

## Genotypic stability analysis of yield and related agronomic characters in wheat-*Agropyron* derivatives under varying watering regimes

A. Moneim Babu Fatih

Institute of Genetics, University of Lund, S-223 62 Lund, Sweden

Received September 9, 1986; Accepted September 25, 1986

Communicated by H. F. Linskens

**Summary.** Genotypic stability of grain yield and yield related traits was estimated for the 8 wheat-*Agropyron* derivatives, 441, 442, 'Vostock', 'PPG 56', 'PPG 56SS', 449, 450 and 441SS, together with two spring wheat controls, 'Drabant' and 'Sv 01382', grown under varying watering regimes for two years. Differences among environments, genotypes and their interactions were highly significant for all traits. The genotypes  $\times$  environments linear response were significant for number of spikelets per main spike, grain number per main spike and single grain weight. No significant linear responses were detected for grain yield or the rest of yield related traits. Deviations from linear responses were highly significant for all traits under study. Grain yield stability was not associated with the stability of yield components. 'PPG 56SS' was identified as the stable variety with the highest mean grain yield per plant under the severe stress environment. Mean grain yields in the severe stress environment were correlated with the genotypic stability parameter " $\alpha$ ". The severe stress environment was recognized as the optimum test environment. The study revealed a shift in the association between grain yield per plant and its components under the varying environments.

**Key words:** Wheat-*Agropyron* derivatives – Genotypic stability analysis – Genotypic environmental interactions – Linear responses

### Introduction

In the absence of adequate knowledge on specific drought resistance mechanisms and the inadequacy of available lab screening techniques, plant breeders

breeding for drought resistance are left with the option of selecting plant genotypes capable of maintaining a reasonable level of yield under drought stress (Fischer and Maurer 1978; Gebeyehou and Knott 1983).

The advances in selection for a complex character as yield are best realized in environments that exhibit maximum variation and provide higher trait heritability (Richards 1978). While Frey (1964) and Johnson and Frey (1967) advocated the use of non-stress environments to select for maximizing yield under unfavourable environments in oats, Hurd (1976) suggested the selection for yield under semi-arid conditions.

The present study was undertaken to evaluate the stability of several wheat-*Agropyron* derivatives, grown under three watering regimes during 1982 and 1983, as part of an extended study aimed at screening for drought tolerance in wheat and wheat-like derivatives.

### Materials and methods

The 10 genotypes investigated included the eight derivatives 441(2), 442(3), 'Vostock' (4), 'PPG 56'(5), 'PPG 56SS'(6), 449(7), 450(8), 441SS(9) and the two wheat controls, 'Drabant' (1) and the breeding line 'Sv 01382'(10). During the years 1982 and 1983, triplicate experimental sets were run in the flats of a nonheated and well ventilated greenhouse at Lund. Each year one of the test groups was kept as a control and received light and frequent irrigations throughout the growing season. The second test group received the same type of irrigation until the late booting stage, after which the water was cut off permanently. This watering regime was meant to induce late and mild water stress. The third test group was watered until the plants established themselves after emergence and then the irrigation was stopped for the rest of the growing season. This treatment was designed to induce early and severe stress.

Each experimental set was laid in a randomized complete block design with three replications. Plant entries were allocated to two-rowed plots, measuring 1.2 m long and spaced 15 cm apart. Seeds were hand sown with 5 cm distance within rows. Fertilizer was applied before sowing at the rate of 120 kg/ha as NPK. Weeds were hand controlled. Each ex-

periment was flanked by nonexperimental rows and the plants at each end of the experimental rows were discarded at harvest. Sowing was on the 28th of April 1982 and the 23rd of March 1983.

Plants were harvested by pulling and then allowed to dry for three weeks in a greenhouse. Twenty plants were selected randomly from each plot and the following data were determined on them: grain yield per plant (GY); effective tiller number per plant (TN); spikelet number per main spike (SNMS); grain number per main spike (GNMS); grain number per plant (GN) grain weight (GW); biological yield (BY); harvest index (HI) and plant height (HT).

#### Statistical procedures

A separate analysis of variance was made for the data collected from each of the six experiments. A combined analysis of variance was carried out with genotypes as fixed effects, while replications and environments were random effects.

