Theor Appl Genet (2001) 103:469–474

R. Ortiz · W.W. Wagoire · J. Hill · S. Chandra
S. Madsen · O. Stølen

Heritability of and correlations among genotype-by-environment stability statistics for grain yield in bread wheat

Received: 25 July 2000 / Accepted: 7 December 2000

Abstract Several genotype-by-environment stability measures are in use, but little information exists about their inheritance or genetic inter-relationships. Among those measures in common use are the linear regression coefficient (b), deviations from regression (s_b), coefficient of determination (R^2), coefficient of phenotypic variation (CPV) and, more recently, interaction principal components (IPCA) of the additive-main-effect-and-multiplicative-interaction (AMMI) model. Because of the factorial structure of the data, the diallel cross is well suited to study these parameters and their relationship to quantitative traits. For this study a complete diallel cross, derived by mating eight lines from a broad based bread wheat breeding population, was grown for several growing seasons at two Ugandan locations, one of which was prone to yellow rust. Stability parameters and grain yield were measured for each cross. CPV had the highest narrow-sense heritability (h^2=0.522) followed by IPCA1 of the AMMI (h^2=0.461). Lowest narrow-sense heritabilities were calculated for b and R^2 (h^2=0.150 and 0.100 respectively). There were high additive genetic correlations (r_A) between grain yield and CPV (r_A=–0.933), grain yield and IPCA1 (r_A=0.707), and grain yield and IPCA2 (r_A=0.751). The genetic association between CPV and IPCA1 was also high and negative (r_A= –0.934). These results suggest that it may be possible to select simultaneously for high and stable grain yield in this broad-based bread wheat breeding pool by selecting outyielders that exhibit a low CPV.

Communicated by P. Tigerstedt

R. Ortiz (✉) · S. Chandra
International Crops Research Institute for the Semi-Arid Tropics,
Patancheru, 502 324 AP, India

J. Hill · W.W. Wagoire · S. Madsen · O. Stølen
The Royal Veterinary and Agricultural University,
40 Thorvaldsensvej, DK-1871 Frederiksberg C, Copenhagen,
Denmark

Keywords AMMI · Coefficient of Phenotypic Variation · Combining Ability · Joint Regression · Stability Parameters

Introduction

The selection of high-yielding genotypes with a stable performance in targeted agro-ecozones remains an important goal in breeding programs. Yield may be affected by the genotype-by-environment (GE) interaction, however, which impedes the selection of promising genotypes with wide adaptation. Likewise, this GE "noise" reduces the heritability of the character, thereby affecting breeding progress owing to inaccurate selections in single environments. Indeed, specific adaptation depends on resistance to biotic and tolerance to abiotic stress(es), and end-user demand(s) (Ortiz 1999). In turn, the latter is influenced by cropping system, derived product(s), and quality for fresh market, storage, and processing.

Plant breeders rely on stability parameters to assess the performance of their crosses or advanced genotypes across environments. The most popular method for determining stability across environments has been the joint regression approach proposed by Yates and Cochran (1938), which was further developed by Finlay and Wilkinson (1963) and Eberhart and Russell (1966). Other measures include the coefficient of phenotypic variation (CPV, Francis and Kanneberg 1978) and the additive-main-effects-and-multiplicative-interaction model (AMMI, Gauch 1992). AMMI has proved useful for understanding complex interactions, gaining accuracy, improving selections, and increasing experimental efficiency (Gauch and Zobel 1996).

The inheritance of some of these stability parameters has been determined for smooth brome grass (Lin and Binns 1991) and for two sorghum populations (Zavala-Garcia et al. 1992), but to the best of our knowledge, no reports exist for bread wheat except for an investigation regarding parent-dependent genotype× enviroment interaction (Bains 1976). This report indicates that linear and non-linear sensivity to the environment in spring wheat appears to be under genetic control and amenable to selection. Hence, this research sought to determine the heritability of, and genetic association between, grain yield, regression coefficient (b), deviations from regression (s_b), coefficient of determination (R^2), CPV, and interaction principal components (IPCA) of the AMMI model. The feasibility of simultaneous selection for high yield and stability across environments in this broad-based bread wheat germplasm adapted to the East African highlands was also explored.

