F4 progeny rows showing good variation for drought tolerance traits at QDPI, Kingaroy, QLD, Australia.

At the inauguration ceremony for the new ACIAR-funded boundary fence at Jalgaon Oilseeds Research Station, Maharashtra, India (*from left*: Dr M.P. Deshmuck, Dr R.B. Patil, Dr G.C. Wright).

Multi-environment Analysis for Indian Sites

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Introduction

GENOTYPE-BY-ENVIRONMENT interactions (GEI) are ubiquitous for quantitative traits of economic importance. Significant GEI tends to hinder genetic progress in a breeding program; in particular, the crossover type of GEI makes it difficult to unambiguously select promising materials that perform consistently better across a wide range of environmental conditions. The first step to deal with the consequences of the presence of GEI is to assess its relative importance through a pooled analysis of data across the testing sites.

Method

Pooled analysis over Indian environments was performed for kernel yield (KY), total transpiration (T), transpiration efficiency (TE), and harvest index (HI) to assess the relative importance of different sources of variation, in particular that of the interaction of major factors like genotypes (G), selection methods (S) and crosses (C) with environments (E). There were 14 environments in total, eight in the kharif (rainy) season and six in the rabi (post-rainy) seasons. These were stratified into four clusters based on water availability as indicated by Rachaputi (2003). Pooled analyses were conducted clusterwise over all 14 environments.

Using the genetic concept of predicted response to selection, predicted selection efficiency of trait-based selection relative to empirical selection was computed:

- for each environment;
- over all 14 environments; and
- for each cluster of environments.

This was used as a measure of potential for further improvement by selection among progenies.

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Biometric analysis

Observation Y_{ijkl} on genotype i recorded in block j of replication k in environment l was modelled as:

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

where:

μ, e_l, r_{kl}, b_{jkl}, g_i, $(ge)_{il,}$ and e_{ijkl}, respectively, denote: 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 to be 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 each random effect were obtained using the restricted maximum likelihood (ReML) method in GenStat computing software. Where necessary, best linear unbiased predictions (BLUPs) were obtained. The plant population was used as a covariate to adjust the estimates for varying plant populations.

As the 192 genotypes were bred from two selection methods (S) and eight crosses (C), with S and C being cross-classified, the genotypes were appropriately grouped into S and C to assess the differences among selection methods and crosses and their interaction (SxC). These effects were assumed to be fixed. Their best linear unbiased estimates (BLUEs) were obtained using ReML. Interaction effects of S and C with E, with E assumed as random, become random. The unbiased estimates of variance components of these random interaction effects were obtained using ReML.

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 the Wald statistic that follows an approximate χ^2 distribution.

Results and Discussion

Components of variance

Table 1 presents the estimates of variance components for the four traits for environments (σ_e^2), genotypes (σ_g^2), GxE (σ_{ge}^2) and residuals (σ_e^2) obtained from data from 14 environments and 192 $F_{2.6}$ progenies. All traits exhibited significant variation among environments, genotypes, and genotype-by-environment interactions. The environments represented the major source of variation, followed by genotype-by-environment interactions, and then genotypes. This is in line with what

Table 1. Estimates of variance components (VC) based on 14 environments and 192 $F_{2:6}$ progenies.

VC	KY (kg/ha)	HI	TE (g/kg)	T (mm)
σ_e^2	302726^{*}	$9\text{x}10^{-3**}$	$215\text{x}10^{-3**}$	60025^{*}
σ_g^2	17571^{***}	$0.6\text{x}10^{-3***}$	$6\text{x}10^{-3***}$	805^{***}
σ_{ge}^2	107769^{***}	$1\text{x}10^{-3***}$	$7\text{x}10^{-3***}$	6994^{***}
σ_e^2	129046	$1.5\text{x}10^{-3}$	$10\text{x}10^{-3}$	3069

Notes: *P<0.05, **P<0.01, ***P<0.001

Table 2. Estimates of variance components for Cluster 3 (Vriddhachalam-rainy, Vriddhachalam-post-rainy, ICRISAT-post-rainy-Midseason) based on 192 $F_{2:6}$ progenies.

