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Crop growth, water-use efficiency and carbon isotope discrimination in groundnut (*Arachis hypogaea* L.) genotypes under end-of season drought conditions*

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Summary

Ten groundnut genotypes were grown under adequately irrigated conditions or subjected to drought during the pod filling phase (83–113 days after sowing) in a medium deep Alfisol at the ICRISAT Centre during the 1986–1987 post-rainy season Crop growth was measured in both treatments but transpiration (*T*) and water-use efficiency (*W*) were quantified only in the drought treatment Leaf samples from both treatments were assayed for discrimination against $^{13}CO_2$ fixed in leaves (Δ) to examine the relationships between Δ crop growth and *W* under field conditions

The shoot dry matter accumulated during the period of drought (*Y*) ranged from 72–150 g m^{-2} and was closely related to transpiration This indicates scope for selection of traits and practices to increase *T* Water-use efficiencies ranged from 1 38–2 50 g kg^{-1} and were inversely related to Δ in eight out of the 10 genotypes For the other two genotypes there was evidence that *T* was under-estimated by field measurements Water-use efficiency and transpiration were not correlated suggesting that these two traits might be combined through breeding Variation between genotypes was greatest for the partitioning of total dry matter to pods (73%) followed by water-use efficiency (31%) and transpiration (29%) Crop growth rates were negatively related to Δ under irrigated conditions but not under drought

Key words *Arachis hypogaea* crop growth rates, partitioning, transpiration, carbon isotope discrimination, water-use efficiency

Introduction

Groundnuts (*Arachis hypogaea* L) are grown predominantly as a rainfed crop in the semi-arid tropics, where season length is variable (Virmani & Piara Singh, 1986) and end-of season drought is common To improve and stabilise yields in drought prone areas, there

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is a need to identify genotypes with superior performance during drought. To develop techniques to screen genotypes for drought tolerance, it is necessary to understand the physiological and genetic factors contributing to crop productivity under drought.

Dry matter production (Y) is linearly related to the amount of water transpired (T) (de Wit, 1958) suggesting that water-use efficiency (W) (defined as the ratio of dry matter produced to amount of water transpired) is constant during growth. However, early work showed variation in W between and within species (Briggs & Shantz, 1913, 1914). Thus, $Y = T \times W$, and pod yield, Yp, is then the product of $T \times W \times p$ where p is the dry matter partitioning ratio (Duncan, McCloud, McGraw & Boote, 1978). The parameters, T, W and p can be used to describe differences in performance of genotypes in a given environment.

However, information on variability for the above parameters in groundnut germplasm is limited. Mathews *et al.* (1988*a*) and Mathews, Harris, Williams & Nageswara Rao (1988*b*) observed that in a prolonged drought that commenced early in the life of the crop, four groundnut cultivars had large differences in Yp that were associated with differences in harvest index (H). No differences were observed among the four cultivars for T, but the differences in Y were associated with W.

Recently, significant variability was reported for W in groundnut genotypes grown in pots under glasshouse (Hubick, Farquhar & Shorter, 1986) and canopy situations (Wright, Hubick & Farquhar, 1988). However, estimates of W in the pot experiments are derived from situations where water available to the root system is fixed and controlled. In the field conditions, water availability varies both temporally and spatially depending on soil characteristics, the distribution of roots and their efficiency in extracting available water.

Water-use efficiency was shown to be negatively related to the discrimination against $^{13}CO_2$ fixed in leaves, Δ, in various crop species (Farquhar, Ball, Von Caemmerer & Roksandic, 1982*a*; Farquhar & Richards, 1984) including groundnut (Hubick *et al.*, 1986; Wright *et al.*, 1988), suggesting a potential use of Δ as a technique to identify genotypes with larger W. The link between Δ and W in groundnut cultivars grown in a glasshouse (Hubick *et al.*, 1986) and field (Wright *et al.*, 1988) under non-limiting conditions was suggested to be associated with the photosynthetic capacity per unit leaf area. However, information is limited on the use of Δ to estimate W, and the relationship between Δ and crop growth under drought conditions in the field.

The objectives of this study were (a) to investigate variability in 10 groundnut genotypes for Y, T, W and p under end-of season drought conditions, and (b) to examine the relationship between Δ and W.