The genotypic stability analysis described by Tai (1971) was followed to calculate the stability parameters of yield and related traits. In this analysis  $\alpha$  measures the linear response of genotypes to environmental effects and  $\lambda$  the deviation from linear response. A perfectly stable genotype has  $(\alpha, \lambda) = (-1, 1)$  and a genotype with average stability has  $(\alpha, \lambda) = (0, 1)$ .

Simple correlation coefficients were determined among traits. Procedures from SPSS 1983, BMDP 1983, and written programmes for Sperry Univac 1100 were used for the analysis.

#### Results

The combined analysis of variance exhibited that the mean differences among environments, genotypes and their interactions were highly significant for all traits (Table 1). The genotypes  $\times$  environments linear responses were highly significant for number of spikelets per main spike (SNMS) and grain number per main spike (GNMS). Significant linear responses were detected for

grain weight (GW). Grain yield (GY) and the rest of related traits showed nonsignificant linear responses. Deviations from linear responses were highly significant for the nine traits under study.

The mean performance and the genotypic stability parameters ( $\alpha$  and  $\lambda$ ) for the 10 genotypes are shown in Table 2a–c. The distribution of  $\alpha$  and  $\lambda$  values of the ten genotypes for grain yield per plant (GY) is shown in Fig. 1. The above average stability area (designed B) contained none of the tested genotypes. None of the genotypes scored a value significantly different from  $\alpha=0$  at the 0.05 probability level for GY. Two genotypes (442(3) and 'Sv 01382'(10)) exhibited significant  $\lambda$  values for GY and were confined to the average stability region (i.e.,  $\alpha=0$  and  $\lambda > 1$ ). The other control variety, 'Drabant' (1), was on the border between stability and instability for GY (Fig. 1). The rest of the derivatives were located in the average stability region (i.e.,  $\alpha=0$  and  $\lambda \leq 1$ ) with 'PPG 56SS'(6) occupying the best position, followed by 'PPG 56'(5) and 449(7).

The genotypes (441SS(9) and 'Sv 01382'(10)) showed  $\hat{\alpha}$  values significantly higher than 0 for TN (Table 2a). 'Drabant' and 'PPG 56SS' scored  $\hat{\lambda}$  values significantly greater than 1 and as such they were regarded, together with 441SS and 'Sv 01382' unstable for TN. 'PPG 56'(5) and 449(7) were considered perfectly stable genotypes for SNMS (i.e.,  $\alpha, \lambda = -1, 1$ ). 441, 442, 'PPG 56SS', 441SS and 'Sv 01382'  $\hat{\lambda}$  values were significantly different from 1 for the same character and they were termed unstable for SNMS (Table 2a). The rest of the genotypes showed average stability performance for SNMS. 'PPG 56SS' with  $-1 \hat{\alpha}$  value and a  $\hat{\lambda}$  value not different from 1, was classified as a perfectly stable genotype for GNMS (Table 2b). 'Drabant', 441, 442, 'PPG 56', 449, 441SS and 'Sv 01382', showing  $\hat{\lambda}$  values

**Table 1.** Combined analysis of variance for eight wheat-*Agropyron* derivatives and two spring wheat controls grown for two years under three watering regimes

Source	DF	GY	TN	SNMS	GNMS	GN	BY	HI	GW	HT
Environments	5	14.04**	6.07***	49.09***	174.50***	7,592.99***	100.04***	122.34	324.73***	2,842.86***
Reps. within environments	12	1.94	0.57	1.83	7.73	878.49	12.22	15.86	25.93	56.73
Genotypes	9	3.80***	0.52***	123.56***	624.57***	5,854.98***	26.37***	25.73***	228.50***	4,382.16***
Genotypes $\times$ environments	45	1.05***	0.21**	5.28***	50.81***	642.76***	5.24**	7.03**	28.07***	55.71***
Linear responses	9	0.55 NS	0.12 NS	5.18***	29.97**	223.21 NS	3.74 NS	3.48 NS	16.64*	26.83 NS
Deviations from linear responses	36	1.17**	0.24***	5.31***	56.02***	747.65***	5.61**	7.92**	30.92***	62.93***
Error	108	0.57	0.11	0.86	9.50	256.23	2.67	3.79	8.07	14.32