Materials and methods

Genotypes derived from an 8×8 diallel crossing scheme of bread wheat cultivars were used in this study. All parents were selected from CIMMYT-derived material according to their host response to yellow rust at Kalengyere, a location in the southwestern highlands of Uganda with a high incidence of this disease (Wagoire et al. 1999). This germplasm has been bred for wide adaptation, including resistance to pests and diseases (Braun et al. 1997). The lines Buri, Kenya Chiriku, and Esda/Lira were rated as resistant to yellow rust, while the lines Vee "S"/JUP73/EMU"S"/GJO"S" (Vee"S" hereafter) and Attila were recorded as being moderately resistance and moderately susceptible, respectively. The remaining three lines were susceptible to yellow rust.

The experiments were planted in two cropping seasons (A and B) extending over a 12-month period at two locations in Uganda (Kalengyere and Buginyanya), both having bimodal rainfall. Kalengyere (1°15′ S 29°45′ E) is at 2400 m above sea level (m.a.s.l.) and has an Andosol of pH 5.7 and an average annual temperature of 16°C. The high rainfall (750 mm) season (B) lasts from September to March and the relatively low rainfall (480 mm) season (A) from March to August. Buginyanya (1°1′ N 34°2′ E) is a low-rust site situated at 2100 m.a.s.l. on the slopes of Mount Elgon. It has an Andosol of pH 5.5 and an average annual temperature of 18°C. The high rainfall (560 mm) season (B) occurs from September to March and the relatively low rainfall (470 mm) season (A) from March to August (470 mm).

The study was carried out for three growing seasons from August 1994 to March 1996. In each season 64 genotypes (8 selfed parents and their 56 F_1 crosses) were sown in two replicates in a randomized complete block design at each site. An additional seventh environment was obtained by applying fungicide to control yellow rust at Kalengyere. Due to the limited availability of F_1 seed, the experimental plot consisted of two rows each 1.5 m long, with 0.3 m between rows and 0.15 m between plants, (i.e., about 20 plants per plot). All plots were fertilized at a rate of 50 kg N ha^{-1} prior to planting. The experiments were hand-weeded, while bird scaring was practiced from anthesis to harvest to minimize losses. Whole plots were hand-harvested, threshed, cleaned, sun-dried, and grain weighed at approximately 12% moisture content. Plot grain yield was transformed to grams per square meter ($g\ m^{-2}$).

Analyses of variance were carried out using plot means. The combining ability effects were calculated using Method I – Model I of Griffing (1956). The phenotypic stability of all characters was investigated using the linear regression coefficient of Finlay and Wilkinson (1963), CPV (Francis and Kanneberg 1978), and AMMI model (Gauch 1992). CPV was calculated as $[100\times (s_i/x_i)]$, where s_i and x_i are the phenotypic standard deviation and the genotypic mean, respectively, of genotype i across the given environments. In this experiment the standard error of the regression line (s_b) was used instead of σ_{di}^2 to assess deviations from the regression model, as suggested by Ortiz and Izquierdo (1994).

AMMI combines into a single model of the analysis of variance for the genotype (G) and environment (E) main effects, with a principal component analysis of the GE interaction. The eigenvectors were scaled as unit vectors, thereby becoming unitless, whereas the singular value for the interaction (λ) has the unit of grain yield. The multiplicative parameters γ_g and δ_e, representing genotype and environment eigenvectors, respectively, were scaled as $\lambda^{0.5}\gamma_g$ and $\lambda^{0.5}\delta_e$ because their product directly delivers the expected value of the interaction terms. The scaled parameters $\lambda^{0.5}\gamma_g$ and $\lambda^{0.5}\delta_e$ represent the genotype and environment IPCA scores.

The genotype-by-environment interaction sum of squares calculated in the original analysis of variance was partitioned into sources of variation due to joint regression and residual deviations using the analysis outlined by Hill et al. (1998) and the single degree of freedom test of non-additivity (Tukey 1949).

Variation between the 64 families for the grain yield stability statistics was partitioned into differences between males, between females, and the interaction among them. After equating the observed mean squares with their Model-II expected values (Griffing 1956), we calculated the components of variance for males, females, and the interaction among them, from which estimates of the additive genetic (σ^2_A) and phenotypic (σ^2_P) components were obtained to determine narrow-sense heritabilities (h^2) following Hill et al. (1998). In addition, additive genetic and phenotypic correlations between the stability parameters were calculated after the analysis of covariance provided the necessary observed cross products and corresponding components of covariance.