Materials and Methods

A field experiment was conducted at the ICRISAT Centre in central India during the 1986–87 post-rainy season (November to April) on a medium deep Alfisol with a water-holding capacity of 100 mm in a 120 cm profile. Basal applications of 18 kg N ha^{-1} and 20 kg P ha^{-1} were incorporated into the soil when the land was prepared into broad beds of 1.2 m width separated by 30 cm furrows (Krantz, Kampen & Virmani, 1978). Ten groundnut genotypes with known responses to end-of season drought were sown in a split-plot design with four replications, with an irrigated control and drought treatments as main plots, and the genotypes as sub-plots. Seeds, treated with Captain and Thiram† both at a rate of 3 g kg^{-1} of seed, were hand-sown on 2 December 1986 at 10 cm intervals in four rows, 30 cm apart on each bed. Each plot consisted of three broad beds (12 rows) of 6 m length.

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†Mention of commercial products or companies does not imply endorsement or recommendation by ICRISAT over others of similar nature.

After sowing, the field was sprayed with a pre-emergence herbicide (Alachlor at 1.75 kg a.i. ha^{-1}) and irrigated uniformly by sprinklers. Thereafter, all plots received sprinkler irrigation (50 mm) at 10-day intervals until February, and at weekly intervals from March to match the increasing evaporative demand. From 85 until 113 days after sowing, irrigation was withheld from the drought treatments, whilst the control plots continued to receive regular irrigation. Plant protection measures were followed as and when necessary to control pests and diseases.

Growth analysis

Plants were sampled from 0.75 m^{-2} ground area in each plot at 30, 60, 85, 90, 97, 105 and 113 days after sowing. Sub-samples of three plants were selected at random from each sample and their green leaf areas measured using a leaf-area meter (LICOR 3100). Green leaf area index (LAI) was calculated by dividing the total leaf area of the sample by ground area harvested.

Weights of leaves, stems and pods were measured after oven-drying at 80°C for 24 h. The dry matter (Y) accumulated during the drought period was estimated as the difference in crop (vegetative + pod) dry matter between 85 and 113 days after sowing. Crop and pod growth rates were estimated from linear regression involving the five sequential harvests during the treatment period. Pod weights were adjusted for their high energy content using a coefficient of 1.65 (Duncan *et al.*, 1978). The partitioning factor (p) was then calculated as the ratio of pod growth rate to crop growth rate during the treatment period.

Water balance

Measurements of evaporation from a Class A open pan were obtained from the ICRISAT meteorological station situated 1 km from the experimental site.

Changes in the soil water content were monitored in the dry treatment. Two neutron probe access tubes (40 mm diameter) per plot were installed to 120 cm depth at the seedling stage. Penetration of access tubes beyond this depth was prevented by a hard pan. Changes in volumetric water content in the soil at 15 cm depth increments were measured at weekly intervals during the drought period using a neutron scanner (Troxler) calibrated against gravimetric measurements in the same field. For convenience of expression of soil water content, the 120-cm soil profile was divided into four horizons of 30 cm each.

Transpiration, T was computed using a simple water balance model, i.e.

$$T = R + I \pm cM - Es$$

where R = rainfall, I = irrigation, and cM = change in the stored soil moisture in 120 cm profile and Es = soil evaporation. The R and I were nil during the drought period. Water loss by drainage from the lowest horizon measured was assumed negligible because there was no increase in water content in the 105–120 cm soil profile following irrigation at 85 days after sowing. Soil evaporation was estimated using the revised version of the soil water balance model (Ritchie, 1972), assuming that the daily soil evaporation depends more on soil hydraulic properties once the crop achieved full ground cover (LAI > 3), i.e.

$$Es = Ct^{1/2} - C(t - 1)^{1/2}$$

where t is the number of days after the last irrigation in the dry treatment, C is a coefficient for soil water transmitting properties which is 2.5 mm day^{-1} for the Alfisol at the ICRISAT Centre. Es was similar in all plots (since the crop achieved full ground cover (LAI = > 3) by the time drought commenced) for the first 5 days following irrigation at 85 days after sowing, after which it was reduced to negligible amounts. Transpiration was calculated as the difference between *cM* measured using a neutron probe and the *Es*. Water-use efficiency was calculated as the ratio of crop dry matter and transpiration during the treatment period.

