 2A). Interestingly, W was also negatively related to SLA (r^2 = 0.84, P < 0.01, Fig. 2B).

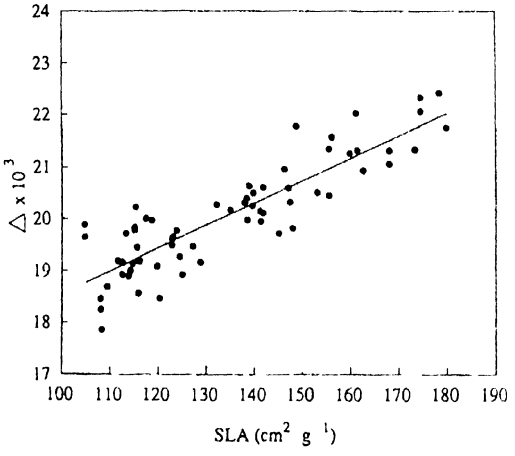

Fig. 3. Relationship between the mean SLA (of H_1 and H_2) and Δ in leaves of four peanut cultivars under the two drought treatments. Δ = 14.2 + 0.04 SLA, (r^2 = 0.81, P < 0.01).

The leaf temperature measurements done at weekly intervals indicated that the difference between plants in pots and adjacent crop was less than 1 °C during the most of the treatment period. In I_1, although leaf temperature in pots increased relative to the crop at 5 wk after imposition of treatments, the difference was less than 2 °C at 7 wk when plants were harvested. In I_2, leaf temperature in pots and the adjacent crop was similar throughout the treatment period, although leaf temperature of Shulamit and Tifton-8 was marginally higher (by 2–3 °C) in pots compared to the bulk crop at 7 wk.

The Δ in pots was well correlated with that of the bulk crop [Δ (crop) = 4.34 + 0.77Δ (pot), r^2 = 0.61, P < 0.05, n = 64]. Similarly, the SLA in pots was well correlated with that of the bulk crop [SLA (crop) = −46.4 + 1.61 SLA (pot), r^2 = 0.73, P < 0.01, n = 32]. Significant correlation of Δ and SLA between plants grown in pots and those in adjacent crop showed that the relative ranking of genotypes for Δ and SLA was consistent in both situations.

The relationship between SLA and Δ was positive and significant (r^2 = 0.81, P < 0.01, Fig. 3) confirming the earlier observation (Fig. 2B) that SLA could be used to identify genotypes with lower Δ and greater W.

DISCUSSION

Genotypes used in this study varied in their phenology, with Chico being a short duration, and McCubbin a medium duration spanish type (var. *vulgaris* of ssp. *fastigiata*), and Shulamit and Tifton-8 being long duration virginia bunch and virginia runner types (i.e., var. *hypogaea* of ssp. *hypogaea*), respectively. Staggered planting of genotypes based on differing thermal time requirements for flowering (Bell et al., 1991) enabled us to match crop phenology with the timing of drought. More than 50% of the plants in all plots had flowered by the beginning of the drought treatments. Genotypes received similar amounts of water in a given drought

treatment (Table 1), yet produced differing amounts of total dry matter, TDM (Table 2) Variation in transpiration, T among genotypes was relatively small compared to variation in TDM with the latter accounting for 80 and 90% of the variation in water use efficiency, W in I_1 and I_2, respectively. The W was measured on single plants grown in mini-lysimeter pots of 58-L capacity which were placed within canopies in the field Canopies of plants in pots and adjacent crops were well intermixed. Earlier studies have indicated that evapotranspiration was not significantly different among large ($3.0\ ^2$), medium ($0.75m\ ^2$) and small ($0.18m\ ^2$) lysimeters after adjusting evapotranspiration for leaf area differences (Dugas and Bland, 1989). The Δ and SLA of plants in pots were well correlated with that of the bulk crop suggesting consistency in relative ranking of genotypes for Δ and SLA in the pot and canopy situations. However, the fact that the slopes and Y Intercepts of these relationships were substantially different from unity and zero, respectively, raises the possibility that some differences in microclimate between pots and adjacent crop may have been present.