\*. \*\*. \*\*\* Significant at 0.05, 0.01 and 0.001 probability levels, respectively

NS = Non-significant

**Table 2a.** Mean grain yield (GN), tiller number per plant (TN), spikelet number per main spike (SNMS) and genotypic stability parameters ( $\alpha$  and  $\lambda$ ) of eight wheat-*Agropyron* derivatives and two spring wheat controls in six environments

Variety or line	GY	$\hat{\alpha}$	$\hat{\lambda}$	TN	$\hat{\alpha}$	$\hat{\lambda}$	SNMS	$\hat{\alpha}$	$\hat{\lambda}$
'Drabant'	4.74	0.794	1.976	3.29	0.074	2.430 <sup>a</sup>	19.31	-0.397	1.863
441	4.42	-0.075	1.315	3.60	0.089	0.250	13.06	1.000	3.574 <sup>a</sup>
442	3.89	-0.373	2.061 <sup>a</sup>	3.39	0.270	0.659	12.78	1.000	3.064 <sup>a</sup>
'Vostock'	4.80	-0.034	0.178	3.34	-0.072	0.539	17.28	-0.325	0.740
'PPG 56'	4.78	-0.573	1.474	3.69	-0.477	1.121	17.58	-0.755*	1.049
'PPG 56SS'	4.90	-0.636	0.879	3.52	-0.624	5.049 <sup>a</sup>	17.92	-0.182	2.652 <sup>a</sup>
449	4.50	-0.306	0.782	3.32	-0.285	0.956	13.80	-1.000*	1.447
450	4.16	0.013	0.443	3.29	0.042	0.637	12.62	-0.318	0.813
441SS	3.58	0.084	0.405	3.21	0.385*	0.101	12.74	0.842	3.324 <sup>a</sup>
'Sv 01382'	4.93	1.000	2.159 <sup>a</sup>	3.17	0.599*	0.268	16.89	-0.160	5.248 <sup>a</sup>
Means	4.47			3.38			15.40		

\* Value significantly different from  $\alpha=0$  at 5% level<sup>a</sup> Value greater than  $F_a$  ( $n_1=4$ ,  $n_2=108$ ) value found from F tables when  $\alpha=5\%$  level (see Tai 1971)**Table 2b.** Mean grain number per main spike (GNMS), grain number per plant (GN), grain weight (GW) and genotypic stability parameters ( $\alpha$  and  $\lambda$ ) of eight wheat-*Agropyron* derivatives and two spring wheat controls in six environments

Variety or line	GNMS	$\hat{\alpha}$	$\hat{\lambda}$	GN	$\hat{\alpha}$	$\hat{\lambda}$	GW	$\hat{\alpha}$	$\hat{\lambda}$
'Drabant'	45.36	-0.344	5.550 <sup>a</sup>	127.68	0.513	5.746 <sup>a</sup>	39.02	-0.067	2.231 <sup>a</sup>
441	30.49	1.000	7.459 <sup>a</sup>	94.38	0.187	3.461 <sup>a</sup>	45.90	0.963	2.178 <sup>a</sup>
442	28.82	1.000	6.920 <sup>a</sup>	84.77	-0.175	2.722 <sup>a</sup>	44.83	-0.296	3.204 <sup>a</sup>
'Vostock'	38.17	-0.353	0.359	110.89	-0.055	0.010	43.06	-0.665*	0.404
'PPG 56'	38.97	-0.908	2.112 <sup>a</sup>	120.64	-0.574	1.541	40.43	-0.156	0.352
'PPG 56SS'	40.52	-1.000*	0.973	121.72	-0.448	0.541	41.82	-0.245	1.733
449	33.38	-1.000	2.131 <sup>a</sup>	93.83	-0.383	1.527	49.14	-0.772	2.587 <sup>a</sup>
450	30.67	0.333	0.603	81.83	-0.161	0.316	50.32	-0.227	0.176
441SS	28.64	1.000	5.152 <sup>a</sup>	80.07	0.104	1.623	43.26	0.771	3.315 <sup>a</sup>
'Sv 01382'	40.60	-0.144	2.437 <sup>a</sup>	114.39	0.992	1.689	44.67	0.693	5.141 <sup>a</sup>
Means	35.56			103.02			44.24		