Leaf transpiration measurements were made in the drought treatment on single leaves for only four genotypes, i.e. ICG 2716, ICGV 86707, ICGV 86635 and ICG 221 using a portable infra-red gas analyser (ADC model) attached to a Parkinson leaf chamber. These measurements were made between 1100 and 1200 h at 3 or 4-day intervals on fully expanded leaves (usually the 3rd leaf from the apex) of three plants selected randomly in each plot. Photosynthetically active radiation during the period of measurement ranged from 1650 to 1790 μmol m^{-2} s^{-1}.

Assay for carbon isotope composition

The leaf samples for carbon isotope analysis were collected from the plants harvested for growth analysis at 113 days after sowing from both the control and drought treatments. The leaves were oven-dried at 80°C for 48 h and ground to pass through a 100 μm sieve. Carbon isotope composition was analysed at the Research School of Biological Sciences, Australian National University, Canberra, as described by Hubick *et al.* (1986).

Results

Weather

The weekly mean minimum and maximum air temperatures at the beginning of the season were 15°C and 27°C (± 3°C), but increased to about 25°C and 37°C (± 3°C) respectively, by the end of the season. Incident radiation was 20–22 MJ m^{-2} day^{-1} during the growing season. The vapour pressure deficit (VPD) followed a diurnal trend, reaching a peak between 1230 and 1430 h. The VPD at mid-day ranged from 1.5 kPa at 85 days after sowing to 3.0 kPa at 113 days after sowing. The high VPD and radiation associated with soil water deficit imposed in the drought treatment from 85 days after sowing resulted in a severe drought condition.

Leaf area

The leaf area index (LAI) increased linearly with time in all genotypes. By 85 days after sowing, the mean LAI was about 3.5 with extremes ranging from about 3 in ICG 476 to 4 in ICGV 86707. Under irrigated conditions, mean LAI increased to 5 by 113 days after sowing, but under drought, a mean LAI of about 3.5 was maintained up to 95 days after sowing followed by a reduction to less than 3 by 113 days after sowing. However, the decline in the LAI in response to drought was variable across genotypes. For example, in ICG 476, LAI decreased rapidly from about 3 to less than 1 in response to drought, whilst ICGV 86707, ICGV 86635 and ICGV 86644 maintained larger LAI of more than 3 during drought. The LAI of other genotypes ranged from 2 to 2.8 at 113 days after sowing.

Crop growth, transpiration and water-use efficiency

The dry matter, *Y* produced by cultivars during drought (85–113 days after sowing) ranged from 72 to 150 g m^{-2} while *T* during the same period ranged from 48 to 68 mm (Table 1). Crop dry matter produced during the drought was positively related to *T* for eight out of 10 genotypes (Fig. 1). ICGV 86635 and ICGV 86644 deviated from this relationship for reasons explained later. Excluding these two genotypes, the relationship between *Y* and *T* was linear ($y = -39.7 + 2.15x$; $r = 0.88$, $P < 0.01$).

Table 1. *Crop dry matter production (Y, g m^{-2}), transpiration (T, mm), water-use efficiency (W, g kg^{-1}), coefficient of partitioning of dry matter to pods (p), and the carbon isotope discrimination ($\Delta \times 10^3$), of 10 groundnut genotypes under drought conditions (85–113 days after sowing)*

Genotype	Y	T	W	p	Δ
ICG 1697	96	62	1.62	0.93	18.69
ICG 2716	119	67	1.78	0.77	18.64
ICGV 86707	133	66	2.01	0.56	18.85
ICG 221	107	56	1.90	0.86	18.83
ICGV 86635	150	59	2.50	0.93	19.09
ICGV 86644	126	53	2.38	0.68	18.87
ICG 476	74	48	1.54	0.97	18.99
ICG 2738	99	68	1.44	0.97	19.19
ICG 5305	84	54	1.38	0.95	19.04
ICGV 86743	72	50	1.43	0.65	18.97
S.E.M. (D.F. = 39)	±11.2	±6.2	±0.18	±0.18	±0.22

Water-use efficiency ranged from 1.38 to 2.50 g kg^{-1}, representing a significant variability (31%) among genotypes for this parameter (Table 1). ICGV 86635 and ICGV 86644, had especially large W values, i.e. 2.50 and 2.38 g kg^{-1}, respectively. From the leaf transpiration measurements, it was apparent that ICGV 86635 maintained a higher rate of transpiration in spite of larger LAI (> 2.7) than the other three cultivars during the period of drought

