

Genotype-Environment Interaction, Heritability Estimates and Interrelationships for Some Traits in Wheat

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ABSTRACT. Four experiments were carried out during the fall-spring seasons of 1978 to 1982 to estimate the genotype-environment interaction, heritability and interrelationships for grain yield, duration of vegetative and grain filling periods, grain filling rate, kernel weight, and test weight in spring wheat (*Triticum aestivum*, L.). Data collected from 27 cultivars grown in a randomized complete block within each season were subjected to analysis of variance, and estimates of variance components were obtained. Heritability estimates for each trait and correlation coefficients among different variables were also obtained.

Genotype x season interactions, though highly significant, were relatively smaller than the seasonal effects. Narrow-sense heritability estimates for the duration of vegetative and grain filling periods, and kernel weight indicated mostly additive effects. Other traits showed larger non-additive proportions. Genotypes with long vegetative periods had higher grain filling rates and yielded better than those with longer grain filling durations. Under the conditions of frequent high temperature stress during the grain filling period, it is suggested that cultivars with moderate or delayed heading and high grain filling rates exhibit high yielding ability in the Near East environment.

The wheat growing season in most of the Near and Middle East Region extends from middle November to the middle of May under arid or semi-arid, continental climates. Since irrigation is a general practice, temperature is the major constraint to yield in this environment. High temperature during the vegetative period reduces the number of tillers and limits sink size. Moreover, hot winds during grain filling force an early maturity and result in poorly filled grains (Sayed and Gadallah 1983). Although it is possible to adjust for tiller number by increase seeding rates, grain shrivelling must be avoided through the selection of genotypes with suitable grain-filling characteristics.

The relationship between grain yield and the duration of vegetative or grain filling period is changeable in response to environmental conditions. In oats (Coffman and Frey 1961) as well as in sorghum (Eastin 1972), genotypes with long vegetative periods (late heading) out-yielded those with long filling periods (early heading) in non-stress environments, but were more susceptible to yield reductions when environmental stress occurred during the grain filling period. Although both growth periods contributed to yield in wheat (Bingham 1969, Evans and Wardlaw 1976), grain-filling duration but not length of the vegetative period, was positively correlated with grain yield. Yet, when the cause-effect relationship was considered, both characteristics showed positive direct effects on kernel weight which, in turn, affected grain yield (Gebeyehou *et al.* 1982). Another indirect effect of the length of vegetative period occurred through grain filling rate.

Kernel weight and test weight are important characteristics of soft wheats. They are strongly correlated which suggests that the factors affecting one trait are likely to affect the other. Test weight is a complex trait for which, under unfavourable environments such as high temperature or water stress, some lines produce shrivelled grains and poor test weight (Ghaderi and Everson 1971). Kernel weight was positively correlated with grain yield, and selection for heavier kernels increased yield (Mc Neal *et al.* 1978).

The objectives of this study were to determine: (1) The extent of genotype x environment interactions for yield and some related traits in wheat cultivars grown in different seasons, and (2) the interrelationships among these traits and their heritability estimates, and the possibility of grain yield improvement through selection.

Material and Methods

Four field experiments were carried out during the fall-winter seasons of 1978/79 (season I), 1979/80 (season II), 1980/81 (season III) and 1981/82 (season IV) at the Experimental Research Station of the College of Agriculture, King Saud University, Riyadh, Saudi Arabia. The soil is a highly calcareous sandy loam. The site was flood irrigated during the growing seasons. Irrigation water was applied when the soil moisture at a depth of 15 cm reached 50-60% of the available water. Planting occurred after summer fallow on the following dates; Dec. 24, 1978; Dec. 12, 1979; Nov. 11, 1980 and Dec. 6, 1981. The experimental design was a randomized complete block with four replications. Each plot (4.5 m²) consisted of six rows, 2.5 m long with 30 cm spacing between rows. The seedling rate was fixed at 100 kg ha⁻¹ (\approx 300 seeds m⁻²) and NPK fertilizers were applied at the recommended rate for the area. Twenty-seven genotypes of spring wheat (*Triticum aestivum*, L.), chosen from the Middle East Regional Yield Trials to include commercial cultivars as well as advanced lines, were used in the study (Table 1).

