

# Genetic and Environmental Variation in Transpiration Efficiency and Its Correlation with Carbon Isotope Discrimination and Specific Leaf Area in Peanut

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## I. Introduction

Identification of physiological traits contributing to superior yield performance of crop plants under drought conditions has been a long-term goal of plant scientists. Transpiration efficiency ( $W$ ), defined as the ratio of dry matter production to transpiration, is one such trait which can contribute to productivity when water resources are scarce. Reviews of literature on this topic over the past decade have concluded that the intraspecific variations in  $W$  are small and are likely to only be increased by either crop management (Fischer, 1979) or modifying the environment (Tanner and Sinclair, 1983). The early work of Briggs and Shantz (1914) showed significant variation in  $W$  among and within species. Their findings have subsequently been confirmed over the past few years, with numerous reports of substantial variation in  $W$  both between and within species (e.g., Farquhar and Richards, 1984; Frank *et al.*, 1985; Hubick and Farquhar, 1989; Dingkuhn *et al.*, 1991).

The difficulty in making accurate measurements of crop transpiration in the field has no doubt made the demonstration of species and cultivar differences in  $W$  difficult. While transpiration may be readily measured in pots in which soil evaporation can be minimized, it is much more difficult to estimate soil evaporation in the field. In the case of dry matter production,

the lack of quality data on root dry matter nearly always results in  $W$  being calculated on an aboveground dry matter basis. Clearly, if differences in partitioning of dry matter to roots and shoots occur due to genetic or environmental effects, considerable error in  $W$  calculations can also arise.

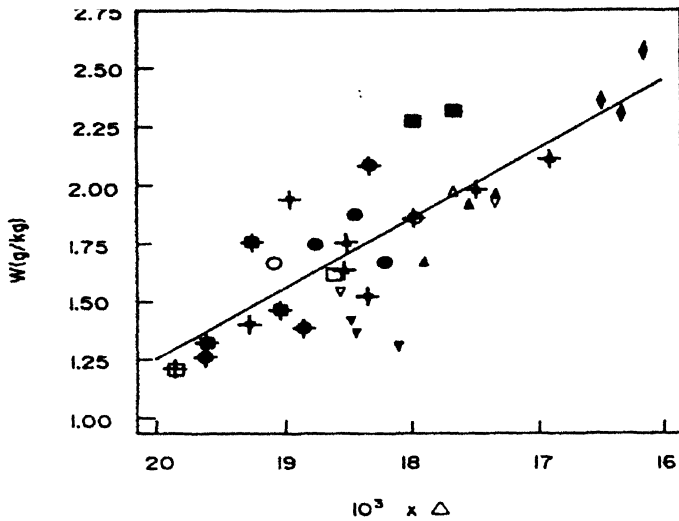
Recently, a new approach has been proposed for identifying variation in  $W$  in  $C_3$  plants, which may overcome the considerable problems involved in field measurement of total dry matter production and transpiration. It exploits theory based upon discrimination against  $^{13}C$  by leaves ( $\Delta$ ) during photosynthesis (Farquhar *et al*, 1982, Farquhar and Richards, 1984), and  $\Delta$  in leaf tissue has been shown to be negatively correlated with  $W$  in numerous species (Farquhar and Richards, 1984, Hubick *et al* 1986, Hubick and Farquhar, 1989, see several chapters in this book). The experimental confirmation of the relationship between  $W$  and  $\Delta$  supported the possibility of using  $\Delta$  as a criterion to exploit variation in  $W$  in breeding programs.

Peanut is a crop of global economic significance not only for its widespread commercial production, but also as an important source of oil and protein in developing countries. In this paper we present results from a series of experiments investigating genotypic and environmental variation in  $W$  in peanut and its correlation with  $\Delta$  under both controlled environment and field conditions. The relationship between pod yield and  $W$  is also investigated, as well as an assessment of whether  $W$  and  $\Delta$  are heritable characters. Such information is needed before  $\Delta$  could be recommended as a selection trait for improving  $W$  in peanut-breeding programs.

## II. Peanut Cultivar Variation in Transpiration Efficiency and Correlation with $\Delta$ at the Whole-Plant Level

Using medium-sized pots (13 kg capacity) in a glasshouse study, Hubick *et al* (1986) showed there was significant variation in  $W$  among seven *Arachis hypogaea* cultivars and two wild *Arachis* species, ranging from 1.41 to 2.29 g/kg. A close negative correlation ( $r^2 = 0.66$ ) between  $W$  and  $\Delta$  was also observed, as expected on the basis of theory and data presented by Farquhar and Richards (1984) (Fig. 1). Differences in photosynthetic capacity were largely responsible for  $W$  variation, as dry matter production was negatively correlated with  $\Delta$ , while water use showed no such relationship with  $\Delta$ . The lack of a relationship between water use and  $\Delta$  may be associated with the use of small pots in this study, where plants were forced to use most of the available water and therefore ended up having the same total water use. Differing responses may occur in the field where access to soil water can be relatively unrestricted.

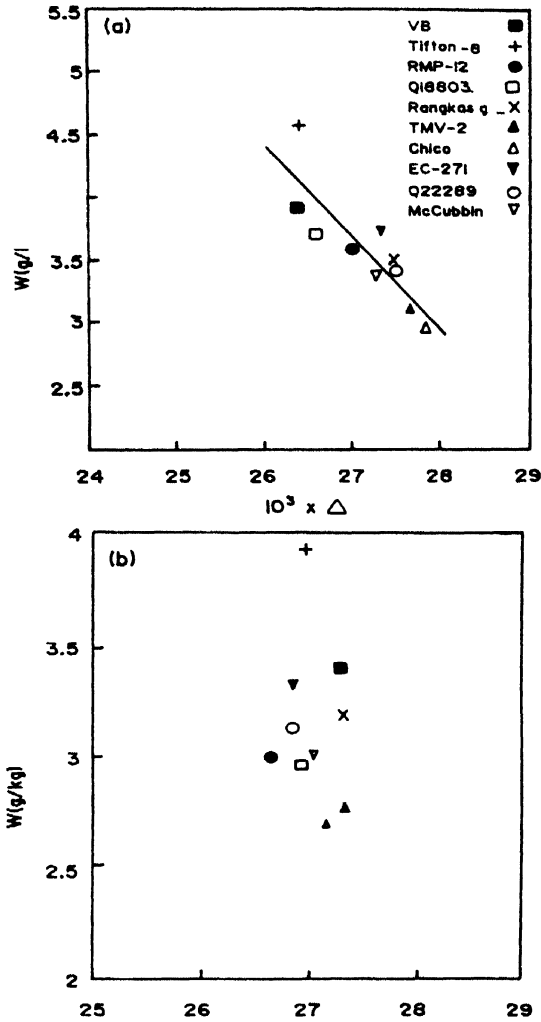
A recent glasshouse experiment (Wright, unpublished observations) using small pots (2 kg capacity) has confirmed that significant  $W$  variation exists among peanut cultivars. Variation in  $W$  among 10 cultivars ranged from 2.96 to 4.58 g/kg under well-watered conditions, and from 3.41 to