VC	KY (kg/ha)	HI	TE (g/kg)	T (mm)
σ_e^2	132485^{ns}	$17\text{x}10^{-3ns}$	$28\text{x}10^{-3ns}$	56062^{ns}
σ_g^2	14802^{**}	$0.1\text{x}10^{-3*}$	$4\text{x}10^{-3***}$	1725^{*}
σ_{ge}^2	77076^{***}	$1\text{x}10^{-3***}$	$3\text{x}10^{-3***}$	12305^{***}
σ_e^2	77272	$0.9\text{x}10^{-3}$	$2.5\text{x}10^{-3}$	2078

Notes: ^{ns}:non-significant at .05 level of significance; *P<0.05, **P<0.01, *** P<0.001

Table 3. Estimates of variance components for Cluster 1 (Anantapur-rainy, ICRISAT-rainy-irrigated, Jalgaon-rainy, Junagadh-rainy, Udaipur-rainy, Junagadh-post-rainy, Tirupati-post-rainy) based on 192 $F_{2:6}$ progenies.

VC	KY (kg/ha)	HI	TE (g/kg)	T (mm)
σ_e^2	455424^{ns}	$8\text{x}10^{-3ns}$	$159\text{x}10^{-3ns}$	22813^{ns}
σ_g^2	22156^{***}	$0.9\text{x}10^{-3***}$	$7\text{x}10^{-3***}$	255^{**}
σ_{ge}^2	102913^{***}	$0.8\text{x}10^{-3***}$	$7\text{x}10^{-3***}$	2346^{***}
σ_e^2	139418	$1.7\text{x}10^{-3}$	$12\text{x}10^{-3}$	2733

Notes: ^{ns} : non-significant at 0.05 level of significance; **P<0.01, ***P<0.001

Table 4. Estimates of variance components for Cluster 2 (Tirupati-rainy, ICRISAT-post-rainy-irrigated, Jalgaon-post-rainy) based on 192 $F_{2:6}$ progenies.

VC	KY (kg/ha)	HI	TE (g/kg)	T (mm)
σ_e^2	319362^{ns}	$11.0\text{x}10^{-3ns}$	$387\text{x}10^{-3ns}$	100703^{ns}
σ_g^2	10257^{ns}	$0.5\text{x}10^{-3***}$	$1\text{x}10^{-3***}$	1703^{**}
σ_{ge}^2	174458^{***}	$1.0\text{x}10^{-3***}$	$1\text{x}10^{-3***}$	14304^{***}
σ_e^2	132506	$1.0\text{x}10^{-3}$	$2\text{x}10^{-3}$	4715

Notes :^{ns}: non-significant at 0.05 level of significance; **P<0.01, ***P<0.001

has usually been observed in multi-environment trials in most crops. The results were similar when the variance components were estimated from 200 genotypes.

Results of cluster-wise pooled analysis for three multiple-environment clusters (Rachapuh, 2003) are presented in Tables 2–4. Results of Cluster 4 are not shown as it had only a single environment (ICRISAT rain-fed, rainy season).

As a result of environmental classification, the variation among environments within clusters became non-significant in all clusters for all four traits. This outcome needs to be viewed with caution, as sample size (the number of environments) in individual clusters is small giving a less precise estimate of variance

Table 5. Difference among selection methods, crosses, and their interactions, and estimates of variance components based on 14 environments and 192 $F_{2:6}$ progenies for KY.

Effect	Wald Statistic	VC Estimate
S	ns (P>0.05)	-
C	P<.001	-
SxC	ns (P>0.05)	-
σ_e^2	-	$271\ 419^{*}$
σ_{Se}^2	-	$0.64\text{x}10^{-3\text{ns}}$
σ_{Ce}^2	-	$35\ 878^{***}$
σ_{SCe}^2	-	$0.14\text{x}10^{-3\text{ns}}$

Note: ^{ns}: non-significant at 0.05 level of significance; *P<0.05, **P<0.01, ***P<0.001

Table 6. Top 20 Progenies or Parents' Mean over all Indian sites.