Table 1. Cultivar names, or pedigree, and country of origin of the 27 genotypes of bread wheat under test

Name/pedigree	Origin	Name/Pedigree	Origin
1. Mexipak 65	Mexico	15. Arz	Lebanon/Saudi Arabia
2. Sakha 8	Egypt/Pakistan	16. Super X	Mexico/Saudi Arabia
3. CM 15517	Mexico/Lebanon/ Egypt	17. Sakha 3	Egypt
4. CM 8625	Mexico/Egypt	18. Sakha 6	Egypt
5. CM 7806	Mexico/Egypt	19. Sakha 62	Egypt
6. Pavon 'S'	Mexico	20. Sakha 79	Egypt
7. QT 4081	Australia	21. Sakha 80	Egypt
8. Mfo 195/69	USA	22. Giza 157	Egypt
9. Bb-Kal	Mexico/Egypt	23. Chenab 70	Pakistan/Egypt
10. CM 5349	Mexico/Egypt	24. Barouk	Lebanon/Saudi Arabia
11. HD 2172	India	25. Vicam	Mexico
12. CM 16045	Mexico/Syria	26. Florence	Tunisia
13. CM 8865	Mexico/Syria	27. Tanori 71	Mexico
14. CM 8237	Mexico/Lebanon		

At maturity, only the four central rows of each plot, which were not affected by intergenotypic competition, were harvested for grain yield (GY: g m⁻²). Kernel weight (KW:mg) and test weight (TW:kg hl⁻¹) were estimated from the cleaned grain.

For each genotype, length of vegetative period (VP) was calculated as the number of days from emergence to anthesis while the length of grain filling period (GFP) was the number of days from anthesis to maturity. The criterion used to estimate anthesis was 75% of the heads reaching the stage of 10.5.3 on the Feekes' scale (Large 1954). Maturity was marked as the day of complete disappearance of green colouration from the plants. The day of maturity probably deviated from the date of maximum grain dry weight but the criterion was applied uniformly across genotypes. Any overestimation of the GFP was the same for all genotypes and relative differences between seasons or genotypes are valid. Grain filling rates (GFR: g m⁻²day⁻¹) were calculated as: grain yield/GFP.

A separate analysis of variance was performed for each trait in each season. A combined analysis of variance was used to test the significance of genotypes, seasons and their interaction; and to estimate the different variance components, *i.e.* σ_g^2 , σ_{gs}^2 and σ_e^2 . Heritability estimates were calculated by two methods. Seasonal variances were used to provide estimates of broad sense heritability (Hb) for each season: $Hb = \sigma_g^2 / (\sigma_g^2 + \sigma_e^2/r)$, (Vogel *et al.* 1981). Then, they were averaged over

seasons. Narrow sense heritability (Hn) estimates were obtained from the variance components:

$$Hn = \sigma_g^2 / (\sigma_e^2 / s + r \sigma_{gs}^2 / s + \sigma_g^2) / r$$

Genotypic coefficient of variability (GCV) and genetic advance (GA) under selection were calculated from variance components as follows:

$$GCV (\%) = (\sqrt{\sigma_g^2} / \bar{X}) \times 100$$

$$GA \text{ (at 5\%)} = 2.06 \times Hn \times \sigma_p^2$$

$$\text{where } \sigma_p^2 = (\sigma_e^2 / rs + \sigma_{gs}^2 / s + \sigma_g^2)$$

Simple correlation coefficients were calculated for each pair of variables within each season and then averaged over seasons.

Results

Analysis of Variance

The means of average daily temperature, relative humidity and rainfall during different seasons are presented in Table 2. The rainfall differed among seasons, but under irrigation such differences were negligible (Sayed and Ghandorah 1984). Low relative humidity was also common to all seasons. High temperatures occurred during the GFP of season II and lower temperatures prevailed during both VP and GFP of season IV. Under the conditions, significant genotypic differences among cultivars were observed for all traits in all seasons with the exception of GY and GFR in season IV (Table 3).