There was significant genotypic variation in production of root biomass during the treatment period, with genotypes with high W having greater root mass (Table 2). Similar observations have been reported for peanut grown in pots (Hubick et al , 1986), and in the field under well-watered conditions (Wright et al., 1988) It is also of interest that while Tifton-8 produced greater root biomass than Chico, there was no significant difference in transpiration during the treatment period. Whether this difference is related to variation in root length density (Cooper et al., 1987), or superior water uptake per unit root length is unknown. This observation does raise the question as to whether some genotypes may produce roots in excess of what is required. Further information on this aspect may have important implications for peanut yield performance under drought con ditions.

Changes in C_i/C_a, and Δ can arise from changes in the balance between leaf stomatal conductance and photosynthetic capacity. Where C_i/C_a changes because of stomatal movements, significant boundary layer resistances to fluxes of water vapor and heat may occur and cause the relationship between W and Δ to break down in plants grown in canopies in the field (Cowan, 1988, Farquhar et al., 1988). Where C_i/C_a changes in response to variation in photosynthetic capacity the problem of poor coupling between the crop canopy and atmosphere may be less important (Farquhar et al., 1988). A strong correlation between W and Δ demonstrated in this study under water-limited conditions in the field therefore suggests that variation in C_i/C_a, and Δ arose mainly from variation in photosynthetic capacity. The negative association between Δ and TDM for the genotypes tested here (Table 2) indeed suggests that variation in photosynthetic capacity, rather than variation in stomatal conductance (and water use), predominated. This finding is in agreement with earlier studies in peanut (Hubick et al., 1986, 1988; Wright et al., 1988) and sunflower (Virgona et al., 1990).

The RUE was significantly less in I_2 compared to I_1, with little change in W (Table 2), although W and RUE were linearly related in both treatments. This result again reinforces the hypothesis that genotypic variation in W occurs due to effects of photosynthetic capacity on dry matter production, rather than to effects of stomatal conductance on water use in peanut Thus, RUE in all genotypes was significantly less in I_2 than in I_1 presumably because of lowered leaf (and canopy) conductance arising from greater levels of soil and crop water deficits reducing photosynthetic activity. This observation suggests the reduction in conductance did not influence the genotypic variation in photosynthetic capacity, as genotypic ranking in RUE was maintained in I_1 and I_2

Significant differences in RUE among peanut genotypes grown under water-limited conditions have been shown previously (Matthews et al., 1988). Our results confirm such variability and suggest that selection for high W (via Δ or SLA) may concurrently improve RUE, which is an important trait for high biomass production under non-limiting conditions.

The strong negative relationship between W and SLA (Fig 2B) suggests that the genotypes with lower SLA (greater leaf thickness) had greater W. The significant relationship between Δ and SLA (Fig. 3) suggests that genotypes with thicker leaves (low SLA) had greater photosynthetic capacity and thereby assimilated more carbon per unit leaf area, as observed in other crops (Dornhoff and Shibles, 1976; Wolf and Blaser, 1972, Bowes et al , 1972). Substantial variation in photosynthetic rates per unit leaf area have been demonstrated in peanut (Pallas and Samish, 1974; Bhagsari and Brown, 1976, Pallas, 1982). The strong correlation between SLA and W (and Δ) suggests that SLA could be used as a rapid and inexpensive selection index to identify genotypes with high W (low Δ), where mass spectrometry facilities are not available However, SLA is influenced by environmental factors such as temperature and water deficit which affect cell elongation and multiplication (Vivekanandan and Gunasena, 1976) and starch accumulation in chloroplasts (Araus et al., 1989). Similarly, Wright et al. (1988) and Hubick and Farquhar (1989) have shown that Δ was strongly influenced by various environmental factors. The G × E interaction for the relationship between SLA and Δ in peanut is further described by Nageswara Rao and Wright (1993).

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