Efficiency of physiological trait-based and empirical selection approaches for drought tolerance in groundnut

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Summary

Drought is the major abiotic constraint affecting groundnut productivity and quality worldwide. Most breeding programmes in groundnut follow an empirical approach to drought resistance breeding, largely based on kernel yield and traits of local adaptation, resulting in slow progress. Recent advances in the use of easily measurable surrogates for complex physiological traits associated with drought tolerance encouraged breeders to integrate these in their selection schemes. However, there has been no direct comparison of the relative efficiency of a physiological trait-based selection approach (*Tr*) *vis-à-vis* an empirical approach (*E*) to ascertain the benefits of the former. The genetic material used in the present study originated from three common crosses and one institute-specific cross from four collaborating institutes in India (total seven crosses). Each institute contributed six genotypes and each followed both the *Tr* and *E* selection approaches in each cross. The field trial of all selections, consisting of 192 genotypes (96 each *Tr* and *E* selections), was grown in 2000/2001 in a 4 × 48 alpha design in 12 season × location environments in India. The selection efficiency of *Tr* relative to *E*, RE_{Tr}, was estimated using the genetic concept of response to selection. Based on all the 12 environments, the two selection methods performed more or less similarly ($RE_{Tr} = 1.045$). When the 12 environments were grouped into rainy season and post-rainy season, the relative response to selection in *Tr* method was higher in the rainy than in the post-rainy season ($RE_{Tr} = 1.220$ *vs* 0.657) due to a higher genetic variance, lower G × E, and high h^2. When the 12 environments were classified into four clusters based on plant extractable soil-water availability, the selection method *Tr* was superior to *E* in three of the four clusters ($RE_{Tr} = 1.495$, 0.612, 1.308, and 1.144) due to an increase in genetic variance and h^2 under *Tr* in clustered environments. Although the crosses exhibited significant differences for kernel yield, the two methods of selection did not interact significantly with crosses. Both methods contributed more or less equally to the 10 highest-yielding selections (six for *E* and four for *Tr*). The six *E* selections had a higher kernel yield, higher transpiration (T), and nearly equal transpiration efficiency (TE) and harvest index (HI) relative to four *Tr* selections. The yield advantage in *E* selections came largely from greater T, which would likely not be an advantage in water-deficient environments. From the results of these multi-environment studies, it is evident that *Tr* method did not show a consistent superiority over *E* method of drought resistance breeding in producing a higher kernel yield in groundnut. Nonetheless, the integration of physiological traits (or their surrogates) in the selection scheme would be advantageous in selecting genotypes which are more efficient water utilisers or partitioners of photosynthates into economic yield. New biotechnological tools are being explored to increase efficiency of physiological trait-based drought resistance breeding in groundnut.

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Introduction

Groundnut is one of the principal oilseed crops in the world. It is a self-pollinated, amphidiploid legume with 2n = 40 (x = 10). It is cultivated on 25.9 million ha with a total production of 34.5 million t and an average productivity of 1.33 t ha^{-1}. Developing countries, where groundnut is grown mostly under rainfed conditions, account for 96.9% of the world groundnut area and 93.8% of total production (FAOSTAT, 2002). Drought is the major abiotic stress factor affecting yield and quality of rainfed groundnut worldwide. Yield losses due to drought are highly variable in nature, depending on the timing, intensity, and duration of the drought, coupled with other location specific environmental factors such as high levels of irradiance and high temperatures. The progress in drought resistance breeding in groundnut, which has normally followed an empirical approach in the past, has been slow and limited. The empirical approach was based mainly on kernel yield, which integrated other adaptation factors at a given location. A physiological trait-based approach has not been widely used in drought resistance breeding due to the cumbersome nature of measurement of proposed resistance traits and the difficulty in applying them for selection in large segregating populations.