The seasonal means of GY were almost similar despite the changes in the minimum and maximum values in different seasons (Table 3). As for other traits, there were noticeable changes in the means of different seasons. For instance, the length of VP in season IV was 11.5, 8.4 and 3.5 days longer than those of seasons, I, II and III, respectively. However, little change occurred in the ranges of means from one season to another. Under the circumstances of stable GY means, seasonal means of GFP's and GFR's were of contrasting order. Another aspect was that KW in season IV showed a 22% increase in the mean and 50% increase in the range of variation compared to those of season II. In contrast, the mean of TW in season III was lowest among seasons but accompanied an increase of more than 200% in the range of variation over seasons I and II.

The combined analysis of variance indicated highly significant genotype \times season interactions for all traits caused by changes in the rankings of cultivars as a

Table 2. Mean temperature, relative humidity and rainfall during the four growing seasons*, the vegetative (VP) and grain filling periods (GFP) for the 27 genotypes of bread wheat under test

Season	Dec.	Jan.	Feb.	Mar.	Apr.	VP	GFP
Mean Temperature (C°)							
I: 1978/79	16.4	14.7	18.9	20.3	25.3	16.8	23.8
II: 1979/80	13.9	13.8	17.0	22.5	27.4	15.3	25.6
III: 1980/81	14.4	16.9	17.0	21.0	26.5	16.6	21.3
IV: 1981/82	15.9	14.6	13.7	19.8	24.5	14.2	21.0
Relative Humidity (%)							
I:	43	52	89	34	26	40	31
II:	41	48	48	34	22	48	30
III:	45	52	44	46	28	47	42
IV:	47	50	46	47	44	48	46
Rainfall (mm)							
I:	0.0	5.6	0.0	4.4	1.7	5.6	6.1
II:	0.6	12.9	39.7	0.2	0.2	53.2	0.4
III:	1.3	2.8	0.5	10.3	0.0	4.6	10.3
IV:	0.6	13.9	16.3	22.6	17.6	36.8	34.2

* Meteorological data were recorded at the experimental site.

Table 3. Mean performance and ranges of six agronomic traits measured on 27 genotypes of bread wheat grown in four seasons

Variable	Season			
	I	II	III	IV
1) GY (g m ⁻²)	339** 210-480	380** 270-490	346** 230-470	345** 260-490
2) VP (days)	78.9** 71.0-87.3	82.0** 72.7-88.0	86.9** 76.3-90.8	90.4** 81.0-94.7
3) GFP (days)	37.7** 31.7-45.8	37.7** 32.7-44.0	43.0** 39.5-49.5	42.3** 38.0-53.0
4) GFR (g m ⁻² day ⁻¹)	9.1** 5.9-14.6	10.2** 6.8-12.7	8.1** 5.2-10.0	8.2** 5.6-10.8
5) KW (mg)	35** 30-40	31** 26-36	31** 24-44	38 ** 32-47
6) TW (kg hl ⁻¹)	72.5** 69.5-75.9	71.1** 66.4-75.9	65.6** 57.9-74.7	66.4** 64.4-70.8

Asterisks denote levels of significance among genotypes in each season.

* and **: Significant at 0.05 and 0.01 levels, respectively.

result of the changes in the environment. Seasonal differences turned out to be an important source of variation since their contributed mean squares were relatively larger than those associated with the interactions (Table 4). The most conspicuous feature of the variance components, however, was the large genetic components (σ_g^2) of VP, GFP and, to some extent, KW compared to the corresponding interaction components (σ_{gs}^2). In this respect, GY, GFR and TW followed a contrasting trend (Table 5).