Results

Grain yields of the 64 genotypes are given in Table 1, together with a summary of their corresponding stability parameters. Differences among genotypes and environment were both highly significant, as was the interaction between them (Table 2). Clearly, however, environmental effects were the major source of variation, with average grain yield ranging from 54 (Kalengyere 1995 A) to 396 $g\ m^{-2}$ (Kalengyere 1995B, with fungicide application). General and specific combining ability effects were also highly significant, but reciprocal differences were only marginally so. Further analysis indicated that the general combining ability (GCA) was the only source of variation that interacted significantly with the environment ($P<0.001$, data not shown).

Both the heterogeneity of regressions and residual deviations were highly significant (Table 2). Re-testing the heterogeneity of regressions against the residual deviations left its significance unaltered. Heterogeneity of the regression lines, i.e., differences between the slopes of the fitted regression lines, accounted for 23% of the GE interaction for grain yield. The single degree of freedom test for non-additivity was also highly significant for both raw and log-transformed data ($P<0.01$ and 0.001, respectively). The R^2 from the regression analysis for individual genotypes varied from 40% to more than 90%, which revealed the extent of the adequacy of fit of the regression model among the different genotypes. Likewise, CPV ranged from more than 30% to less than 100% (Table 1), indicating the wide response exhibited by the genotypes included in this multi-environment experiment.

Environments accounted for 70.5% of the total variation, while genotypes and the GE interaction explained 8.7% and 19.6%, respectively, of the total variation for grain yield. IPCA 1 and IPCA 2 were highly significant and accounted for 24.3% and 22.7%, respectively, of the

Table 1 Some stability statistics for grain yield in a 8×8 diallel cross. In descending order: grain yield (g m^{-2}), coefficient of phenotypic variation (CPV, %), regression slope (b), deviation from regression (s_b), coefficient of determination (R^2, %), interaction principal components of the AMMI 1 and 2

Parent ♀	♂ (1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Buri	226	223	207	205	202	235	200	143
(1)	45.0	76.4	55.2	43.4	57.8	55.3	71.8	84.4
	0.859	0.815	1.011	0.737	1.038	1.141	1.237	0.832
	0.158	0.126	0.114	0.153	0.110	0.147	0.200	0.322
	85.6	89.3	94.0	82.3	94.6	92.3	88.5	57.2
	0.038	0.020	–0.002	0.007	–0.038	0.049	–0.182	–0.147
	–0.041	–0.040	0.062	–0.120	–0.021	0.093	0.069	–0.151
K. Chiriku	217	172	190	207	188	183	179	213
(2)	72.6	31.3	45.9	66.8	68.2	48.2	62.2	77.6
	1.360	0.467	0.751	1.127	1.096	0.510	0.786	1.354
	0.212	0.070	0.117	0.254	0.186	0.279	0.288	0.300
	89.2	89.8	89.2	79.7	87.4	40.0	59.9	80.3
	–0.020	0.128	0.120	0.165	0.044	0.179	0.120	–0.025
	0.240	–0.168	–0.062	0.098	0.161	–0.163	–0.158	0.270
Esda/Lira	223	180	226	205	198	206	256	207
(3)	56.3	54.6	51.4	62.7	65.3	55.9	46.4	51.9
	1.128	0.721	0.908	0.785	1.082	0.879	0.926	0.902
	0.089	0.240	0.247	0.389	0.213	0.258	0.253	0.172
	97.0	64.3	72.9	44.9	83.8	69.9	72.8	84.6
	–0.025	0.029	0.209	0.329	0.109	0.157	0.071	0.096
	0.035	–0.051	0.039	0.117	0.175	0.080	0.115	–0.057
Vee ‘S’/	231	191	214	211	213	225	150	140
(4)	62.8	58.3	54.4	61.1	63.8	49.5	73.6	84.0
	1.269	0.939	0.756	1.161	1.240	0.955	0.922	0.956
	0.175	0.173	0.334	0.096	0.176	0.160	0.183	0.222
	91.3	85.4	50.5	96.7	90.8	87.7	83.5	78.7
	–0.038	0.025	0.236	–0.000	–0.074	–0.021	–0.019	–0.129
	0.157	0.077	0.092	0.082	0.150	–0.030	–0.076	0.066
Attila	269	255	172	234	199	188	200	181
(5)	40.5	49.1	48.3	55.5	72.4	78.5	93.7	93.7
	0.921	1.096	0.551	0.922	1.268	1.314	1.607	1.412
	0.167	0.148	0.233	0.334	0.164	0.127	0.263	0.283
	85.8	91.7	52.9	60.3	92.3	95.6	88.4	83.3
	0.027	–0.004	0.256	0.150	0.045	–0.141	–0.304	–0.294
	–0.047	–0.002	–0.007	–0.012	0.155	0.033	0.140	0.025
CY8801/	213	197	195	153	201	130	152	111
(6)	52.0	46.9	51.0	54.5	87.9	69.8	72.7	77.9
	0.966	0.687	0.853	0.723	1.571	0.779	0.874	0.681
	0.139	0.219	0.142	0.112	0.171	0.127	0.226	0.179
	90.6	66.1	87.7	89.3	94.5	88.2	74.9	74.3
	0.008	0.068	0.065	–0.013	–0.208	0.063	–0.103	–0.004
	–0.081	–0.183	0.005	–0.155	0.205	–0.120	–0.175	–0.220
F6603147/	171	168	187	181	151	163	140	106
(7)	58.6	79.9	63.3	85.4	87.3	82.5	97.7	84.2
	0.910	1.139	1.024	1.385	1.130	1.153	1.138	0.721
	0.041	0.206	0.154	0.121	0.186	0.188	0.233	0.169
	99.0	85.9	89.8	96.3	88.1	88.3	82.7	78.4
	0.010	0.079	0.056	–0.166	–0.144	–0.108	–0.157	–0.033
	–0.048	0.172	0.119	0.035	–0.030	–0.095	0.002	–0.180
Car853/	188	207	243	146	184	134	143	115
(8)	83.2	52.3	63.6	73.7	94.4	72.8	88.3	89.3
	1.389	0.922	1.303	0.797	1.525	0.680	1.053	0.862
	0.156	0.159	0.241	0.260	0.197	0.258	0.209	0.247
	94.1	87.1	85.4	65.3	92.3	58.2	83.5	71.0
	–0.138	0.013	0.035	–0.082	–0.224	–0.010	–0.130	–0.025
	0.075	–0.025	0.196	–0.184	0.058	–0.272	–0.093	–0.197