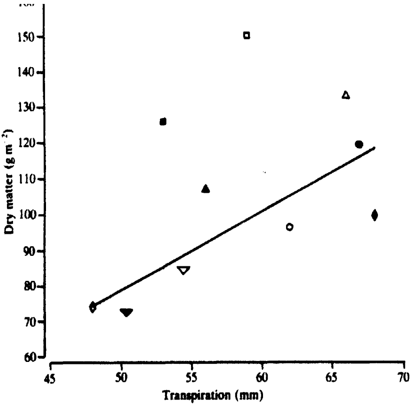

Fig. 1. Relationship between dry matter production during the period of drought, 85–113 days after sowing and transpiration of 10 groundnut genotypes. ○ = ICG 1697, ● = ICG 2716, △ = ICGV 86707, ▲ = ICG 221, □ = ICGV 86635, ■ = ICGV 86644, ◇ = ICG 476, ◆ = ICG 2738, ▽ = ICG 5305, ▼ = ICGV 86743.

Table 2. *Leaf area indices and single leaf transpiration rates (g H_2O dm^{-2} h^{-1}) of 10 groundnut genotypes during the drought*

	Days after sowing			
	98	102	109	112
Genotype		Leaf area index		
ICG 2716	2.5	2.4	ND†	2.4
ICGV 86707	3.3	3.0	ND	2.7
ICG 221	3.0	2.4	ND	2.2
ICGV 86635	3.2	3.0	ND	2.9
ICGV 86644	2.9	2.8	ND	2.7
S.E.M. (D.F. = 19)	±0.09	±0.04	—	±0.11
Genotype		Transpiration rate		
ICG 2716	0.9	0.7	0.3	0.3
ICGV 86707	0.8	1.3	0.6	0.4
ICG 221	0.8	1.5	0.6	0.4
ICGV 86635	0.9	1.0	1.0	0.8
ICGV 86644	ND	ND	ND	ND
S.E.M. (D.F. = 15)	±0.20	±0.22	±0.13	±0.10

†ND = Not determined.

(Table 2), suggesting sufficient supply of water by the roots. However, the higher transpiration rate of ICGV 86635 was not proportional to total water extraction in the 120-cm soil profile. Transpiration measurements were done during mid-day and it is possible that there could be temporal differences among genotypes for transpiration. The total amount of water extracted by ICGV 86635 from the measured profile was, in fact, less than either ICGV 86707 and ICG 2716 (Table 1), which generally had lower transpiration rates during the end-of drought period (Table 2). This observation suggested that water extraction from beyond the 120-cm soil profile by ICGV 86635 might have resulted in an underestimation of *T* (overestimation of *W*). Leaf transpiration rates were not measured for ICGV 86644, but maintenance of larger LAI, no visual signs of canopy wilting during the drought, and the deviation from the relationship between *Y* and *T* also indicate that water may have been extracted from deeper soil layers. Excluding these two deviating points, the variability (between the worst and the best genotypes) for *W* was 31%.

Water extraction pattern

During the drought period, about 25% of total water was extracted from 0–30 cm horizon (Table 3). In general, there was less water extraction from the 30–60 cm horizon, while water uptake from the 60–90 and 90–120 cm horizons accounted for 26% and 30%, respectively, of the total water extraction during drought. The variability in genotypes for water extraction was greater from 90–120 cm, than that from the upper horizons. For example, ICG 476 extracted only 9 mm of water from 90–120 cm depth, whilst ICG 1697, ICGV 86635 and ICG 2738 extracted about 20 mm indicating a significant variability amongst genotypes for efficiency in soil water extraction.

Crop growth rate and partitioning

Under irrigated conditions crop growth rates ranged from 12 to 17 g m^{-2} day^{-1} declining to 2 to 8 g m^{-2} day^{-1} under drought. Pod growth rates ranged from 6 to 8 g m^{-2} day^{-1} under irrigated conditions and from 2 to 4 g m^{-2} day^{-1} under drought.