Table 4. Mean squares from combined ANOVA of six traits measured on 27 genotypes of bread wheat grown in four seasons

Source	df	GY	VP	GFP	GFR	KW	TW
Genotypes (G)	26	2.91*	173.**	120.**	2,395.**	121.**	37.6**
Seasons (S)	3	3.57	2,762.**	899.**	10,849.**	1,299.**	479.5**
G × S	78	1.45**	20.**	16.**	905.**	29.**	17.5**
Pooled Error	324	0.68	7.	10.	486.	8.	2.5

* and **: Significant at 0.05 and 0.01 levels, respectively.

Table 5. Estimates of variance components, broad and narrow sense heritability (Hb, Hn), genetic coefficient of variation (GCV) and genetic advance under selection (GA) for six traits, of bread wheat

Parameter	GY	VP	GFP	GFR	KW	TW
1) σ_g^2	0.09	9.59	6.51	93.19	5.76	1.26
2) σ_{gs}^2	0.19	3.15	1.52	104.50	4.93	3.76
3) σ_c^2	0.68	7.67	9.88	486.20	8.34	2.47
4) Hb	0.60	0.96	0.93	0.76	0.94	0.93
5) Hn	0.50	0.88	0.87	0.62	0.77	0.54
6) GCV(%)	8.50	3.70	6.40	10.88	7.19	1.63
7) GA(% of \bar{X})	12.00	7.00	12.00	18.00	13.30	2.00

Heritability

As might be expected, the Hb estimates were higher than the Hn estimates for all traits (Table 5). Both Hb and Hn estimates were large for VP and GFP whereas KW and TW showed large Hb and relatively smaller Hn estimates. Fowler *et al.* (1981) used the ratio of $\sigma_g^2/(\sigma_g^2 + \sigma_c^2/r)$ or the Hb value as an estimate of repeatability measuring the relationship between variation due to genotypes and that due to error in measurements. Applying such parameters to the present study,

VP, GFP, KW and TW showed high repeatability of more than 90%, GFP and GY showed moderate repeatability values.

The traits; GFP, GY, KW and GFR, respectively, showed GCV values ranging from 6.4 to 10.9% and GA values of more than 10%. TW and VP expressed extremely small GCV's, subsequently less than 10% GA values.

Correlation Coefficients

The phenotypic correlation coefficients among the six traits varied from one season to another. Subsequently their averages over seasons produced better estimates. Since the $G \times S$ interactions were highly significant the genotypic correlation coefficients were also calculated (Table 6). For phenotypic correlations, GY was positively correlated to GFR, KW, and TW but not to the length of VP or GFP. Test weight was also correlated to GFR. The lengths of VP and GFP were negatively correlated. Except for the relationships between GY and GFP; VP and GFP; the genotypic correlations revealed more significant relationships. The two traits measuring kernel weight (KW) and kernel density (TW) were interrelated and both were correlated with GY, VP and GFP. Grain filling rate (GFR) was also correlated with VP, GFP and KW.

Table 6. Phenotypic (top right) and genotypic (bottom left) correlation coefficients matrices calculated for six traits of bread wheat

	GY	VP	GFP	GFR	KW	TW
1) GY	—	-0.16	-0.01	+0.80**	+0.19*	+0.28**
2) VP	0.14	—	-0.83**	-0.03	-0.11	+0.13
3) GFP	0.11	0.16	—	-0.07	+0.15	-0.08
4) GFR	0.03	0.67**	0.59**	—	+0.10	+0.30**
5) KW	0.52**	0.71**	0.70**	0.36**	—	+0.18
6) TW	0.36**	0.20**	0.23**	0.09	0.027**	—

* and **: Significant at 0.05 and 0.01 levels, respectively.

Discussion

The present study involved five agronomic traits known for their direct or indirect effects on GY. Two of these traits *vis*: VP and GFP related to the phenological events of the plant and strongly respond to environmental stresses (Wiegand and Cuellar 1981). The other three; GFR, KW and TW, control grain characteristics. The traditional yield components, *i.e.* number of spikes per unit

area and kernels per spike, were not included since they are subject to compensation and could be easily adjusted through cultural practices (Mc Neal *et al.* 1978). The results obtained in the study, however, depend largely on the sample of genotypes chosen and the environments used. The present genotypes were a representative sample of currently grown cultivars and acceptable advanced lines from wide genetic background. Therefore, they were expected to respond differently during the seasons of testing which can result in reasonable estimates of variance components.