\* Value significantly different from  $\alpha=0$  at 5% level<sup>a</sup> Value greater than  $F_a$  ( $n_1=4$ ,  $n_2=108$ ) value found from F tables when  $\alpha=5\%$  level (see Tai 1971)**Table 2c.** Mean biological yield (BY), harvest index (HI), plant height (HT) and genotypic stability parameters ( $\alpha$  and  $\lambda$ ) of eight wheat-*Agropyron* derivatives and two spring wheat controls in six environments

Variety or line	BY	$\hat{\alpha}$	$\hat{\lambda}$	HI	$\hat{\alpha}$	$\lambda$	HT	$\hat{\alpha}$	$\hat{\lambda}$
'Drabant'	11.78	0.760	1.680	40.18	0.012	0.518	99.62	0.191	6.059 <sup>a</sup>
441	11.05	-0.424	0.856	39.29	0.201	2.085 <sup>a</sup>	88.46	-0.243*	0.303
442	9.89	-0.710	1.025	38.53	0.742	2.353 <sup>a</sup>	91.40	-0.463*	0.444
'Vostock'	12.13	0.139	0.122	39.84	0.135	1.655	126.33	0.042	4.763 <sup>a</sup>
'PPG 56'	12.74	-0.077	2.189 <sup>a</sup>	37.65	-0.163	3.195 <sup>a</sup>	128.63	0.203	6.639 <sup>a</sup>
'PPG 56SS'	12.94	-0.378	1.187	37.64	-0.254	1.939	124.38	0.226	2.461 <sup>a</sup>
449	11.56	-0.179	1.275	38.56	-0.208	0.418	105.30	0.098	1.521
450	10.72	-0.065	0.539	38.22	0.078	1.022	102.94	0.114	3.749 <sup>a</sup>
441SS	9.08	-0.134	0.805	38.42	-0.049	0.669	87.68	-0.296*	0.670
'Sv 013822'	11.74	1.000*	0.347	41.77	-0.494	1.571	103.18	0.128	0.831
Means	11.36			39.01			105.69		

\* Value significantly different from  $\alpha=0$  at 5% level<sup>a</sup> Value greater than  $F_a$  ( $n_1=4$ ,  $n_2=108$ ) value found from F tables when  $\alpha=5\%$  level

**Table 3a.** Simple correlation coefficients among grain yield/plant, yield components and agronomic characters for eight wheat-*Agropyron* derivatives and two spring wheat controls, in six environments

Characteristics	TN	SNMS	GNMS	GN	BY	HI	GW	HT
Grain yield/plant (GY)	0.71***	0.50***	0.58***	0.88***	0.96***	0.34***	0.09 NS	0.49***
Tiller no./plant (TN)		0.14 NS	0.10 NS	0.62***	0.76***	-0.03 NS	0.02 NS	0.36***
Spikelet no./main spike (SNMS)			0.93***	0.77***	0.45***	0.36***	-0.58***	0.41***
Grain no./main spike (GNMS)				0.80***	0.52***	0.35***	-0.43***	0.40***
Grain no./plant (GN)					0.85***	0.30***	-0.36***	0.47***
Biological yield (BY)						0.06 NS	0.08 NS	0.62***
Harvest index (HI)							-0.02 NS	-0.25***
Grain weight (GW)								0.02 NS
Plant height (HT)								

\*\*\* Significant at the 0.001 probability level

NS = Non-significant

**Table 3b.** Simple correlation coefficients among grain yield/plant, yield components and agronomic characters for eight wheat-*Agropyron* derivatives and two spring wheat controls, in the severe stress environment