Rank	Progeny or Parent	Selection Method	KY (kg/ha)	HI	TE (g/kg)	T (mm)
1	JAL 30	Emp	2153	0.27	2.16	438.60
2	JAL 01	Trait	2111	0.26	2.15	460.70
3	TIR 31	Emp	2096	0.26	2.10	470.00
4	JAL 29	Emp	2095	0.25	2.14	477.70
5	ICR 24	Trait	2093	0.28	2.07	454.50
6	ICR 39	Emp	2084	0.28	1.93	455.80
7	ICR 09	Trait	2083	0.29	2.09	424.30
8	ICR 45	Emp	2079	0.29	2.03	438.60
9	ICR 43	Emp	2077	0.28	2.09	472.70
10	JAL 13	Trait	2073	0.26	2.17	457.10
11	TIR 16	Trait	2072	0.28	1.98	440.70
12	ICR 40	Emp	2070	0.27	1.99	531.60
13	TIR 18	Trait	2068	0.27	1.98	452.40
14	ICR 07	Trait	2064	0.27	2.11	451.00
15	JUG 13	Trait	2055	0.26	2.20	450.00
16	JAL 15	Trait	2044	0.26	2.19	431.60
17	ICR 13	Trait	2034	0.25	2.06	488.10
18	JAL 02	Trait	2027	0.24	2.17	473.60
19	JUG 03	Trait	2019	0.27	2.18	435.00
20	JAL 05	Trait	2014	0.27	1.97	474.10
	ICGS 76		2046			
	ICGS 44		1949			
	TAG 24		1853			
	CSMG 84-1		1766			
	ICGV 86031		1765			
	GG 2		1744			
	JL 220		1702			
	K 134		1645			
	LSD (5%)		148.6	24.44	0.044	0.017
	Mean	Emp (n = 7)	2093	469.30	2.06	0.27
		Trait (n = 13)	2058	453.30	2.10	0.26
	Maximum	Emp	2153	531.60	2.16	0.29
		Trait	2111	488.10	2.20	0.29
	Minimum	Emp	2070	438.60	1.93	0.25
		Trait	2014	424.30	1.97	0.24

component σ_e^2. The general trend of relative magnitude of variation for E, GxE, and G remained nearly similar to that in Table 1 for all 14 environments analysed together. A casualty of clustering was the absence of significant genetic variation for KY in Cluster 4.

Methods, crosses, and interactions

The results of statistical significance of difference among selection methods, crosses, and their interactions with environments, and estimates of variance components for SxE, CxE, and SxCxE are presented in Table 5 for KY for 14 environments and 192 $F_{2.6}$ progenies.

The two selection methods, trait-based and empirical, did not significantly differ from each other. There were large and significant differences among the eight 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 performance of the two methods in each of the 14 environments.

Empirical v trait-based selection

The top 20 progenies (ca.10% of 192) for KY that were significantly superior ($P<0.05$) to parents are listed in Table 6. The first-ranked progeny JAL 30, an empirical selection, had KY of 2153 kg/ha, whereas the 20th ranked progeny JAL 05, a trait-based selection, had KY of 2014 kg/ha. The frequency of empirical and trait-based progenies among these top 20 progenies was 7/20 for empirical and 13/20 for trait-based. The eight parents/checks differed in their KY from 1645 kg/ha (K 134) to 2046 kg/ha (ICGS 76). None of the top 20 progenies differed significantly ($P>0.05$) from ICGS 76. Only the first-ranked and second-ranked progenies (JAL 30 & JAL 01) had significantly higher KY ($P<0.05$) than the second best

Table 7. Predicted Relative efficiency of trait-based selection (RE_T) for KY in 14 Indian environments for 96 $F_{2:6}$ progenies.

Parameter	*ATP-K*	*ICR-IR-K*	*ICR-RF*	*JAL-K*	*JUN-K*	*TIR-K*	*UDAI-K*
$\sigma_g^2(E)$	26 159**	68 760**	32 591^{ns}	48 542**	62 339**	65 038***	295 619***
$\sigma_g^2(T)$	19 608^{ns}	55 353*	49 736**	56 389***	82 339***	57 945***	280 031***
$h^2(E)$	0.449	0.422	0.300	0.456	0.503	0.583	0.948
$h^2(T)$	0.330	0.365	0.440	0.524	0.630	0.574	0.924
RE_T	**0.742**	**0.834**	**1.495**	**1.155**	**1.286**	**0.937**	**0.961**