**Figure 1.** Transpiration efficiency (shoots plus roots) versus carbon isotope discrimination in leaves ( $r = -0.81$ ). Open symbols represent well-watered plants and closed symbols represent plants that were droughted. Symbols represent genotypes as follows: *Arachis villosa*,  $\nabla$ ; *A. glabrata*,  $\blacktriangledown$ ; *A. hypogaea* cultivars—Chico,  $\blacklozenge$ ; PI314817,  $\blacklozenge$ ; PI259747,  $\bullet$ ; UF78114-3,  $\blacksquare$ ; VB187,  $\blackstar$ ; Florunner,  $\blacktriangle$ ; Tifton-8,  $\blacklozenge$  (redrawn from Hubick *et al.*, 1986).

4.74 g/kg under a terminal drought stress during vegetative growth (which killed all plants). A highly significant correlation between  $W$  and  $\Delta$  ( $r^2 = 0.74$ ) was observed under well-watered conditions (Fig. 2a); however, under droughted conditions no relationship was detected (Fig. 2b). Interestingly, the ranking of cultivars for  $W$  was not significantly affected by the drought treatment, as is illustrated in Fig. 3a where a highly significant correlation ( $r^2 = 0.87$ ) between  $W$  under well-watered and droughted conditions was observed. In contrast,  $\Delta$  under both watering regimes was poorly correlated (Fig. 3b), which could imply that under the severely water-stressed treatment,  $\Delta$  was somehow affected such that the relationship between  $W$  and  $\Delta$  broke down. Conversely, it could be interpreted that for a given  $\Delta$ ,  $W$  in the stressed treatment was less than in the well-watered treatment because of greater respiratory losses as a proportion of carbon gained,  $\phi_c$ . Theory suggests that, at reduced growth rates,  $\phi_c$  is increased (Masle *et al.*, 1990).

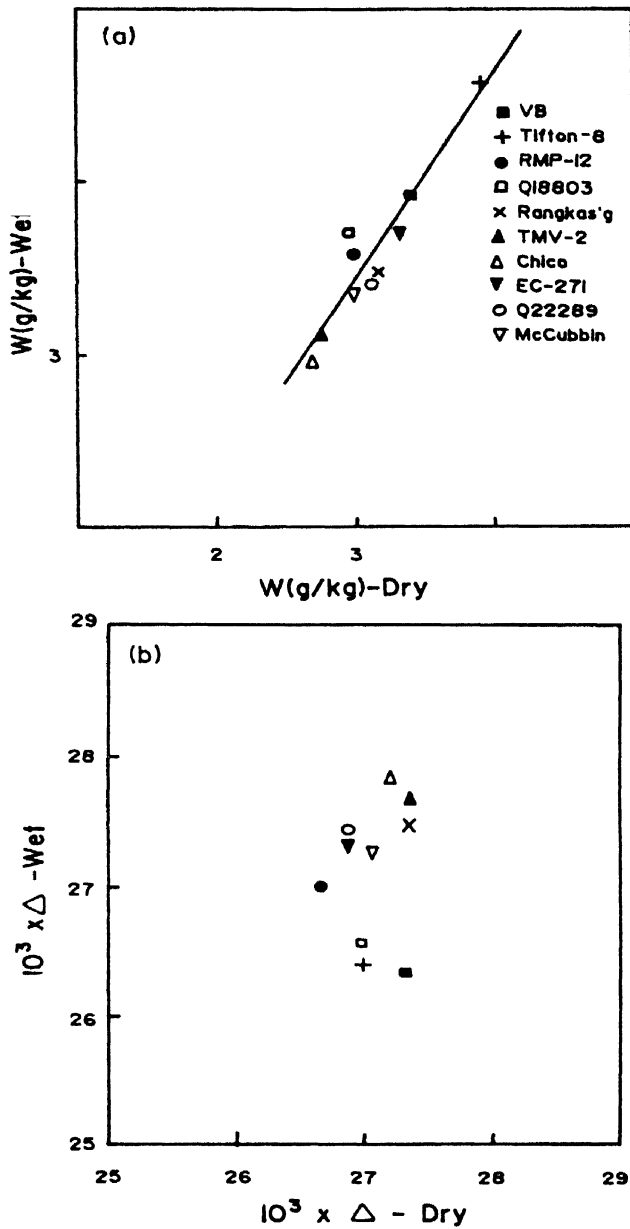
The experimental confirmation that variation in  $W$  exists among peanut cultivars, and that a strong relationship between  $W$  and  $\Delta$  often exists under glasshouse conditions, suggests that  $\Delta$  could be used as a criterion to exploit variation in  $W$  in breeding programs. There are however a number



**Figure 2.** Transpiration efficiency (shoots plus roots) versus carbon isotope discrimination in leaves of 10 peanut cultivars grown in small pots in a glasshouse for (a) well-watered plants and (b) plants droughted from emergence to 50 days after emergence (unpublished data of Wright)

of potential sources of discrepancy between results from glasshouse plants in pots and plants grown under field conditions. For example,

1. There are difficulties in correctly apportioning water use into that lost by transpiration and that lost by evaporation. In field studies there are problems in measuring and estimating soil evaporation, in contrast



**Figure 3.** Transpiration efficiency under well-watered and droughted conditions (a) and carbon isotope discrimination under well-watered and droughted conditions (b) for 10 cultivars grown in small pots in a glasshouse (unpublished data of Wright)

to pots where it can be minimized (Turner, 1986). Complications can also arise from differences between cultivars in the extent and timing of soil evaporation (Condon *et al.*, 1991).

2. There is generally a lack of data on root dry matter in field studies and  $W$  usually is based on aboveground dry matter. Differences among cultivars in apportioning of dry matter to roots and shoots may lead to erroneous comparisons of  $W$  defined on this basis. This error may be particularly large in severe drought conditions where total dry matter accumulation may be dominated by roots.