Passioura (1986) suggested that for a trait to be useful in improving yield under stress, it must benefit one of the main functional components in the following biological model for seed yield: Seed yield = Water transpired (T) × Water-use efficiency (WUE or TE) × Harvest index (HI). Substantial genetic variation has been demonstrated in groundnut for each of these functional components (Hebbar *et al*., 1994; Rao *et al*., 1993). However, for the reasons stated earlier, these traits could not be used as selection criteria in a large-scale breeding programme. Further studies led to identification of surrogate traits of TE (WUE) such as carbon isotope discrimination (Hubick *et al*., 1986; Wright *et al*., 1994), specific leaf area (Rao & Wright, 1994), and SPAD chlorophyll meter reading (Rao *et al*., 2001) in groundnut, which are relatively easy to measure. These developments in the understanding of underlying mechanisms of drought resistance, and in efficient ways of measuring genotype differences in trait expression in groundnut, encouraged breeders to attempt a physiological trait-based selection approach in drought resistance breeding in groundnut with a hope that it would result in greater and speedier progress. Simultaneously, it was also thought appropriate to compare the efficiency of selection between trait-based and empirical approaches so that an effective strategy could be devised for drought resistance breeding in groundnut.

This paper presents the results of a multi-institute study on comparing the efficacy of selection between physiological trait-based and empirical approaches in drought resistance breeding in groundnut, which was conducted during 1997–2002 in India.

Materials and Methods

Genetic materials, experimental design and test environments

The study material consisted of 192 $F_{2:6}$ genotypes that originated from four collaborating research institutes (ICRISAT, Patancheru, MPKV, Jalgaon, NRCG, Junagadh, & ARS, Tirupati) in India as described in Chandra *et al*., (2003). Each institute made four crosses in 1997; three crosses were common across institutes, and the fourth was institute specific. All four crosses at each institute were simultaneously advanced from the F_2 to F_6 generation following a common selection scheme (Nigam *et al.,* 2003) with both a physiological trait-based selection index as outlined in Chandra *et al*., (2003) and empirical approach, largely based on kernel yield and traits of local adaptation, followed by the respective breeder.

The F_2 population of each cross at each institute was divided into two equal parts, each containing about 500 plants, for carrying out physiological trait-based (*Tr*) and empirical (*E*) selection in 1998. Thus for each selection method in each cross, 500 $F_{2:3}$ families constituted the base population. For selection method *Tr*, harvest index (HI), water-use efficiency (TE), and water transpired (T) were recorded on 10 plants randomly selected from each $F_{2:3}$ family grown under no-moisture-stress conditions. These three traits were combined into a selection index (SI), which gave equal weight to each trait. This SI was used to select the top 10% of the $F_{2:3}$ families to get 50 $F_{2:4}$ families in each cross. Under selection method *E*, the top 10% $F_{2:3}$ families, based on pod yield under no-moisture-stress conditions, were selected to generate 50 $F_{2:4}$ families. The no-moisture-stress condition was opted for both selection methods, in order to have sufficient seed from each selected plant for the progeny rows in the next generation. The 50 $F_{2:4}$ *Tr*-based families were grown under no-moisture-stress as well as managed moisture stress conditions (akin to a long dry spell in the rainy season) during the rainy season of 1999. The 50 $F_{2:4}$ *E*-based families were grown under no-moisture-stress and rainfed conditions, the latter as per practice for drought resistance breeding at individual institutes. Using the SI (selection method *Tr*) or pod yield (selection method *E*), the top five (10%) $F_{2:4}$ families were selected to generate five $F_{2:5}$ families from each growing condition for each selection method. These selected $F_{2:5}$ families were further evaluated following both selection methods during the 1999/2000 post-rainy season and their seed increased as they were nearly stabilised.

The final set of lines used to compare selection methods consisted of $F_{2:6}$ families, three from no-moisture-stress and three from managed moisture stress for selection method *Tr* and six for selection method *E,* for each cross. The trial thus had 192 families [(six *Tr*-based + six *E*-based) families × 4 crosses × 4 institutes]. Of the 192 genotypes, 96 emanated from trait-based (*Tr*) and 96 from empirical (*E*) selection approach, each institute contributing six each *Tr* and *E* based selections from each cross. The genotypes were field-tested in 12 season-location environments in India during 2000-2001 using, in each environment, a 4 × 48 alpha design with three replications. The 12 environments encompassed two seasons (2000 rainy and 2000/2001 post-rainy) and six distinct locations (Anantapur, Patancheru, Jalgaon, Junagadh, Tirupati & Udaipur) in India.