Characteristics	TN	SNMS	GNMS	GN	BY	HI	GW	HT
Grain yield/plant (GY)	0.89***	0.27 NS	0.31 NS	0.92***	0.98***	0.04 NS	0.26 NS	0.55***
Tiller no./plant (TN)		0.13 NS	0.10 NS	0.88***	0.93***	-0.26 NS	0.12 NS	0.51**
Spikelet no./main spike (SNMS)			0.87***	0.47**	0.24 NS	0.26 NS	-0.53**	0.44**
Grain no./main spike (GNMS)				0.49**	0.26 NS	0.33 NS	-0.47**	0.34 NS
Grain no./plant (GN)					0.92***	-0.03 NS	-0.13 NS	0.55**
Biological yield (BY)						-0.17 NS	0.22 NS	0.56***
Harvest index (HI)							-0.11 NS	-0.06 NS
Grain weight (GW)								0.10 NS
Plant height (HT)								

\*\*, \*\*\* Significant at the 0.01 and 0.001 probability levels, respectively

NS = Non-significant

**Table 3c.** Simple correlation coefficients among grain yield/plant, yield components and agronomic characters for eight wheat-*Agropyron* derivatives and two spring wheat controls, in the fully irrigated environment

Characteristics	TN	SNMS	GNMS	GN	BY	HI	GW	HT
Grain yield/plant (GY)	0.12 NS	0.70***	0.71***	0.85***	0.95***	0.62***	-0.05 NS	0.35 NS
Tiller no./plant (TN)		-0.23 NS	-0.26 NS	-0.02 NS	0.09 NS	0.21 NS	0.29 NS	-0.33 NS
Spikelet no./main spike (SNMS)			0.99***	0.93***	0.82***	0.02 NS	-0.68***	0.71***
Grain no./main spike (GNMS)				0.94***	0.83***	0.03 NS	-0.67***	0.67***
Grain no./plant (GN)					0.92***	0.23 NS	-0.56***	0.54**
Biological yield (BY)						0.36*	-0.26 NS	0.57***
Harvest index (HI)							0.57***	-0.35 NS
Grain weight (GW)								-0.56***
Plant height (HT)								

\*, \*\*, \*\*\* Significant at the 0.05, 0.01 and 0.001 probability levels, respectively

NS = Non-significant

significantly greater than 1, were unstable for GNMS. The remaining genotypes showed average stability performance for this trait. All genotypes with the exception of 'Drabant', 441 and 442 were stable for GN (Table 2b). While 'Vostock' showed a perfect stability for GW, 'Drabant', 441, 442, 449, 441SS and 'Sv 01382', behaved as unstable genotypes for the same character (Table 2b). 'PPG 56', 'PPG 56SS' and 450 exhibited an

average stability performance for GW. 'Sv 01382' with an  $\hat{\alpha}$  value significantly greater than 0 for BY was classified as unstable, together with PPG 56, which had an  $\lambda$  value significantly higher than 1, for the same character. The rest of the genotypes aggregated in the average stability category (Table 2c). 441, 442 and 'PPG 56' were the only genotypes that were classified unstable for HI (Table 2c). 441, 442 and 441SS ex-

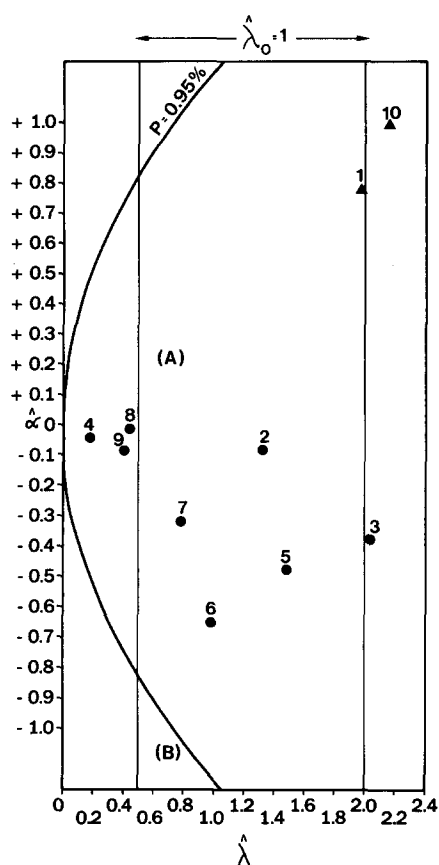


Fig. 1. Statistical stability distribution of 8 wheat-*Agropyron* derivatives and two wheat strains in 6 environments. (A=average stability region, B=above average stability region)