3. The aerial environment of field canopies is characterized by complex interactions involving transfer of heat and water vapor, and the interactions are different from those around isolated potted plants. Reduced  $W$  of isolated plants that occurs because of reduced stomatal conductance may not necessarily be reflected at the canopy level, if the crop boundary layer conductance is relatively small (Cowan, 1971, 1977, 1988; Jarvis and McNaughton, 1985; Farquhar *et al.*, 1989).

Definitive experiments aimed at assessing variation in  $W$  among peanut cultivars, and the correlation between  $W$  and  $\Delta$ , therefore, need to be conducted in canopies under field conditions. This information is essential in order to ascertain that we are sure  $W$  variation actually exists under field conditions and that  $\Delta$  can be confidently used as a selection criteria for  $W$ . Also, this assessment needs to be conducted under both well-watered and water-limited conditions; as evidence shown in this section indicates, the correlation between  $W$  and  $\Delta$  may break down under severe plant water deficits.

### **III. Peanut Cultivar Variation in Transpiration Efficiency and Correlation with $\Delta$ in Field Canopies**

#### **A. Measurement of $W$ under Field Conditions**

Wright *et al.* (1988) described a minilysimeter facility in combination with a portable rain-out shelter (Hatfield *et al.*, 1989) which allowed an effective and low-cost assessment of plant performance in a canopy situation. It enabled isolation of the root zone, for accurate water application and measurement, and recovery of total root and shoot dry matter.

Briefly, intact soil cores were excavated using a soil-coring machine. As the core was being dug, a PVC storm water pipe (dimensions 0.30 m i.d. 0.31 m o.d. and 0.8 m deep) was slid over the core. After digging, the intact soil core and pipe were lifted aboveground using a gantry device, and a galvanized iron circular cap (1 mm thick) was screwed into the base of the pipe. A 1-mm-thick galvanized iron sheet (0.8 m deep) was then fitted around the circumference of the hole where the core had been removed, to prevent loose soil from falling back into the excavation, and the core was replaced. Plants were then established in and around the minilysimeters to simulate a field canopy. Water loss from pots was estimated by weighing

with an electronic load cell (accuracy of  $\pm 0.1$  kg) mounted on a tractor-driven gantry which straddled the plot area. This facility allowed rapid and repeated measurement of minilyimeter weights and hence transpiration. Soil evaporation was estimated from the changes in water content (weight) of bare soil minilyimeters, adjusted for fractional radiation interception by the canopy (Cooper *et al.*, 1983).

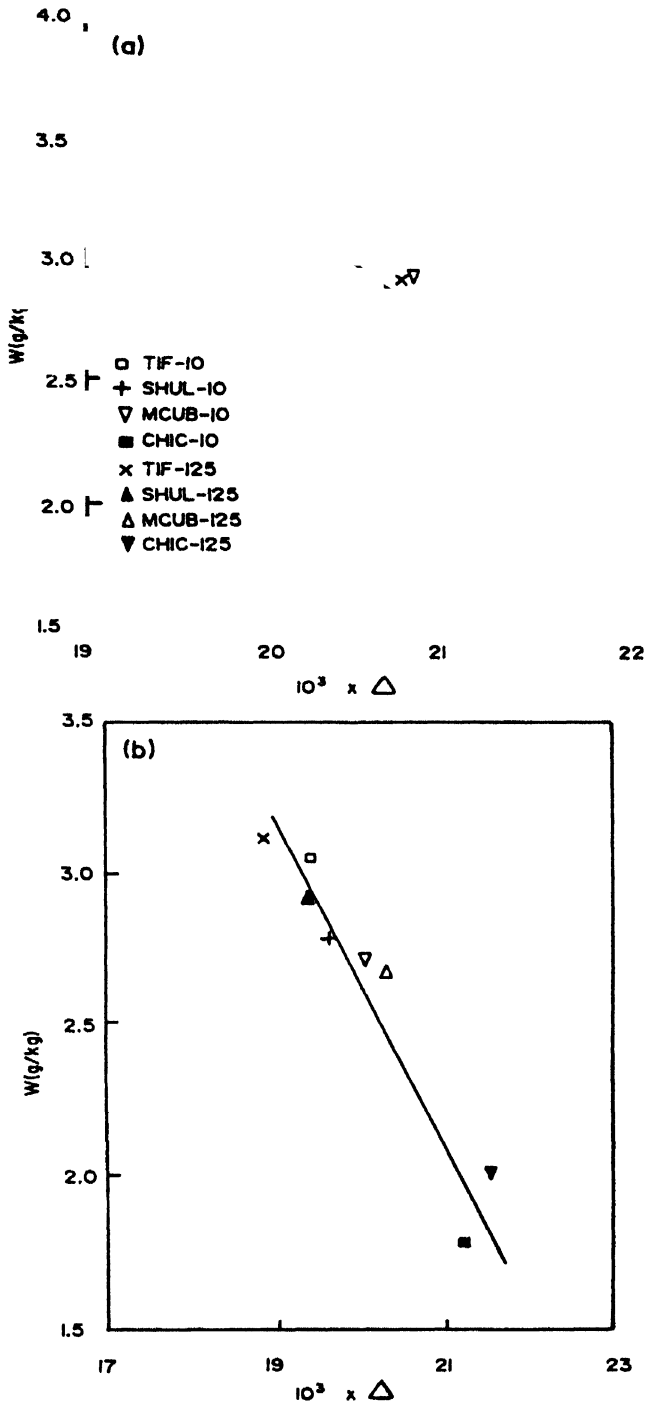
### B. Variation in $W$ under Well-Watered and Water-Limited Conditions

Two large field experiments using the minilyimeter facility described above were conducted to determine whether cultivar differences in  $W$  were occurring in small field canopies. One experiment was conducted under full irrigation (Wright *et al.*, 1988), while the other imposed two levels of soil water deficit (Wright *et al.*, 1993). In both experiments  $W$  was measured only during the period between full canopy development (ca. 45 days after planting, DAP) and early podfilling (ca. 90 DAP). This was done to minimize the effects of soil evaporation and avoid any confounding effects arising from maturity differences among cultivars.

The results from experiments clearly indicates that significant differences in  $W$  existed among peanut cultivars in the field, under both water nonlimiting and limiting conditions (Table I). In general, variation in  $W$  among cultivars was associated with differences in dry matter accumulation rather than to differences in transpiration. This result indicates that photosynthetic capacity, rather than leaf/canopy stomatal conductance, was dominating the  $W$  differences among peanut cultivars.