Table 2 Analysis of variance of combining ability and the genotype-by-environment interaction in a 8×8 diallel cross for grain yield using the joint regression analysis, the single degree of freedom Tukey's test for non-additivity, and the additive main effect multiplicative interaction (AMMI) model

Source of variation	Degrees of freedom	Mean squares	*P*>F
Joint regression analysis			
Heterogeneity of regressions	63	9537.63	<0.001
Residual deviations	315	6224.26	<0.001
Error	441	3080.75	
Tukey's test (log-transformed data in brackets below raw data)			
Non-additivity	1	22955.10 (19.33)	<0.01 (<0.001)
Residual	377	3336.34 (0.06)	
AMMI (percentage of variation in brackets after mean square)			
Environments (E)	6	1532737.20	<0.001
Replications/E	7	21627.27	<0.001
Genotypes (G)	63	17940.43	<0.001
General combining ability	7	80969.46	<0.001
Specific combining ability	28	12211.38	<0.001
Reciprocal differences	28	7932.09	<0.05
G×E	378	6776.47	<0.001
IPCA 1	68	6067.90 (24.3)	<0.001
IPCA 2	66	5437.29 (22.7)	<0.001
IPCA 3	64	2486.07 (16.1)	NS[a]
IPCA 4	62	2395.65 (14.6)	NS
IPCA 5	60	1984.98 (13.0)	NS
IPCA 6	58	1028.09 (9.2)	NS
Error	441	3080.75	
Coefficient of Variation (%)		29.26	
Mean		190	

[a] NS, Non-significant source of variation

Table 3 Mean squares (MS), variance components (σ^2) and narrow-sense heritabilities (h^2) of stability statistics for grain yield (GY, g m^{-2}), and the associated stability parameters

	GY	b[a]	s_b[b]	R^2[c]	CPV[d]	IPCA1[e]	IPCA2[e]
$MS_{♂}$[f]	3073.301	0.134	0.008	307.9	777.2	0.042	0.030
$MS_{♀}$	3584.801	0.062	0.006	177.4	580.4	0.038	0.022
$MS_{♂\times♀}$	697.832	0.057	0.004	168.1	126.4	0.009	0.013
$\sigma^2_{♂}$[g]	296.934	0.010	0.001	17.5	81.3	0.004	0.002
$\sigma^2_{♀}$	360.871	0.001	0.0003	1.2	56.7	0.004	0.001
σ^2_A	657.805	0.010	0.001	18.6	138.1	0.008	0.003
σ^2_P	1355.637	0.068	0.005	186.8	264.5	0.017	0.016
h^2	0.485	0.150	0.176	0.100	0.522	0.461	0.200