Measurement of selection efficiency

The selection efficiency under *Tr*, relative to *E*, for kernel yield was estimated using the genetic concept of response to selection, computed as $RE_{Tr} = R_{Tr}/R_E$, where $R_{Tr} = i_{Tr}\, h_{Tr}\, \sigma_{GTr}$ is the response to selection under *Tr* and $R_E = i_E\, h_E\, \sigma_{GE}$ is the response to selection under *E*. This gives the efficiency of *Tr* relative to *E* as $RE_{Tr} = \{i_{Tr}/i_E\}\ \{h_{Tr}/h_E\}\ \{\sigma_{GTr}/\sigma_{GE}\} = \{h_{Tr}/h_E\}\ \{\sigma_{GTr}/\sigma_{GE}\}$ for $i_{Tr} = i_E$ (1)
where, i is the selection intensity, h^2 is the heritability, and $\sigma_G{}^2$ is the genetic variance. For selection method *Tr* to be superior to *E*, RE_{Tr} should exceed 1. This, under the assumption of equal selection intensity under *Tr* and *E*, can happen when any one of the following three conditions hold: (i) $h_{Tr} > h_E$ for $\sigma_{GTr} = \sigma_{GE}$, (ii) $\sigma_{GTr} > \sigma_{GE}$ for $h_{Tr} = h_E$, or (iii) $\{h_{Tr}/\sigma_{GTr}\} > \{h_E/\sigma_{GE}\}$. The above formulation of relative efficiency assumes the genotype effects as random. The heritability was estimated on entry-mean basis as $h^2 = \sigma_G{}^2/[\sigma_G{}^2 + (\sigma\varepsilon^2/r)]$ for individual environments and $h^2 = \sigma_G{}^2/[\sigma_G{}^2 + (\sigma_{Ge}{}^2/e) + (\sigma\varepsilon^2/er)]$ across environments, where r is the number of replications, e the number of environments, $\sigma_{Ge}{}^2$ the genotype-by-environment interaction variance, and $\sigma_\varepsilon{}^2$ the residual variance.

Biometric analyses

Efficiency of selection, as described above, was estimated for each of the 12 individual environments separately as well as across the environments. The across environments selection efficiency was also estimated after grouping the environments in two ways: by season (rainy or post-rainy) and by pattern of seasonal plant extractable soil-water availability (P_esw) computed through APSIM peanut model (Rachaputi, 2003). The latter grouped the 12 environments into four clusters as shown in Table 1.

The estimation of genetic parameters to compute the selection efficiency in equation (1) required analysis of plot-wise data for each selection method separately. This analysis for each selection method in an individual environment was based on the

Table 1. *Environment clusters based on similarity of pattern of plant extractable soil-water availability (P_esw)*

Cluster	Number of environments	Name of environments (Abbreviation)[a]
Cluster 1	1	ICRISAT rainy season (ICR-R)
Cluster 2	1	ICRISAT post-rainy season-imposed mid-season drought (ICR-PRM)
Cluster 3	7	Anantapur rainy season (ATP-R) ICRISAT rainy season-irrigated (ICR-RIR) Jalgaon rainy season (JAL-R) Udaipur rainy season (UDA-R) Junagadh rainy season (JUN-R) Junagadh post-rainy season (JUN-PR) Tirupati post-rainy season (TIR-PR)
Cluster 4	3	Tirupati rainy season (TIR-R) ICRISAT post-rainy season (ICR-PR) Jalgaon post-rainy season (JAL-PR)

[a] All rainy season environments are rainfed unless stated otherwise. Similarly, all post-rainy season environments are irrigated unless stated otherwise

following linear additive model

$$Y_{ijk} = \mu + r_k + b_{jk} + g_i + \varepsilon_{ijk} \qquad (2)$$

where, Y_{ijk}, μ, r_k, b_{jk}, g_i, and ε_{ijk}, respectively, denote the observation on genotype i in block j of replication k, general mean, effect of replication k, effect of block j within replication k, effect of genotype i, and the residual effect. All terms on the right hand side of the model, except μ, were assumed random. Each random effect was assumed to be identically and independently normally distributed with a mean of zero and a constant variance.