**Table I** Dry Matter (Including Roots), Transpiration,  $W$  and  $\Delta$  in Peanut Cultivars Grown in Minilyimeters in Field Canopies under Well-Watered Conditions (Wright *et al.*, 1988) and Two Levels of Water-Limited Conditions (Wright *et al.*, 1993)

Study	Cultivar	Biomass (kg)	Water use (kg)	$W$ (g/kg)	$\Delta$ ( $\times 10^3$ )	
Well watered	Tifton-8	63.1	17.0	3.71	19.7	
	VB-81	46.9	16.2	2.90	20.1	
	Robut 33-1	55.3	19.0	2.91	20.8	
	Shulamit	51.6	16.8	3.07	20.8	
	McCubbin	48.6	16.9	2.88	20.8	
	Cianjur	43.4	16.3	2.66	20.9	
	Rangkasbitung	41.6	16.9	2.46	20.9	
	Pidie	47.3	16.6	2.85	20.6	
lsd $P = 0.05$		7.0	1.5	0.3	0.55	
Water limited	(intermittent stress)	Tifton-8	37.5	12.2	3.07	19.4
		Shulamit	35.7	12.8	2.79	19.9
		McCubbin	36.3	13.4	2.71	20.7
		Chico	20.5	11.4	1.80	21.1
	(terminal stress)	Tifton-8	31.3	10.0	3.13	18.6
		Shulamit	29.0	9.9	2.93	18.8
		McCubbin	26.8	10.0	2.68	19.4
		Chico	17.8	8.8	2.20	20.9
lsd $P = 0.05$		5.61	1.90	0.38	0.93	



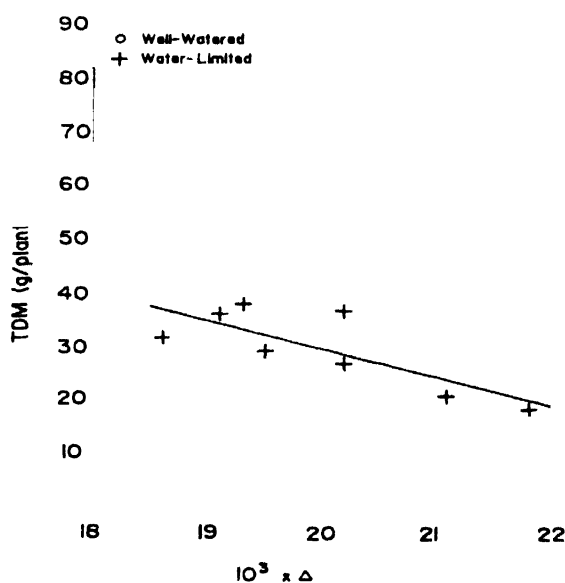
**Figure 4.** Relationship between transpiration efficiency and carbon isotope discrimination under well-watered (redrawn from Wright *et al.*, 1988) and droughted (redrawn from Wright *et al.*, 1993) conditions for a range of peanut cultivars growing in a field.



### C. Correlation between $W$ and $\Delta$ in the Field

Highly significant negative correlations were observed between  $\Delta$  and  $W$  under both well-watered ( $r^2 = 0.67$ ) and water-limited conditions ( $r^2 = 0.92$ ) (Figs. 4a and 4b). These relationships for field-grown peanuts support the suitability of  $\Delta$  as a selection criterion for screening for high  $W$ .

Changes in  $p_i/p_a$ , the ratio of internal  $\text{CO}_2$  concentration in the leaf to ambient  $\text{CO}_2$  concentration and  $\Delta$ , can arise from changes in the balance between leaf stomatal conductance and photosynthetic capacity. Where  $p_i/p_a$  changes are due to stomatal movements, the relationship between  $W$  and  $\Delta$  observed for well-ventilated, isolated leaves may break down in plants grown in canopies in the field because of significant canopy boundary-layer resistances to fluxes of water vapor and heat (Cowan, 1977, 1988; Farquhar *et al.*, 1989). Where  $p_i/p_a$  changes in response to variation in photosynthetic capacity, the problem associated with weak coupling between the crop canopy and atmosphere is not as important, as increased  $p_i/p_a$  and  $\Delta$  arise because of decreased assimilation rate, which causes a relatively small change in the  $\text{CO}_2$  concentration in the air above the canopy and no effect on heat and vapor transfer through the boundary layer. The observation that total dry matter production (TDM) was negatively correlated with  $\Delta$  for the peanut cultivars examined in the field studies of Wright *et al.* (1988, 1993) (Fig. 5) suggests that variation in  $p_i/p_a$  in photosynthetic capacity was the predominant source of variation in  $p_i/p_a$  (and therefore  $\Delta$ ). Indeed, a very



**Figure 5.** Total dry matter (shoots plus roots) versus carbon isotope discrimination in leaves for well-watered (Wright *et al.*, 1988) and droughted (Wright *et al.*, 1993) peanut cultivars growing in a field.

**Table II Regression Equations Relating Total Dry Matter Production (TDM Includes Roots) to  $\Delta$  from a Range of Glasshouse Experiments**

Expt	Fitted regression	$r^2$	Comments	Source
1	TDM = 74.3 - 3.24( $\Delta \times 10^3$ )	0.44	Glasshouse, well-watered	Hubick <i>et al.</i> (1986)
	TDM = 43.6 - 1.95( $\Delta \times 10^3$ )	0.75	Glasshouse, droughted	Hubick <i>et al.</i> (1986)
2	TDM = 687.6 - 26.46( $\Delta \times 10^3$ )	0.84	Glasshouse, well watered, min N	Hubick (1990)
	TDM = 679.9 - 28.70( $\Delta \times 10^3$ )	0.93	Glasshouse, well watered, nodule N	Hubick (1990)
	TDM = 149.5 - 5.61( $\Delta \times 10^3$ )	0.95	Glasshouse, droughted, min N	Hubick (1990)
	TDM = 223.1 - 9.17( $\Delta \times 10^3$ )	0.97	Glasshouse, droughted, nodule N	Hubick (1990)
3	TDM = 364.0 - 16.46( $\Delta \times 10^3$ )	0.84	Glasshouse, well watered, 3 cv	Hubick <i>et al.</i> (1990)
	TDM = 303.0 - 11.85( $\Delta \times 10^3$ )	0.64	Glasshouse, well watered, F2 plants	Hubick <i>et al.</i> (1990)

strong negative relationship between TDM and  $\Delta$  has been observed in peanut cultivars over a wide range of experimental conditions (provided well-watered and droughted treatments are not mixed). Table II summarizes the statistical parameters of this relationship measured in a number of glasshouse studies and shows that extremely strong correlations (range in  $r^2 = 0.44$  to  $0.97$ ) exist over a wide range of environmental conditions.