hibited a perfectly stable performance with regard to HT (Table 2c). 'Drabant', 'Vostock', 'PPG 56', 'PPG 56SS' and 450 were unstable for the same character. The remaining genotypes were average in stability for plant height. Correlation coefficients among the nine characters, under the six environments, severe stress environment and fully irrigated environment are shown in Table 3a-c, respectively. Some change in magnitude and sign was noticed for these coefficients under different environments. The correlation coefficients between yield and yield components, under severe stress and fully irrigated environments, were further partitioned into direct and indirect effects (Table 4) with the help of path coefficient analysis (Wright 1921) and as explained by Li (1956) and described by Dewey and Lu (1959).

### Discussion

The combined analysis (Table 1) revealed higher environmental mean squares in comparison to mean squares of genotypes or interactions between genotypes and environments, with regard to grain yield per plant, effective tiller number per plant, grain number per plant, biological yield and grain weight. This suggested that the environmental effects on the means of these traits were generally more profound than the mean differences between the genotypes and even more important than the genotypic environmental interactions. On the other hand, the genotypic mean squares

Table 4. Phenotypic path-coefficient analysis of grain yield per plant and yield components under severe stress and fully irrigated environments

Pathway	Severe stress	Fully irrigated
Grain yield per plant vs. grain weight		
Direct effect	0.344	0.720
Indirect effect via		
Tiller no. per plant	0.100	0.066
Grain no. per main spike	-0.186	-0.840
Total correlation	0.258	-0.054
Grain yield per plant vs. tiller no. per plant		
Direct effect	0.805	0.228
Indirect effect via		
Grain weight	0.043	-0.322
Grain no. per main spike	0.039	0.209
Total correlation	0.887	0.115
Grain yield per plant vs. grain no per main spike		
Direct effect	0.395	1.252
Indirect effect via		
Tiller no per plant	-0.162	-0.483
Grain weight	0.080	-0.058
Total correlation	0.313	0.711
R <sup>2</sup>	0.926	0.879

were higher than the environmental and the genotypic environmental interactions for spikelet number per spike, grain number per main spike and plant height, suggesting a bigger role for the differences between genotypes in the expression of these characters.

When the genotypes  $\times$  environments interactions were further partitioned into interactions due to linear responses and deviation from linear responses, the former were insignificant, while the latter were highly significant for GY. Similar results have been reported by Breese (1969) in grasses, Tai (1971) in potato and Yassin (1973) in field beans. Nonsignificant linear response and highly significant deviations were also evident for TN, GN, BY, HI and HT. Both highly significant linear responses as well as deviations from linear responses, were detected for both SNMS and GNMS. GW exhibited significant linear responses and highly significant deviations from linearity (Table 1). For such characters as SNMS and GNMS, exhibiting higher genotypic mean squares in comparison to environmental mean squares and genotypic environmental mean squares that are several times greater than the error mean squares, it is worth noting that a significant linear response to environments is reported for the trait in question.

The genotype ('PPG 56SS') identified as the most stable genotype for grain yield per plant (Fig. 1), behaved as an unstable genotype with regard to TN, SNMS and plant height and perfectly stable for GNMS (Table 2 a–c). This behaviour suggested that the stabilities of grain yield per plant and these traits are not related in this material (Singh and Bains 1984). Talukdar and Bains (1982) reported that the yield components varied in a compensating fashion to ensure a stable performance of grain yield in wheat under varying environments. Singh and Bains (1984), while working with chickpea, explained this phenomenon in analogous terms to what Grafius (1956) concluded from his studies in oats. If the same argument is adopted here, the grain yield stability reported for 'PPG 56SS' could have been brought about by the plasticity of TN and SNMS.

This compensating shift of grain yield related traits could be elucidated by analysing the correlations between grain yield and related agronomic traits given in Tables (3 a–c) and the path coefficient analysis between yield and yield components under severe stress and fully irrigated environments (Table 4).