Across environments analysis for each selection method was based on the following extension of model (2)

$$Y_{ijkl} = \mu + e_l + r_{kl} + b_{jkl} + g_i + (ge)_{il} + \varepsilon_{ijkl} \qquad (3)$$

where, Y_{ijkl}, μ, e_l, r_{kl}, b_{jkl}, g_i, $(ge)_{il}$ and ε_{ijkl}, respectively, denote the observation on genotype i in block j of replication k in environment l, the general mean, effect of environment l, effect of replication k within environment l, effect of block j within replication k within environment l, effect of genotype i, effect of interaction of genotype i with environment l, and the residual effect. All terms in the model, except μ, were assumed random. Each random effect was assumed to be identically and independently normally distributed with a mean of zero and a constant variance.

The unbiased estimates of variance components for random effects in models (2) and (3), as required to compute the selection efficiency in equation (1), were obtained using the restricted maximum likelihood (ReML) method in GenStat statistical computing software (Payne, 2002). ReML was also used to obtain the best linear unbiased predictions (BLUPs) of the performance of genotypes in individual and across environments. Plant population varied from plot to plot and had a positive/negative relationship with the variables considered in this study. The plant population was therefore used as a covariate to adjust the estimates for various effects in models (2) and (3) for varying plant populations.

To assess significance of the differences between selection methods (S), among crosses (C), selection method × cross interactions (S × C), and their interactions (S × e, C × e, S × C × e) with environments (e), a pooled ReML analysis of data across the 12 environments, using a linear additive model containing the seven effects, was conducted assuming the effects S and C as fixed and that of environments (e) as random. The statistical significance of estimates of variance components was tested using their respective standard errors, assuming an asymptotic normal distribution. The significance of differences among levels of a fixed-effects-factor was tested using Wald statistic that follows an approximate χ^2 distribution.

Results and Discussion

Selection efficiency

The results of selection efficiency for kernel yield, based on response to selection, are presented in Table 2 for individual environments and in Table 3 for environments clustered into four groups.

Grouping of 12 environments into two classes – rainy season and post-rainy season – shows that selection method *Tr* provides higher response to selection in rainy season, but not in post-rainy season. This happens because *Tr* in rainy season generates a higher genetic variance, lower G × E interaction variance, and hence, higher heritability than those of the post-rainy season. Taken over all 12 environments, two selection methods more or less perform the same with RE_{Tr} being 1.045 (Table

Table 2. *Relative efficiency of trait-based selection (Tr)* vis-à-vis *empirical selection (E) for kernel yield in 96 $F_{2:6}$ progenies each under Tr and E in 12 Indian environments*

Parameter	ATP-R	ICR-RIR	ICR-R	JAL-R	JUN-R	TIR-R
$\sigma_g^2(E)$	26159^{**}	68760^{**}	32591^{ns}	48542^{**}	62339^{**}	65038^{***}
$\sigma_g^2(Tr)$	19608^{ns}	55353^{*}	49736^{**}	56389^{***}	82339^{***}	57945^{***}
h^2 (*E*)	0.449	0.422	0.300	0.456	0.503	0.583
h^2 (*Tr*)	0.33	0.365	0.440	0.524	0.630	0.574
RE_{Tr}	0.742	0.834	1.495	1.155	1.286	0.937

Parameter	UDA-R	ICR-PR	ICR-PRM	JAL-PR	JUN-PR	TIR-PR
$\sigma_g^2(E)$	295619^{***}	267176^{***}	99210^{***}	166677^{***}	201914^{***}	138816^{***}
$\sigma_g^2(Tr)$	280031^{***}	390542^{***}	53487^{*}	152826^{***}	251083^{***}	162425^{***}
h^2 (*E*)	0.948	0.754	0.583	0.912	0.854	0.724
h^2 (*Tr*)	0.924	0.810	0.405	0.918	0.915	0.752
RE_{Tr}	0.961	1.254	0.612	0.961	1.154	1.103