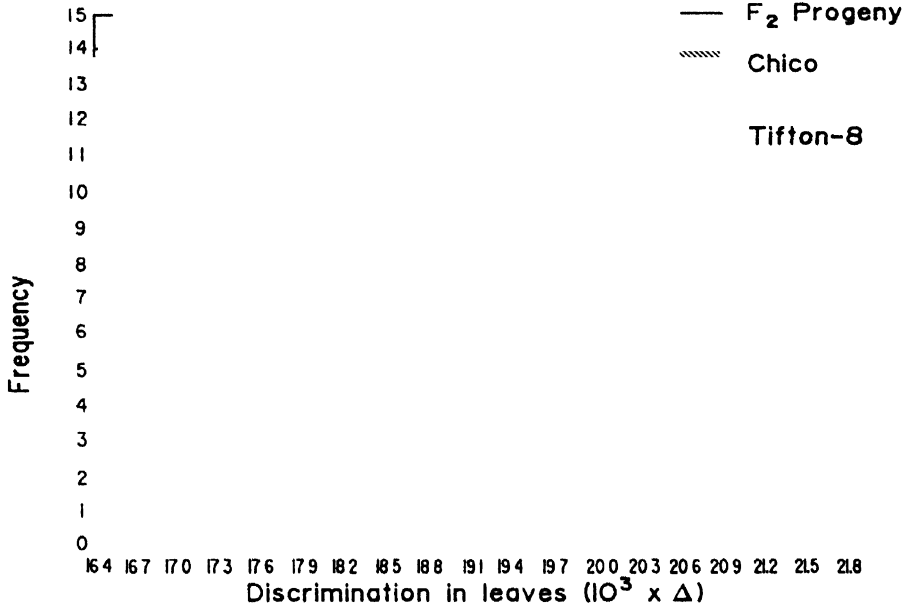
#### IV. Genotype X Environment Interaction and Heritability for $W$ and $\Delta$

Genotype  $\times$  environment interaction for  $W$  appears to be small in peanut. Wright *et al.* (1988) found that although there were large differences in  $W$  and  $\Delta$  in "above-ground" as compared to "in-ground" minilysimeters, cultivar ranking in these parameters was largely maintained across the two contrasting environments. Correlation coefficients ( $r$ ) for  $W$  and  $\Delta$  in in-ground versus aboveground minilysimeters were 0.91 and 0.83, respectively.  $W$  was strongly correlated ( $r^2 = 0.74$ ) with  $\Delta$  under well-watered and droughted environments in the pot study reported earlier (see Fig. 2a) which again indicates there is low genotype  $\times$  environment interaction for  $W$ . Hubick *et al.* (1986, 1988) also reported that the ranking of  $W$  and  $\Delta$  was consistent in a range of cultivars under two contrasting water regimes in glasshouse studies. Hubick (1990) showed that, although  $W$  and  $\Delta$  varied significantly in response to watering treatment and source of nitrogen (mineral N versus nodule N), the ranking of  $W$  and  $\Delta$  was similar under each treatment, again indicating there is low genotype  $\times$  environment interaction for these parameters.

In 16 peanut cultivars grown at 10 sites with widely different rainfall patterns in subtropical and tropical areas of Queensland, Australia, there was significant genotypic variation in  $\Delta$ , with no significant interaction between genotype and environment (Hubick *et al.*, 1988). A broad sense heritability (ratio of genotypic variance to the total or phenotypic variance) or repeatability of  $\Delta$  in this experiment was 81%.

Inheritance of  $\Delta$  was studied in plants grown in pots using crosses of cultivars with contrasting  $\Delta$  and  $W$  (Hubick *et al.*, 1988). The  $F_1$  progeny had  $\Delta$  values similar to those of the low  $\Delta$  cultivar, Tifton-8, and considerably smaller than those of Chico, the high  $\Delta$  cultivar. This response suggests a degree of dominance for small  $\Delta$  or large  $W$  in these genotypes. In the  $F_2$  generation, the distribution of  $\Delta$  exceeded the range between Tifton-8 and Chico, with two  $F_2$  plants having smaller  $\Delta$  values than those of the low  $\Delta$  parent, Tifton-8 (Fig. 6). The  $F_2$  distribution for  $\Delta$  strongly suggested quantitative rather than qualitative inheritance for this trait.

The results from the study of Hubick *et al.* (1988), in combination with the evidence we present here indicating that  $W$  and  $\Delta$  have low genotype  $\times$  environment interaction, suggests that effective selection for  $\Delta$ , and hence  $W$ , could be conducted in a restricted number of environments. Indeed,