[a] b, Regression slope

[b] s_b, Deviation from regression

[c] R^2, Coefficient of determination (%)

[d] CPV, coefficient of phenotypic variation (%)

[e] IPCA1, First interaction principal component; IPCA2, second interaction principal component

[f] $MS_{♂}$, mean square males; MS=mean square females; $MS_{♂\times♀}$=mean square male×female interaction

[g] $\sigma^2_{♂}$;=Variance among males; $\sigma^2_{♀}$ variance among females; σ^2_A=additive genetic variance, σ^2_P, total phenotypic variance

significant GE interaction (Table 2). The AMMI1 model (main effects plus IPCA1) thus explained up to 84% of the variation for grain yield in this multi-environment experiment, whereas in the AMMI2 model, IPCA1 and IPCA2 jointly accounted for 47% of the GE interaction, or only 9% of the total variation for grain yield. IPCA1 and IPCA2 scores are listed for the 64 genotypes in Table 1. Most of the reciprocal crosses, especially if at least one parent was resistant (R), were near each other in the AMMI1 model (bi-plot not shown). In one of the quadrants, R×R crosses were grouped together with most of the R× susceptible (S) crosses. In an opposite quadrant were almost all the S×S crosses, whereas the S×R crosses were close to the center of the bi-plot or split be-

Table 4 Genetic (above diagonal) and phenotypic (below diagonal) correlations[a] between grain yield and its stability parameters

	GY	b	s_b	R^2	CPV	IPCA1	IPCA2
GY		−0.302	−0.332	−0.011	−0.933	0.707	0.751
b	0.257		−0.165	0.616	0.640	−0.719	0.014
s_b	−0.049	−0.056		−0.959	0.219	0.039	−0.330
R^2	0.183	0.581	−0.803		0.273	−0.564	0.168
CPV	−0.561	0.562	0.221	0.130		−0.934	−0.675
IPCA1	0.283	−0.630	0.180	−0.486	−0.706		0.644
IPCA2	0.577	0.687	0.067	0.328	0.071	0.022	

[a] See footnotes and legend to Table 3 for clarification of abbreviations and terms

Table 5 General combining ability effects[a] for the eight lines (see Table 1 for codes)

Line	GY	b	s_b	R^2	CPV	IPCA1	IPCA2
(1)	21.453	0.029	−0.041	7.033	−5.841	−0.024	0.009
(2)	6.641	−0.110	−0.004	−1.798	−8.259	0.067	0.000
(3)	18.703	−0.095	0.020	−5.698	−11.009	0.122	0.056
(4)	5.078	−0.010	0.007	−1.530	−2.697	0.023	0.015
(5)	12.391	0.190	0.000	4.389	4.691	−0.047	0.071
(6)	−13.734	−0.091	−0.016	−1.123	−1.784	0.003	−0.075
(7)	−21.797	0.071	0.002	2.427	11.972	−0.073	−0.013
(8)	−28.734	0.016	0.031	−3.698	12.928	−0.070	−0.064
SE[b] (g_i)	9.340	0.084	0.022	4.584	3.975	0.034	0.040
SE (g_i–g_j)	13.208	0.119	0.032	6.483	5.621	0.047	0.057

[a] See footnotes and legend to Table 3 for clarification of abbreviations and terms
[b] SE, Standard error

tween both R and S quadrants. No single cross approached the lowest yielding season at Kalengyere (1995 A), indicating that there were no genotypes adapted to this highly stressed environment.

The mean squares, variance components, and narrow-sense heritability for grain yield and grain yield stability parameters are shown in Table 3. The largest significant variation among parents was observed for grain yield, CPV and IPCA1. Consequently, these characteristics had the highest heritabilities (h^2=0.485, 0.522 and 0.461, respectively). The remaining stability parameters had low heritabilities, reflecting the relatively low variation between parents, especially for b, s_b, and R^2.

High additive genetic correlations (r_A) existed between grain yield and CPV, grain yield and IPCA1, and grain yield and IPCA2 (Table 4). The genetic association between CPV and IPCA1 was high and negative, as was that between s_b and R^2, suggesting that these stability parameters may be accounting inversely for the same variation across environments and that one of the two suffices to indicate the dispersion of phenotypic values. These particular additive genetic correlations also exceeded their corresponding phenotypic correlations.