Table 3. *Amount of water (mm) used from different soil horizons by 10 groundnut genotypes during the drought period (85–113 days after sowing)*

Genotype	Soil horizons			
	0–30	30–60	60–90	90–120 cm
ICG 1697	14	11	17	20
ICG 2716	20	12	19	16
ICGV 86707	16	13	18	18
ICG 221	12	9	15	19
ICGV 86635	16	10	14	20
ICGV 86644	12	10	16	16
ICG 476	13	13	13	9
ICG 2738	18	10	20	21
ICG 5305	16	12	16	18
ICGV 86743	13	9	12	17
Mean	14	11	16	17
S.E.M. (D.F. = 39)	±2.2	±1.6	±2.1	±2.5

Partitioning (p) of dry matter to pods during the drought period ranged from 0.56 in ICGV 86707 to more than 0.95 in early maturing genotypes, ICG 476, ICG 2738 and ICG 5305 representing a maximum variability (73%) amongst genotypes for p.

Relationship between water-use efficiency, crop growth rate and Δ

Water-use efficiency, which ranged from 1.2 to 2.5 g kg^{-1} among genotypes was negatively correlated with Δ in eight out of 10 genotypes ($y = 16.6 - 0.79x$; $r = -0.66$, $P < 0.05$, Fig. 2). ICGV 86635 and ICGV 86644 deviated from this relationship presumably, because of overestimation of W.

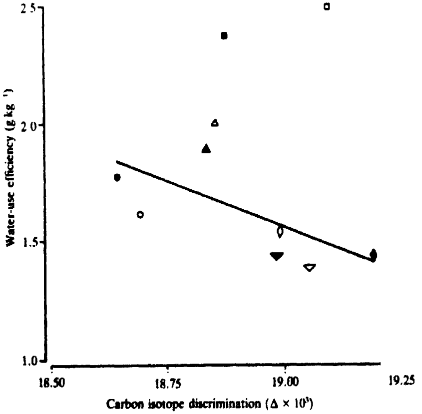

Fig. 2. Correlation between carbon isotope discrimination and water-use efficiency in 10 groundnut genotypes. Symbols are as in Fig. 1.

Crop growth rates were negatively related to Δ under irrigated conditions ($y = 82.6 \cdot 3.6x$; $r = -0.81$, $P < 0.01$, Fig. 3*a*), but not under drought conditions (Fig. 3*b*). However, there was no relationship between Δ and pod growth rates under irrigated conditions (Fig. 3*c*), but a trend of a positive relationship between Δ and pod growth rates was apparent under drought conditions ($y = -17.8 + 1.097x$; $r = 0.54$, Fig. 3*d*).

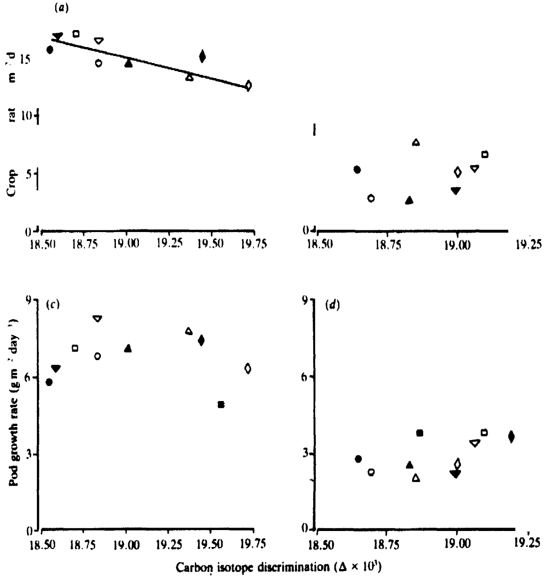

Fig. 3. Relationship between carbon isotope discrimination and, crop growth rates (*a* and *b*) and pod growth rates (*c* and *d*) of 10 groundnut genotypes under irrigated and drought conditions. Symbols are as in Fig. 1.

The pod filling phase is most sensitive to drought in groundnut (Pallas, Stansell & Koske, 1979; Boote, Stansell, Schubert & Stone, 1982; Nageswara Rao *et al.*, 1985). Any strategy to alleviate drought effects during pod filling will be of importance to farmers in the semi-arid tropics. Early maturing genotypes may escape end-of season drought, but the early maturity may not always be successful in overcoming drought effects under unpredictable rainfall situations. Drought occurring during the pod filling phase of an early maturing cultivar may result in a major crop loss (e.g., ICG 476 in the present study). Thus, it is necessary to include drought tolerance as an important objective in crop improvement for rainfed agriculture.