^{ns} = non-significant at .05 level of significance, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, RE_{Tr} = Efficiency of *Tr* relative to *E*

Table 3. *Relative efficiency of trait-based selection (Tr)* vis-à-vis *empirical selection (E) for kernel yield in 96 $F_{2:6}$ progenies each under Tr and E in two seasons and four clusters of environments*

Parameter	Rainy season	Post-rainy season	12-En	CL-1	CL-2	CL-3	CL-4
$\sigma_g^2(E)$	14479^{**}	43179^{***}	22106^{***}	32591^{ns}	99210^{***}	18022^{**}	7712^{ns}
$\sigma_g^2(Tr)$	18451^{***}	27028^{*}	23872^{***}	49736^{**}	53487^{*}	25761^{***}	9486^{ns}
$\sigma_{ge}^2(E)$	74740^{***}	132522^{***}	103101^{***}	-[1]	-[1]	102965^{***}	159553^{***}
$\sigma_{ge}^2(Tr)$	70517^{***}	176359^{***}	112680^{***}	-[1]	-[1]	104042^{***}	191440^{***}
$h^2(E)$	0.444	0.540	0.631	0.300	0.583	0.453	0.099
$h^2(Tr)$	0.520	0.372	0.638	0.440	0.405	0.543	0.106
RE_{Tr}	1.220	0.657	1.045	1.495	0.612	1.308	1.144

^{ns}= non-significant at .05 level of significance, $^{*}= P < 0.05$, $^{**}= P < 0.01$, $^{***}= P < 0.001$, En = environments; CL = environment clusters; RE_{Tr}= Efficiency of *Tr* relative to *E*; 1 = single environment clusters

Table 4. *Difference among selection methods (S), crosses (C), and their interactions, and estimates of variance components (VC) based on 12 environments and 192 $F_{2:6}$ progenies for kernel yield*

Effect	Wald Statistic	VC Estimate
S	ns ($P > 0.05$)	-
C	$P < 0.001$	-
S × C	ns ($P > 0.05$)	-
σ_e^2	-	313547*
σ_{Se}^2	-	0.74×10^{-3ns}
σ_{Ce}^2	-	41184^{***}
σ_{SCe}^2	-	0.13×10^{-2ns}

ns = non-significant at 0.05 level of significance, $^{**}P < 0.01$, $^{***}P < 0.001$

2). Classification of the 12 environments into four clusters (CL-1, CL-2, CL-3, CL-4) according to plant extractable soil-water availability indicates that selection method *Tr* was superior to *E* in CL-1 (single environment cluster), CL-3, and CL-4. This is because of an increase in genetic variance and heritability under *Tr* in these clusters. All three of these clusters had declining soil-water availability with varying patterns during the later phase of crop growth. In CL-2 (another single environment cluster), which experienced mid-season moisture stress, *E* was superior to *Tr* as the former had higher genetic variance and higher heritability.

Selection methods, crosses, and their interactions with environments

The results of variance analysis for effects of selection methods (S), crosses (C), and their interactions, and estimates of variance components for S × e, C × e, and S × C × e are presented in Table 4 for kernel yield based on 12 environments and 192 $F_{2:6}$ progenies.

Across all environments the two selection methods, *Tr* and *E,* did not differ significantly from each other for kernel yield. There was, in contrast, large and significant difference among crosses. There was no significant interaction between selection methods and crosses. The crosses significantly interacted with environments. The two selection methods, however, did not exhibit significant interaction with environments, indicating a similar ranking of the two methods in each of the 12 environments.