The nonsignificant correlation coefficient between grain yield per plant, under the fully irrigated environment (Table 3 c), shifted to a high significant correlation coefficient ( $P < 0.001$ ) under the severe stress environment (Table 3 b). A reverse shift took place for the correlation of yield with spikelet number per main spike (i.e., from a highly significant correlation ( $P < 0.001$ ) under the fully irrigated environment to a nonsignificant coefficient of correlation under the severe stress environment). Grain number per spike was highly correlated with grain yield under the fully irrigated environment ( $P < 0.001$ ) and showed a nonsignificant positive correlation with yield under the severe stress environment (Table 3 b). Grain number per plant and biological yield showed highly significant positive correlations with grain yield per plant under both the environments (Table 3 b–c). Harvest index,

which showed a highly significant positive correlation with grain yield under the fully irrigated environment ( $P < 0.001$ ), was not correlated with grain yield under the severe stress environment (Table 3 b). Grain weight was uncorrelated with grain yield under both environments (Table 3 b–c). Plant height, which showed a low and positive but nonsignificant correlation with grain yield under the fully irrigated environment (Table 3 c), was highly correlated with grain yield per plant ( $P < 0.001$ ) under the severe stress environment.

When the shift in the association between grain yield per plant and its yield components (i.e., GW, TN and GNMS) under the two environments was further partitioned into direct and indirect effects with the help of path coefficient analysis (Table 4), the following was found:

The change in the correlation coefficient between GY and TN, under the varying environments was mainly brought about by an increase in the direct effect of TN on GY (i.e., increasing from a direct effect of 0.228 under the fully irrigated environment to a 0.805 under the severe stress environment). A change in the sign of the indirect contribution of GW added to the increase of the association between GY and TN in the stress environment (Table 4). The change in the association between GY and GNMS under the two environments was mainly brought about by a drastic decrease in the direct effect of GNMS on GY from 1.252 under the fully irrigated environment to 0.395 under the severe stress environment.

Although the direct effect of GW on GY was as high as 0.720 under the fully irrigated environment, the stress environment with only a direct contribution of GW on GY of 0.343 showed a total correlation between GY and GW of 0.258 compared to the  $-0.053$  recorded in the fully irrigated environment. The cause of the shift was due to a big negative indirect effect on GY via GNMS ( $-0.840$ ) under the fully irrigated environment. The coefficient of determination of the three yield components increased from 0.879 under the fully irrigated environment to 0.926 under the severe stress environment (Table 4).

The shift in the association between grain yield and yield components under varying environments, encountered in this study and reported by others, e.g., Talukdar and Bains (1982), is of special importance in plant breeding. This importance stems from the fact that most plant breeders argue that selection for yield components is more efficient than selection for yield per se (Grafius 1956) and consequently resort to indirect selection for yield in early generations. Such indirect selection methods might prove to be ineffective under varying environments, since genetic differences might be confounded by environmental effects on the phenotypic expression.

The shift in the association between yield components and grain yield from one environment to another raises the question: In which environment should one practise selection for drought tolerance? This question has already divided plant breeders into different schools of thought. While Frey (1964) considered the nonstress environment as the optimum environment for practising selection for grain yield in oats, Hurd (1976) suggested the selection for yield under semi-arid conditions. Still others, e.g., Byth et al. (1969), found no difference in genetic advance in yield in soyabeans between lines selected in high and low performance environments. Allen et al. (1978) suggested a procedure for defining the optimum test environment. In this procedure, the value of a macro-environment (i.e., the fully irrigated, mild stress or severe stress) is properly measured by the product,  $r\sqrt{H}$ . Here  $r$  is the correlation coefficient between the deviations of genotype values with respect to the test environment ( $\bar{y}$ ) and the deviations of the genotype values with respect to the entire target population of environments ( $\bar{y}$ ).  $H$ =heritability defined relative to the test environment and obtained by dividing the variance of  $\bar{y}$  ( $\sigma^2\bar{y}$ ) by the variance of the phenotypic mean value employed as the basis for selection ( $\sigma^2\bar{p}$ ). The  $r$  values in this study were -0.09, 0.18 and 1.00 for fully irrigated, mild stress and severe stress test environments, respectively. The  $H$  values for the fully irrigated, mild stress and severe stress test environments were 0.8478, 0.8357 and 0.8316 respectively. While the  $r$  values were very variable, the  $H$  values were very close. The fully irrigated test environment showed the highest genotypic and error variances as has been reported in many other studies, e.g., Allen et al. (1978). These results rank the severe stress environment as the optimum test environment, followed by the mild stress environment. The  $r$  coefficient of 1.00 showed that the severe stress environment is "typical" of the target population of environments (Allen et al. 1978). Indeed the severe stress environment was the only environment which exhibited a significantly negative correlation with the genotypic stability parameter  $\alpha$  (-0.717) for grain yield per plant, thereby indicating high mean yield in association of low  $\alpha$  values.