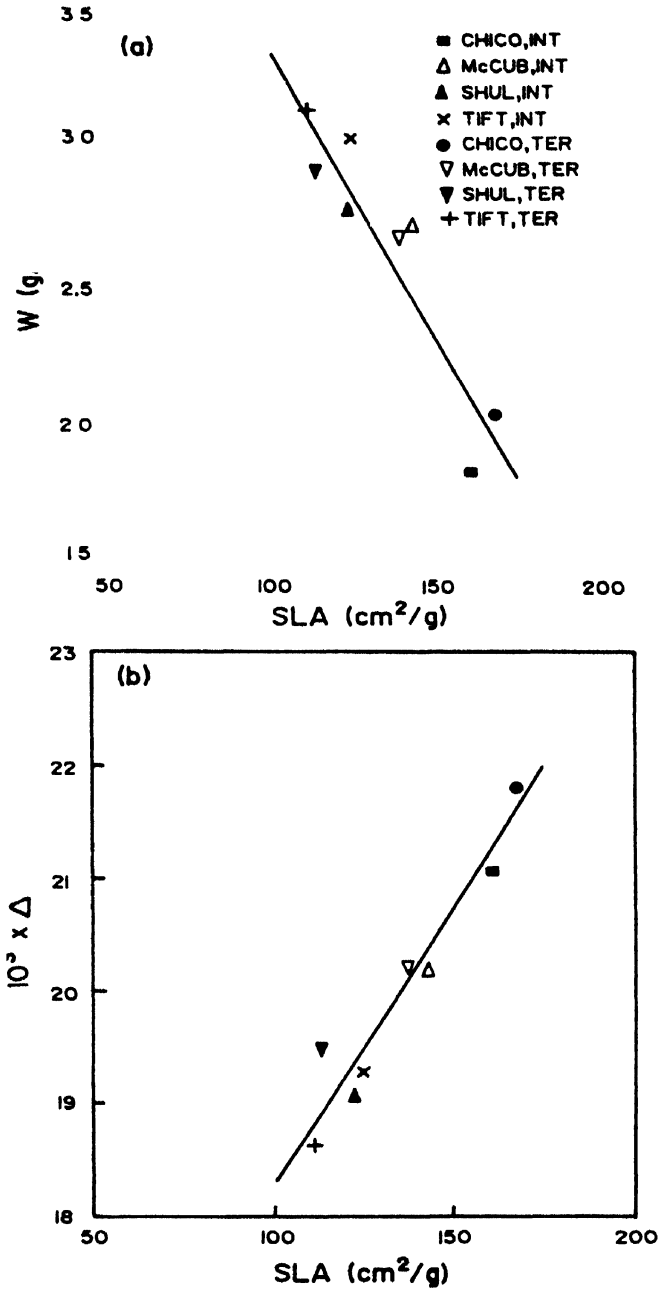


**Figure 6.** Frequency distribution of carbon isotope discrimination in leaves of well-watered plants of peanut cultivars Tifton-8 and Chico and their F<sub>1</sub> and F<sub>2</sub> progeny population grown together in one glasshouse environment (redrawn from Hubick *et al.*, 1988)

the results indicate selection could possibly take place in a single environment, be it well watered or water limited, and in a glasshouse or field situation.

**V. Relationships between Specific Leaf Area, *W*, and  $\Delta$**

It has been observed over many experiments that specific leaf area (SLA, cm<sup>2</sup>/g, which is negatively related to leaf thickness) is closely and negatively correlated with *W* and also that SLA and  $\Delta$  are positively correlated. Examples of the relationships between SLA and *W*, and SLA and  $\Delta$ , measured in the minilysimeter study by Wright *et al.* (1993) are illustrated in Figs. 7a and 7b, respectively. These observations are consistent with our earlier hypothesis that cultivars with high *W* have higher photosynthetic capacity. If it is assumed that the N : C ratio does not vary among cultivars then it is possible that those cultivars with thicker leaves had more photosynthetic machinery and the potential for greater assimilation per unit of leaf area. Indeed, Nageswara Rao and Wright (unpublished observations) have shown that specific leaf nitrogen (gN/m<sup>2</sup>) is linearly related with SLA, such that thicker leaves had higher nitrogen contents (data not shown). Similar relationships between *W* and SLA, and  $\Delta$  and SLA, have been reported



**Figure 7.** Transpiration efficiency versus specific leaf area (a) and carbon isotope discrimination in leaves versus specific leaf area (b) for four peanut cultivars grown under two levels of drought in the field (data derived from Wright *et al.*, 1993)

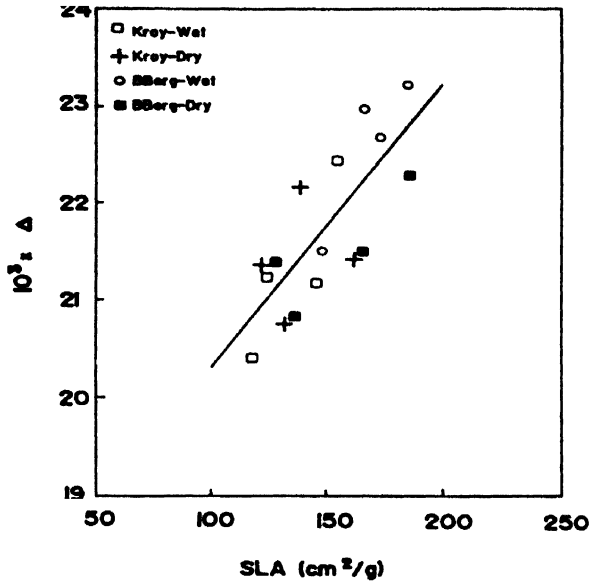
elsewhere (Wright *et al.*, 1988). A highly significant relationship between  $\Delta$  and SLA was also observed for some 300 F<sub>3</sub> plants derived from a single cross of high and low  $\Delta$  Indonesian cultivars grown in the field (Wright *et al.*, 1992). Thus, there is considerable evidence to support the hypothesis that a very strong association between  $\Delta$  and SLA exists. This finding has significant implications for breeding programs, where selection for  $W$  may be practiced, as SLA is simple and inexpensive to measure, compared to the  $\Delta$  measurement, which requires an isotope ratio mass spectrometer.

An experiment has recently been conducted to determine the generality of the SLA relationship with  $\Delta$  by growing four cultivars with contrasting  $\Delta$  in two contrasting temperature environments, under irrigated and rain-fed conditions (Nageswara Rao and Wright, unpublished data). The two sites, Kingaroy and Bundaberg, were similar except for their minimum night temperatures, in that mean minimum temperatures during the season were 16°C at Kingaroy compared to 20°C at Bundaberg. Table III shows how environment, cultivar, and watering regime all influenced the magnitude of SLA and  $\Delta$ . For instance, SLA and  $\Delta$  for each cultivar were significantly higher in the warmer Bundaberg environment, while water deficits associated with the rain-fed treatment tended to reduce SLA and  $\Delta$  for each cultivar but not in Kingaroy. This effect was particularly apparent at Bundaberg where lower rainfall resulted in greater crop water deficits. The data clearly show that leaves of all cultivars became "thicker" in response to low temperature and water deficits, possibly due to effects on leaf expansion and translocation of assimilate from the leaf (Bagnall *et al.*, 1988). Of more interest, however, was the observation that cultivar ranking for SLA and  $\Delta$  remained the same in each environment and watering regime. Analysis of variance indeed showed the main effects of location, irrigation treatments, and cultivar were highly significant ( $P < 0.05$ ) for SLA and  $\Delta$ , while the genotype  $\times$  environment interactions were nonsignificant. These results are consistent with the low genotype  $\times$  environment interactions for  $W$  and  $\Delta$  reported earlier.

The strong correlation between  $\Delta$  and SLA reported previously (Fig. 7b) was again apparent for this data set (Fig. 8) even given the interactions noted above.