The effect of high temperature stress was noted on some traits during different periods of plant growth. Compared to season I, lower temperatures during pre-anthesis stages in season IV resulted in delayed heading and long VP's. Similarly, compared to seasons III and IV, GFP's measured during seasons I and II were shorter and reflected the high temperatures encountered during the later half of the GFP's. These results are in agreement with Wiegand and Cuellar (1981) that temperature affects the duration of various growth stages of the wheat plant.

The genotype \times season interaction, which is a measure of non-additive gene action, is an indication of some environmental aspects whose pattern among seasons were different. Being highly significant in the present study, it indicated that certain genotypes consistently performed differently during the years of testing. On the other hand, the large seasonal variances indicated that individual seasons exerted major influence on the relative performance of genotypes. In view of these results, breeding of wheat cultivars with a broad spectrum of adaptation, is recommended for these conditions, as suggested by Comstock and Moll (1963). This will require the evaluation of different genotypes in a range of environments to select those best adapted.

The reduction in the Hn relative to the Hb estimates reflect the importance of the non-additive variance component. Estimation of GY in yield trials is usually associated with high experimental errors (Fowler *et al.* 1976). Confounding and interactions caused by environmental effects further decreased the Hb estimate or repeatability for GY, therefore it approached the Hn estimate (0.60 vs 0.50). Such behaviour contrasted that of TW, which is precisely measured in the laboratory, therefore expressed a high Hb or repeatability estimate (0.93). Despite such differences, both traits expressed similar proportions of additive variance (0.50 and 0.54, respectively). Ghaderi and Everson (1971) reported a similar value (0.48) for TW.

Edwards *et al.* (1976) reported only additive gene effects for KW and mostly additive for VP. The present findings indicate the presence of only small proportions of non-additive genes for KW, VP and GFP. Such strict genetic control (high Hn), and the relatively small G \times S interactions for these traits, indicated

little variation in genotypic response to environmental stresses. Water and high temperature stresses have been associated with the duration of VP and GFP (Lal *et al.* 1978, Wiegand and Cuellar 1981, Sayed and Ghandorah 1984). Since soil moisture was sufficiently available during the seasons of testing, it appears that temperature was the most probable major factor affecting these traits. Under the conditions, the relative genotypic response to temperature, however, was similar among cultivars. Pirasteh and Welsh (1980) indicated that wheat genotypes, though heading earlier under higher temperatures, maintained their relative rankings at each temperature. This argument suggests that although selection can successfully alter the duration of these traits (due to high heritability), it should be practiced each season, on a scaled manner, among genotypes grown within the same environment.

The negative relationship ($r = -0.83$) between the lengths of vegetative and grain filling periods seemed to be of developmental rather than genetic nature (Adams 1967). These traits though they develop in sequential pattern, they are free to vary in response to environmental conditions and are dependent on the time of heading. This view was supported by the insignificant genotypic correlation between the two traits. Under the circumstances of almost stable grain yields across seasons, KW which was highly correlated with GY, seemed to better explain the hidden dependency of GY on GFR and, in turn, the durations of VP and GFP (pre-anthesis and post-anthesis contributions). When the conditions during GFP were favourable, mild temperatures as in season III, genotypes having long GFP's showed higher GFR's ($r = + 0.7$). Otherwise, high temperatures during the GFP in season II favoured genotypes with long VP's which showed high GFR's ($r = + 0.7$). These findings confirm that the pre-anthesis and post-anthesis contributions to GY, which stabilizes KW via GFR, are not only equally important (Bingham 1969, Gebeyhou *et al.* 1982) but also show that the pre-anthesis contribution could be of more importance under stress conditions (Yoshida 1972, Gallagher *et al.* 1975).