In the present study, high temperatures (> 35°C), high VPD (2 to 3 kPa), and large leaf areas (with LAI > 3.5) at the onset of drought favoured rapid development of drought stress. LAI declined in response to drought particularly in the case of ICG 476, due to leaf drying and senescence.

Genotypic differences existed for *T* and *W* during the drought period (Table 1). The differences in *T* accounted for over 75% of variability in *Y* under drought conditions (Fig. 1), suggesting that yields can be improved by traits and practices that increase transpiration. However, variability in *T* was mainly due to differences among genotypes to extract soil water from various depths during the drought period (Table 3). Ketring (1984) observed significant variation in groundnut genotypes for rooting.

Water-use efficiency of genotypes ranged from 1.3 to 2.5 g kg^{-1}, with two genotypes (ICGV 86635 and ICGV 86644) deviating from the general relationship between *Y* and *T* (Fig. 1) and from that between *W* and Δ (Fig. 2). Greater transpiration coupled with larger leaf area indices during drought (Table 3) suggested that the larger estimates of *W* for these two genotypes were presumably due to an underestimation of transpiration in the field experiment. Except for these two deviations, *W*s of the genotypes (1.3–1.9 g kg^{-1}) were comparable with those measured by other workers (Mathews *et al.*, 1988*a*; Wright *et al.*, 1988). Water-use efficiency of ICGV 86635 and ICGV 86644 estimated using the Δ (from the regression equation of Fig. 2) was 1.52 and 1.69 g kg^{-1} respectively.

Dry matter produced by a crop is a product of *T* and *W*. These two factors should however be at their optimum levels to achieve greater yields under water-limiting conditions. The lack of relationship between *T* and *W* in the present study (Table 1) suggests scope for selecting and combining genotypes with greater *T* and *W*. However, selection of genotypes for *T* and *W* from the field is difficult. Farquhar *et al.* (1982*a*) and Farquhar, O'Leary & Berry (1982*b*) demonstrated a negative relationship between Δ and the transpiration efficiency (mmol C/mol H_2O) of C_3 plants. Experiments with potted plants showed the expected negative relationship between Δ and *W* in various crops (Farquhar & Richards, 1984; Hubick *et al.*, 1986; Wright *et al.*, 1988). The present study provides evidence of a negative relationship between Δ and *W* ($r = -0.66$, $P < 0.05$) under drought conditions in the field. However, the relationship between these two parameters was not as strong in the field as it was in pot experiments (Hubick *et al.*, 1986). The weaker relationship between *W* measured in the field (relative to the pot experiments) and Δ could be due to (a) less precise measurement of *T*, and (b) lack of accounting for root dry matter in field experiments.

A strong negative correlation between Δ and crop growth rates under irrigated conditions (Fig. 3) suggests yet another application of the carbon isotope technique, i.e. to select for greater water-use efficiency and crop growth rates under irrigated conditions (Wright *et al.*, 1988). Carbon isotope discrimination under non-limiting conditions, might be closely linked with crop growth *via* photosynthetic rate per unit leaf area (Hubick *et al.*, 1986). Lack of association between Δ and crop growth rate under drought conditions (Fig. 3*b*) could be due to (a) a shift in allocation of carbon to roots (which were not included in the estimation of crop dry matter) and pods, and (b) loss of assimilated carbon through increased respiration under drought conditions (McCree, 1986).

Lack of relationship of Δ and *W* with crop growth rates under severe drought conditions suggest that other factors (like *T*) might play a dominant role in contributing to productivity under severe drought conditions (Wright, Hubick & Farquhar, 1991). The intensity of drought required to affect the relationship between Δ and crop growth rate was unclear in the present study. However, *W* as a trait is desirable to take advantage of periods with variable water supply under unpredictable rainfall conditions.

Selection for "earliness" is considered as the best strategy in areas prone to end-of-season drought (Nageswara Rao, Williams & Murari Singh, 1989). However, the present study provides evidence for variability among genotypes with similar maturity for *T*, *W* and *p* suggesting a scope for selection of genotypes for these traits and combining to maximise the productivity in drought-prone environments.

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