Promising $F_{2:6}$ progenies under empirical and trait-based selection methods

Top 20 selections (≈10% of 192) for kernel yield are listed in Table 5. This is based on a pooled ReML analysis of all 192 genotypes across the 12 environments, assuming a fully random model. The rank 1 selection JAL 30, developed from empirical approach (*E*), had kernel yield of 2212 kg ha^{-1}, whereas the rank 20 selection JAL 17, developed from trait-based approach (*Tr*), had kernel yield of 2037 kg ha^{-1}. The frequency of *E* and *Tr* selections among these top 20 selections was six for *E* and 14 for *Tr*. Among the top 10 of the top 20, the frequency of *E* and *Tr* selections is nearly equal (6*E* : 4*Tr*). The lower 10 of top 20 selections are all *Tr*. The eight parents/checks differed in their kernel yields, which ranged from 1635 kg ha^{-1} (Parent 8) to 2115 kg ha^{-1} (Parent 2). None of the top 20 selections differed significantly ($P > 0.05$) from the best parent in the trial (Parent 2). All top nine selections had significantly higher kernel yield ($P < 0.05$) than the second best parent (Parent 1) that had a kernel yield of 1948 kg ha^{-1}. All top 20 selections, however, had significantly higher kernel yield ($P < 0.05$) than each of the other five parents (Parents 3-8).

Mean T, TE, and HI for the top 20 high-yielding selections are also presented in Table 5. On an average, the six *E*-based selections had higher kernel yield, higher T, and nearly equal TE and HI relative to the 14 *Tr*-based selections. The minimum and maximum values of T (390.5 – 439.2, with a range of 48.7 mm) for *E*-based selections were higher than that for Tr-based selections (366.7 – 424.9, with a range of 58.2 mm). The ranges of TE and HI values were similar for both *Tr* and *E* selections.

From the results of these multi-environment analyses, it is evident that the physiological trait-

Table 5. *Top 20 selections having significantly (indicated by ✓) higher kernel yield than parents*

Rank	Selection	Selection method	Parent 2	Parent 1	Parents 3-8	Kernel yield (kg ha^{-1})	T (mm)	TE (g kg^{-1})	HI (kernel)
1	JAL 30	*E*	None	✓	✓	2212	405.2	2.11	0.30
2	ICR 24	*Tr*		✓	✓	2161	418.6	2.05	0.30
3	ICR 45	*E*		✓	✓	2160	408.7	2.03	0.31
4	ICR 39	*E*		✓	✓	2157	398.1	1.97	0.31
5	ICR 43	*E*		✓	✓	2151	390.5	2.10	0.31
6	TIR 31	*E*		✓	✓	2144	439.2	2.05	0.28
7	JAL 29	*E*		✓	✓	2141	431.2	2.07	0.27
8	JAL 01	*Tr*		✓	✓	2132	410.1	2.10	0.29
9	TIR 16	*Tr*		✓	✓	2129	376.9	2.06	0.30
10	JAL 13	*Tr*			✓	2116	423.7	2.10	0.29
11	TIR 18	*Tr*			✓	2106	401.4	2.05	0.29
12	ICR 09	*Tr*			✓	2100	366.7	2.15	0.31
13	JUG 13	*Tr*			✓	2089	413.7	2.15	0.28
14	JAL 18	*Tr*			✓	2065	397.3	2.07	0.29
15	JAL 03	*Tr*			✓	2062	407.8	2.07	0.28
16	ICR 10	*Tr*			✓	2061	407.9	2.06	0.28
17	ICR 07	*Tr*			✓	2059	389.9	2.14	0.29
18	JAL 02	*Tr*			✓	2051	424.9	2.10	0.26
19	ICR 23	*Tr*			✓	2044	400.1	2.04	0.29
20	JAL 17	*Tr*			✓	2037	388.6	2.03	0.30
		E:*Tr* :: 6:14							
				LSD (5%)		172.2	27.52	0.051	0.019
				Mean	*E* (6)	2161	412.2	2.06	0.30
					Tr (14)	2087	402.0	2.08	0.29
				Max	*E*	2212	439.2	2.11	0.31
					Tr	2161	424.9	2.15	0.31
				Min	*E*	2141	390.5	1.97	0.27
					Tr	2037	366.7	2.03	0.26

Parent 1: ICGS 44 (1948)[*]
Parent 2: ICGS 76 (2115)
Parent 3: CSMG 84-1 (1861)
Parent 4: ICGV 86031 (1721)
Parent 5: TAG 24 (1783)
Parent 6: JL 220 (1755)
Parent 7: GG 2 (1722)
Parent 8: K 134 (1635)