For grain yield the two resistant lines Buri and Esda/Lira had the highest GCA (Table 5). Esda/Lira (line 3) also combined a significantly negative GCA for CPV with a significantly positive GCA for IPCA1, converting this line in a potential parent of offspring with a high and stable grain yield in these East African environments. Conversely, the susceptible lines exhibited significantly negative GCA for grain yield across the environments.

Discussion

The highly significant environmental effects could be attributed to the abiotic and biotic differences across locations and seasons. For example, the amount of precipitation received in each season as well as the annual total precipitation per site were different. Also, Kalengyere had a lower mean temperature than Buginyanya. In addition, one of the experiments in the 1995 (B) season at Kalengyere was sprayed with fungicide to control yellow rust, which significantly affected grain yield (Wagoire et al. 1999). Likewise, the experiments at Buginyanya were yellow rust-free during the test period, while those at Kalengyere always had yellow rust infestation that varied in severity between seasons. Yellow rust severity, as measured by the coefficient of infection, at Kalengyere averaged 7.89% in 1994 (B), 30.17% in 1995 (A) and 24.05% in 1995 (B) (Wagoire et al. 1999). It was not surprising, therefore, that genotypic effects were also highly significant because the parental lines were selected to provide a full range of variation in host response to yellow rust, a fact which partially explained the significant genotype-by-environment effects for grain yield in this multi-environment trial.

The joint regression analysis (Table 2) suggested that the linear model offered an incomplete explanation of the genotype-by-environment interaction for grain yield. Nevertheless, the regression approach may still be of value in identifying those genotypes that are specifically adapted to favorable or unfavorable environments. For example, most of the crosses having K. Chiriku and

Esda/Lira as one parent, had significant regression slopes when tested against their respective error mean squares (data not shown). These crosses are of particular interest since K. Chiriku and Esda/Lira are known to have a high resistance to yellow rust. These two lines also had the lowest (best) GCA for CPV (Table 5). Not surprisingly, therefore, crosses to yellow rust-resistant parents produced high yields in environments where yellow rust was present. Similarly, crosses to the yellow rust-susceptible line 8 exhibited significant regression slopes, although this parent had the most inferior (highest) GCA for CPV, suggesting that offspring of line 8 gave high yields in rust-free environments and very low yields in environments where disease incidence was high. For such genotypes, small differences in the regression slope become important in extreme environments (Becker and León 1988).

The joint regression term, which corresponds to a linear-by-linear interaction, is essentially Tukey's test for removable additivity (Mayo 1987). A highly significant value indicated that analysis should be carried out on the log scale. The significant single degree of freedom test for non-additivity for grain yield, transformed in a log scale, as observed in this multi-environment trial (Table 2), confirmed that some genotypes were showing relatively greater variation in the so-called "poorest" environments as against "best" environments. This occurred because yellow rust, as the most important limiting factor for grain yield in these environments, did not affect all genotypes equally. For example, the poorest environment was season 1995 A at Kalengyere, when the average coefficient of infection was 30% (Wagoire et al. 1999), although it varied from 0.11% (highly resistant genotype) to 99% (highly susceptible genotype). Hence, yellow rust may have been responsible for the significant residual deviations for grain yield in this experiment. This finding suggests that new wheat cultivars for release in Uganda must be resistant to this disease. In this context, the CPV, which measures the dispersion of the data set, may be of interest because a low CPV reflects data that are more closely clustered around the mean; e.g., for the high-yielding offspring derived from the yellow rust-resistant line Esda/Lira.

It has been suggested that a decrease in yield stability may occur in bread wheat while achieving genetic gains in yield potential (Calderini and Slafer 1999). The results from our multi-environment trial suggest that it should be possible to improve both simultaneously using a combined index based upon a stability parameter and grain yield itself. For this material, CPV appears to be the best option because it had the highest h^2 in this experiment, which confirms the results of Lin and Binns (1991) that the variance of a genotype across environments appears to be heritable. Likewise, CPV showed a high additive genetic correlation with IPCA1 of AMMI analysis, whose calculation requires more sophisticated procedures.

Within this material Esda/Lira appears to be the most promising parental line from which to breed high- and stable-yielding cultivars because it combines superior GCA for both grain yield and CPV. Furthermore, these results confirm previous work that indicated that offspring derived from this line displayed better parent heterosis for grain yield (Hill et al. 2000). Hence, recombinant inbred lines having Esda/Lira as one parent offer the best prospect of producing cultivars adapted to rust-prone environments in the East African highlands.

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