Examination of the yielding strategies of different genotypes, indicated that 18 days separated the earliest heading genotype, Sakha-3, from the latest genotype, Bb-Kal (Table 7). The top 10 yielders headed nine or more days later than Sakha-3, of which three were not significantly different from Bb-Kal, KW and TW were more or less the same among these genotypes. It seems that delayed heading or long vegetative period was favoured by these genotypes as a high yielding strategy. Therefore, they have the advantage of relying on a large pre-anthesis storage to secure high grain filling rates under stress conditions.

In conclusion, the above discussion indicates that environmental conditions during the growing season determine the lengths of vegetative and grain filling periods with respect to their possible contribution to grain yield. Therefore, under

the conditions of frequent high temperature stress during the grain filling period, which results in strong seasonal effects, it is suggested to breed cultivars with a broad spectrum of adaptation. Genotypes with moderate or long vegetative duration and high grain filling rates seem to meet these conditions. The high heritability estimates for these traits warrant their selection.

Table 7. Mean performance of the 10 top yielders, the earliest and the latest to heading genotypes (averages of 4 seasons) of 27 genotypes of bread wheat

Cultivar	GY (g m ⁻²)	VP (days)	GFP (days)	GFR (g m ⁻² day)	KW (mg)	TW (kg hl ⁻¹)
1) Giza 157	436	81	43	10.1	35	71
2) Sakha 80	419	89	37	11.6	33	72
3) Barouk	416	82	42	9.9	35	70
4) Chenab 70	412	83	43	9.7	34	73
5) Sakha 61	405	81	44	9.2	35	72
6) Tanouri	397	81	44	9.1	35	71
7) Sakha 62	391	88	36	11.0	32	72
8) Sakha 79	389	89	37	10.7	34	71
9) Arz	372	84	40	9.6	35	72
10) CM 15517	362	82	43	8.5	34	67
11) Sakha 3	327	72	47	7.0	33	70
12) Bb-Kal.	303	90	38	8.1	31	65
Overall mean	353	84	40	8.9	33	69
L.S.D. (.05)	29	1.9	0.8	1.5	2	1.8

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دراسة التفاعل بين التركيب الوراثي والبيئة وعلاقة ذلك بدرجة التوارث والعلاقات بين بعض الصفات في القمح

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المملكة العربية السعودية

أجريت أربع تجارب خلال موسمي الخريف والربيع وللسنين ١٩٧٨ - ١٩٨٢ م وذلك لاختبار التفاعل بين التركيب الوراثي والبيئة، ودرجة التوارث والعلاقات لصفات المحصول - طول مراحل النمو الخضري، وامتلاء الحبوب، ووزن الحبة، والوزن النوعي لبعض أصناف قمح الخبز الربيعي. وقد سجلت البيانات على ٢٧ صنفاً زرعت في تصميم ذي قطاعات كاملة العشوائية، وأجري عليها تحليل للتباين وتقدير لمكوناته. كما قدرت درجة التوارث ومعاملات التلازم للمتغيرات المختلفة. وتشير النتائج إلى أن التفاعل بين التركيب الوراثي والموسم، رغم معنويته، إلا أنه كان أقل بكثير من تأثير الموسم. واعتمدت درجة التوارث بالمعنى المحدود لصفات طول مراحل النمو الخضري وامتلاء الحبوب، وكذلك لوزن الحبة على التأثير المتجمع للجينات، بينما أظهرت الصفات الأخرى مزيداً من التأثير غير المتجمع. وأظهرت التراكيب الوراثية ذات المراحل الطويلة للنمو الخضري معدلاً أعلى لامتلاء الحبوب، وكذلك تفوقاً في المحصول على التراكيب ذات المراحل الطويلة للإمتلاء، وتحت ظروف زيادة الإجهاد الناجم عن ارتفاع درجة الحرارة خلال مرحلة الامتلاء فإنه يقترح أن الأصناف ذات التزهير المتوسط أو المتأخر مع ارتفاع في معدل الامتلاء هي أكثر مناسبة للمحصول العالي تحت ظروف البيئة السائدة في المنطقة.