[*] Mean kernel yield of parent (kg ha^{-1})

based selection index approach did not demonstrate a consistent superiority over empirical approach in selecting for kernel yield in groundnut across the environments. The yield advantage in selections based on empirical approach came largely from greater T (amount of water transpired), which may limit the yield of these genotypes in water-deficit environments. Therefore, it may be advantageous to include physiological traits (or their easily measurable surrogates) in the selection scheme to select genotypes that are efficient water utilisers and partitioners of photosynthates into economic yield, for environments in which T is limited by stress. Such genotypes would be successful in both water-deficit and irrigated environments, as water is becoming a scarce resource in agriculture. The SPAD chlorophyll meter provides an easy opportunity to integrate a surrogate measure of water-use-efficiency with pod yield, in the selection scheme of a drought resistance breeding programme in groundnut. As the meter is hand held, it can be used in the field and on a large number of plants in a short time.

It is hoped that new biotechnological tools will make drought resistance breeding more effective and efficient. A search for QTLs for water-use efficiency in groundnut is in progress at ICRISAT. Initial indications from experiments at ICRISAT with genetically transformed groundnuts with

Drought Responsive Elements from *Arabidopsis* are encouraging (ICRISAT, unpublished).

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References

Chandra S, Nigam S N, Cruickshank A W, Bandyopadhyaya A, Harikrishna S. 2003. Selection index for identifying high-yielding groundnut genotypes in irrigated and rainfed environments. *Annals of Applied Biology* **143**:303–310.

FAOSTAT. 2002. Database results (www.fao.org).

Hebbar K B, Sashidhar V R, Udayakumar M, Devendra R, Rao Nageswara R C. 1994. A comparative assessment of water use efficiency in groundnut (*Arachis hypogaea*) grown in containers and in the field under water-limited conditions. *Journal of Agricultural Science, Cambridge* **122**:429–434.

Hubick K T, Farquhar G D, Shorter R. 1986. Correlation between water-use efficiency and carbon isotope discrimination in diverse peanut (*Arachis*) germplasm. *Australian Journal of Plant Physiology* **13**:803–816.

Nigam S N, Basu M S, Cruickshank A W. 2003. Hybridization and description of the trait-based and empirical selection programs. In *Breeding for drought-resistant peanuts*, pp. 15–17. Eds A W Cruickshank, N C Rachaputi, G C Wright and S N Nigam. Report of a workshop held at ICRISAT Centre, Andhra Pradesh, India, 25–27 February 2002. *ACIAR Proceedings No. 112.*

Passioura J B. 1986. Resistance to drought and salinity: avenues for improvement. *Australian Journal of Plant Physiology* **13**:191–201.

Payne R W. (Ed.) 2002. *The Guide to GenStat®*, Release 6.1, Part 2: Statistics. Oxford, UK: VSN International Ltd.

Rachaputi N C. 2003. Environmental characterization of experimental sites in India and Australia. In *Breeding for drought-resistant peanuts*, pp. 61–66. Eds A W Cruickshank, N C Rachaputi, G C Wright and S N Nigam. Report of a workshop held at ICRISAT Centre, Andhra Pradesh, India, 25–27 February 2002. *ACIAR Proceedings No. 112.*

Rao Nageswara R C, Wright G C. 1994. Stability of the relationship between specific leaf area and carbon isotope discrimination across environments in peanut. *Crop Science* **34**:98–103.

Rao Nageswara R C, Williams J H, Wadia K R D, Hubick K T, Farquhar G D. 1993. Crop growth, water-use efficiency and carbon isotope discrimination in groundnut (*Arachis hypogaea* L.) genotypes under end-of-season drought conditions. *Annals of Applied Biology* **122**:357–367.

Rao Nageswara R C, Talwar H S, Wright G C. 2001. Rapid assessment of specific leaf area and leaf nitrogen in peanut (*Arachis hypogaea* L.) using a chlorophyll meter. *Journal of Agronomy and Crop Science* **186**:175–182.

Wright G C, Rao Nageswara R C, Farquhar G D. 1994. Water-use efficiency and carbon isotope discrimination in peanut under water deficit conditions. *Crop Science* **34**:92–97.

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