Parameter	*VRI-K*	*ICR-IR-R*	*ICR-MD*	*JAL-R*	*JUN-R*	*TIR-R*	*VRI-R*
$\sigma_g^2(E)$	84 398***	267 176***	99 210***	166 677***	201 914***	138 816***	90 755***
$\sigma_g^2(T)$	89 001***	390 542***	53 487*	152 826***	251 083***	162 425***	129 201***
$h^2(E)$	0.973	0.754	0.583	0.912	0.854	0.724	0.995
$h^2(T)$	0.974	0.810	0.405	0.918	0.915	0.752	0.994
RE_T	**1.028**	**1.254**	**0.612**	**0.961**	**1.154**	**1.103**	**1.192**

Notes: ^{ns}: non-significant at 0.05 level of significance; * $P<0.05$, **$P<0.01$, ***$P<0.001$; E = empirical. T = trait-based.

Table 8. Relative efficiency of trait-based selection (RE_T) for KY in pooled environments for 96 $F_{2:6}$ progenies.

Parameter	Rainy season	Post-rainy season	All 14	Cluster 1	Cluster 2	Cluster 3	Cluster 4
$\sigma_g^2(E)$	9 053*	29 333***	16 289***	32 591^{ns}	13 105^{ns}	18 022**	7 712^{ns}
$\sigma_g^2(T)$	12 346**	21 529**	18 676***	49 736**	14 488^{ns}	25 761***	9 486^{ns}
$\sigma_{ge}^2(E)$	77 260***	131 924***	103 614***	-	78 470***	102 965***	159 553***
$\sigma_{ge}^2(T)$	74 776***	168 994***	114 006***	-	76 097***	104 042***	191 440***
$h^2(E)$	0.367	0.501	0.606	0.300	0.277	0.453	0.099
$h^2(T)$	0.451	0.378	0.625	0.440	0.295	0.543	0.106
RE_T	**1.29**	**0.744**	**1.087**	**1.495**	**1.086**	**1.308**	**1.144**

Notes: ^{ns}: non-significant at 0.05 level of significance; *$P<0.05$, **$P<0.01$, ***$P<0.001$; Cluster 1: ICR-RF; Cluster 2: VRI-K, ICR-MD, VRI-R; Cluster 3: ATP-K, JAL-K, UDA-K, ICR-K, JUN-K, JUN-R, TIR-R; TIR-K, ICR-R, JAL-R; RE_T.: Efficiency of T relative to E.

parent (ICGS 44, KY = 1949 kg/ha). All top 20 progenies, however, had significantly higher KY ($P<0.05$) than the other parents (CSMG 84-1, TAG 24, ICGV 86031, GG 2, JL 220 and K 134).

Mean T, TE, and HI for the top 20 high-yielding progenies are presented in Table 6. On average, the seven empirical progenies had higher KY, higher T, lower TE, and nearly equal HI relative to the 13 trait-based progenies. The maximum and minimum values of T (531.6 - 438.6 = 93.0 mm) for empirical progeny were higher than that (488.1 - 424.3 = 63.8 mm) for trait-based progenies. The reverse was true for TE, with trait-based progenies having generally higher TE values. The range of HI values was similar for both trait and empirical progenies. Thus, trait-based progenies had relatively lower KY, but generally exhibited higher TE values than empirical progenies.

Potential for Further Improvement

The predicted selection efficiencies for KY, based on predicted response to selection, are presented in Table 7 for individual environments and in Table 8 for environments pooled or clustered in different ways.

Grouping of 14 environments into two classes – rainy season and post-rainy season – shows that the trait-based selection method has more potential for improvement in the rainy season, but not in the post-rainy. This happens because in the rainy season this material generates a higher genetic variance, lower GxE interaction variance, and hence higher heritability. Taken over all 14 environments, the two selection methods more-or-less perform the same with RE_T being 1.087. Classification of the 14 environments into four clusters according to pattern of water availability shows trait-based selection to be generally superior to empirical. This is because of an increase in genetic variance and heritability under trait-based selection resulting from this water-availability-based grouping of the environments.

This predictable outcome is consistent with the raison d'être of the project – trait-based selection would be expected to select genotypes that will express greater genetic variance and less GEI over environments differing in available water.

Reference

Rachaputi, N.C. (2003). Environmental characterisation of experimental sites in India and Australia. These Proceedings.