**Table III** Specific Leaf Area (cm<sup>2</sup>/g) and  $\Delta$  (%) Measured at Maturity for Four Peanut Cultivars Grown at Two Sites (Bundaberg and Kingaroy) under Two Watering Regimes (Irrigated and Rain Fed)

Site	Treatment	Chico		McCubbin		Shulamit		Tifton	
		SLA	$\Delta$	SLA	$\Delta$	SLA	$\Delta$	SLA	$\Delta$
Kingaroy	Irrigated	155.2	22.44	145.9	21.17	124.0	21.24	117.7	20.40
	Rain fed	138.9	22.15	164.8	21.45	124.9	21.95	132.7	20.77
Bundaberg	Irrigated	184.9	23.21	174.2	22.68	166.8	22.97	148.3	21.50
	Rain fed	186.3	22.29	166.2	21.50	128.5	21.39	136.8	20.84

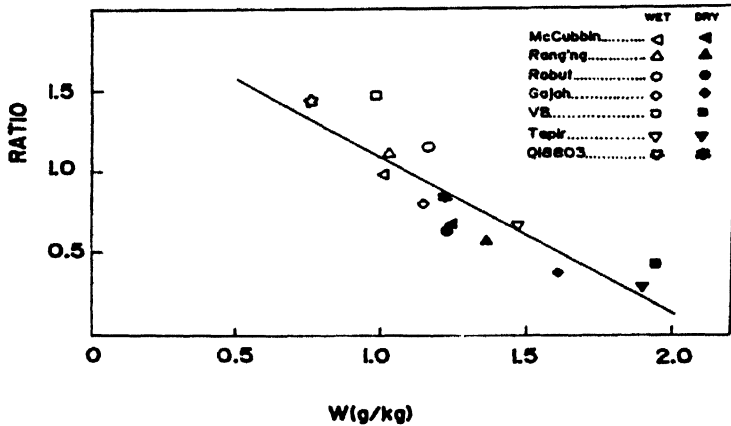


**Figure 8.** Carbon isotope discrimination in leaves versus specific leaf area for four peanut cultivars grown in the field at Bundaberg and Kingaroy, Qld, Australia (unpublished data of Nageswara Rao and Wright)

Interestingly, the data from the contrasting temperature and water-stress environment form a universal relationship. Even the data presented in Fig. 7b, and other data we have measured elsewhere (e.g., Wright *et al.*, 1992), fit well onto this relationship. The physiological mechanisms involved are unknown and need further investigation. The significant application of the relationship is however obvious, in that breeders could use the inexpensively measured SLA, in lieu of  $\Delta$ , to screen for high  $W$  among peanut germplasm within particular environments.

## VI. Negative Association between $W$ and Harvest Index

A number of glasshouse and field experiments have shown that while TDM at maturity was negatively correlated with  $W$  and  $\Delta$ , pod yield was not, suggesting that selection for low  $\Delta$  would substantially increase TDM while having only minimal influence on pod yield improvement (see Hubick *et al.*, 1988; Wright *et al.*, 1988, 1993). An example of the negative relationship between  $W$  and partitioning ratio (calculated as the proportion of total dry matter allocated to pods during the podfilling period) for seven cultivars contrasting in  $W$  characteristics is shown in Fig. 9. The relationship still exists when dry matter is converted to glucose equivalent (to account for



**Figure 9.** Transpiration efficiency versus partitioning ratio (the proportion of total biomass partitioned to pods between early podfill and maturity) for seven peanut cultivars grown under well-watered (open symbols) and droughted (closed symbols) conditions in pots in a glasshouse (unpublished data of Wright).

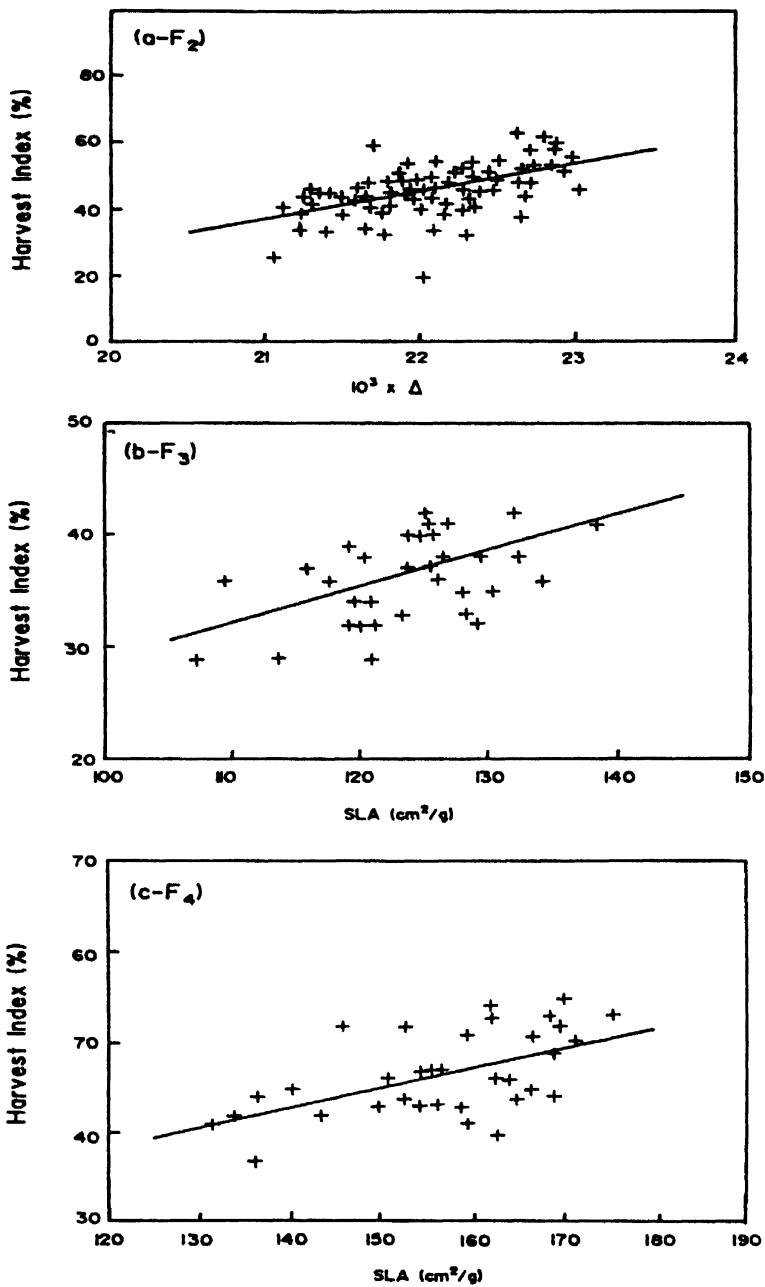
the higher energy costs of synthesizing oil in kernels, data not shown), indicating that the relationship is not an artifact of dry matter energy costs. It is also of interest that Hubick (1990) recently found that much of the increased dry matter produced in plants given mineral N compared to nodulated plants was allocated to leaves, not pods. Thus variation in harvest index (HI) resulted in no correlation between  $W$ , or  $\Delta$ , and pod yield.