**Acknowledgements.** I wish to record my gratitude to the undermentioned: Prof. Arne Lundqvist for provision of facilities, supervision and critical reviewing of the manuscript. Dr. Arnulf Merker for supervision. Dr. Thore Denward for support and encouragement. F. K. Lena Ghatnekar and F. K. Ann-Christine Sjögren for qualified technical assistance. Mr. Egon Emanuelson, Mr. Bengt Jacobsson and Mr. Algot Olsson for their excellent assistance in the sowing, handling and harvesting of the material. F. K. Agneta Sternerup-Hansson and Mr. Mohammad Mahloujian for computer programming. F. K. Karin Andersson, Lund University, and Mrs. Margaretha Nornemark, Markett Företagsservice, for typing the manuscript. The study was supported by SAREC's project no. 9.491 SAREC Ans 83/105.

## References

- Allen FL, Comstock RE, Rasmusson DC (1978) Optimal environments for yield testing. *Crop Sci* 18:747-751
- BMDP (1983) (Biomedical computer programs) Statistical software manual. University of California Press, Los Angeles
- Breese EL (1969) The measurement and significance of genotype-environment interactions in grasses. *Heredity* 24: 27-44
- Byth DE, Caldwell BE, Weber CR (1969) Specific and non-specific index selection in soybeans, *Glycine max* L. (Merrill). *Crop Sci* 9:702-705
- Dewey DR, Lu KH (1959) A correlation and path-coefficient analysis of components of crested wheatgrass seed production. *Agron J* 51:515-518
- Fischer RA, Maurer R (1978) Drought resistance in spring wheat cultivars. 1. Grain yield responses. *Aust J Agric Res* 29:897-912
- Frey KJ (1964) Adaptation reaction of oat strains selected under stress and non-stress environmental conditions. *Crop Sci* 4:55-58
- Gebeyehou G, Knott DR (1983) Response of durum wheat cultivars to water stress in the field and greenhouse. *Can J Plant Sci* 63:801-814
- Grafius JE (1956) Components of yield in oats: a geometrical interpretation. *Agron J* 48:419-423
- Hurd EA (1976) Plant breeding for drought resistance. In: Kozlowski TT (ed) *Water deficits and plant growth*, vol 4. Academic Press, New York, pp 137-353
- Johnson GR, Frey KJ (1967) Heritabilities of quantitative attributes of oats (*Avena* sp.) at varying levels of environmental stress. *Crop Sci* 7:43-46
- Li CC (1956) The concept of path coefficient and its impact on population genetics. *Biometrics* 12:190-210
- Richards RA (1978) Genetic analysis of drought stress response in rapeseed (*Brassica campestris* and *B. napus*). 1. Assessment of environments for maximum selection response in grain yield. *Euphytica* 27:609-615
- Singh H, Bains KS (1984) Stability analysis of varietal mixtures in chickpea (*Cicer arietinum* L.). *Z Pflanzenzücht* 92: 159-167
- SPSS (1983) (Statistical package for the social sciences) User's guide. McGraw Hill, New York
- Tai GCC (1971) Genotypic stability analysis and its application to potato regional trials. *Crop Sci* 11:184-190
- Talukdar P, Bains KS (1982) Genotype  $\times$  environment interaction in a diallel cross of wheat. *Z Pflanzenzücht* 89: 197-205
- Wright S (1921) Correlation and causation. *J Agric Res* (Washington DC) 20:557-585
- Yassin TE (1973) Analysis of yield stability in field beans (*Vicia faba* L.) in the Northern Province of the Sudan. *J Agric Sci* 80:119-124