The negative association observed between  $\Delta$  and partitioning in peanut may be limited to the particular set of cultivars used in our studies to date. Some preliminary genetic studies have been conducted to determine whether these traits are genetically linked, and whether the linkage could be broken through breeding. In this study (Cruickshank and Wright, unpublished data), a cross between a low  $W$ , high HI Indonesian line (Rangkasbitung) and a high  $W$ , low HI Indonesian line (Tapir) was made. Both these lines were spanish botanical types, with similar maturity of about 120 days in the Kingaroy environment.

The  $F_2$  progeny were grown under well-watered conditions in the glasshouse, and  $W$  (via  $\Delta$ ) and HI were measured at maturity. Figure 10a shows that HI and  $\Delta$  were negatively correlated, although considerable scatter in the relationship suggested crossing may have disturbed the association.

A number of  $F_3$  and  $F_4$  families derived from individual  $F_2$  plants were selected on the basis of low  $\Delta$ , high HI, or the best of both traits and grown in the field under well-watered and rain-fed conditions. Figures 10b and 10c again shown that  $W$  (via SLA measurements) and HI were negatively associated, with no obvious outliers possessing both high  $W$  and high HI. The moderate strengths of the correlation (ca.  $r = -0.55$ ) suggest that concurrent improvement in these traits may be difficult, but should be





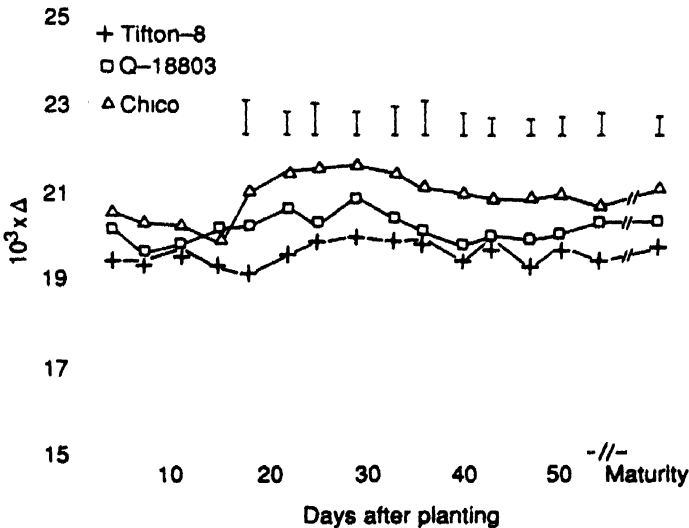
**Figure 10.** Relationship between (a) harvest index and carbon isotope discrimination for  $F_2$  progeny, and harvest index and specific leaf area for  $F_3$  progeny (b) and  $F_4$  progeny (c), derived from a cross between Tapir and Rangkasbitung growing in a well-watered field environment (redrawn from Wright *et al.*, 1992)

possible. The extent of the negative association needs to be investigated using a wider range of peanut germplasm.

### VII. Selection for *W* in Peanut-Breeding Programs

To screen large numbers of lines for *W* would be extremely difficult because of the need to accurately measure both transpiration and total biomass (including roots) under glasshouse or field condition. This is no doubt the major reason why cultivar variation in *W* in a range of species has not been widely demonstrated, or pursued as a selection trait in breeding programs. For maximum effectiveness in developing cultivars with improved *W*, selection should be conducted in the large segregating heterogeneous populations that occur at various stages of a breeding program. The results of numerous studies which have been reviewed here indicate that  $\Delta$  or SLA could be used to effectively select for *W* in such large populations.

Hubick *et al.* (1986) found that  $\Delta$  of all plant components were highly correlated with the  $\Delta$  of leaf material. It is therefore considered that  $\Delta$  in leaves should provide a reasonable guide to select peanut cultivars for improved *W*. Hall *et al.* (1993) cautioned that  $\Delta$  may be different in plant material produced during stress periods, so sampling procedures would need to be developed to account for this effect. In terms of purely seeking improved *W* there may be an advantage in selecting for low  $\Delta$  (or low SLA)



**Figure 11.** Change in carbon isotope discrimination in leaves and error variation with time for well-watered plants of cultivars Tifton-8, Q18803, and Chico grown in a glasshouse (redrawn from Wright *et al.*, 1992).

under well-watered conditions, so as to minimize potential drought effects on  $\Delta$ .

The question of how early in a plant's life cycle  $\Delta$  (or SLA) could be selected for and still represent its  $W$  characteristics is also pertinent in relation to selection in a breeding program. Figure 11 shows the temporal change in  $\Delta$  at four daily intervals until 54 days after emergence (and also at maturity). It is clear that after about 15 days after emergence,  $\Delta$  remains very constant. A similar procedure (at two weekly intervals) was also carried out for four cultivars in a field experiment under well-watered and droughted conditions (Wright *et al.*, 1991). There was no significant interaction for  $\Delta$  between irrigation treatment and time of sampling for the four cultivars. Based on these observations, the stability of  $\Delta$  throughout crop ontogeny indicates that selection could take place very early during crop development.

### VIII. Summary

Significant variation among peanut cultivars in transpiration efficiency ( $W$ ) under well-watered and water-limited conditions has been shown in isolated plants in the glasshouse and in small canopies in the field. There is considerable scope for  $W$  improvement in currently grown commercial cultivars.  $W$  was shown to be highly correlated with carbon isotope discrimination in leaves ( $\Delta$ ), and also with specific leaf area (SLA), or leaf thickness.

Genotype  $\times$  environment interaction for  $W$ ,  $\Delta$ , and SLA was shown to be very low, while heritability of  $\Delta$  was high, indicating that these traits could be used for selecting high  $W$  in peanut-breeding programs. The results indicate that selection could take place in a single environment, be it well watered or water limited, and in a glasshouse or field situation.

A worrying negative association between  $W$  and partitioning of dry matter to pods among peanut cultivars is apparent. Preliminary genetic studies aimed at assessing whether the association is due to a genetic linkage indicated that the negative association persisted up to the  $F_4$  generation in a cross of two contrasting Indonesian peanut cultivars. Further research aimed at identifying cultivars with high levels of both  $W$  and harvest index is warranted.

Based on our observations to date, it would seem that selection for low  $\Delta$  or SLA in peanut may be appropriate in certain water-limited cropping systems, for instance in developing countries, where both pod yield for human consumption and vegetative yield for animal fodder need to be maximized. In cropping systems where pod yield is of primary concern, breeders will need to be aware of the potential negative association between harvest index and  $\Delta$  in any breeding program incorporating  $\Delta$  as a selection trait.

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