

CROP BREEDING, GENETICS & CYTOLOGY

Genotype-by-Environment Interactions of Barley in the Mediterranean Region

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ABSTRACT

In the Mediterranean region, progress in selection for yield in harsh environments is hampered by large environmental variation between seasons and locations. This study analyzes the genotype-by-environment (GE) interaction of 36 two-rowed genotypes of barley (*Hordeum vulgare* L.), grown in 14 environments in Syria and North Africa. It assesses the effect of growth type (winter or spring type) and heading date on the GE interaction and determines whether or not high-yielding (HY) environments are representative of low-yielding (LY) ones. Average grain yield per environment ranged from 7 to 513 g m⁻². Genotypes and environments were classified by a cluster analysis and the interaction was analyzed with an additive main effects and multiplicative interaction model. Genotypes were classified into four clusters, related to their growth type and earliness of heading. Environments were clustered in a HY and LY group; this classification was related to seasonal rainfall and temperature. Medium-early heading winter types had a positive interaction with LY environments and a negative interaction with HY environments, whereas late heading genotypes (spring and winter types) had the opposite interaction pattern. Early heading spring types had above-average mean yields; the highest-yielding among them tended to have a low interaction with environments. High-yielding environments did not discriminate well between genotypes with high or low yields in LY environments, and may thus have limited value for yield selection for LY environments. For a breeding program aimed at improving yield in environments where favorable conditions are rare, selection for yield should be done in representative less-favorable environments.

GRAIN YIELD OF BARLEY in the east Mediterranean region is limited by seasonal rainfall, rainfall distribution, and temperature (Hadjichristodoulou, 1982; Ceccarelli et al., 1991). Ceccarelli et al. (1991) reported, for barley in northern Syria, average yields of 1562 kg ha⁻¹ and 32 kg ha⁻¹ from the same site in two successive seasons with minor differences in total rainfall. The crop failure was due to the combined effect of low temperatures and drought stress. Under such variable conditions, GE interactions are large.

The GE interaction can be partitioned by parametric linear regression techniques (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) or multivariate techniques (Kempton, 1984; Lin et al., 1986; Zobel et al., 1988; Nachit et al., 1992a). Since genotype responses are multivariate rather than univariate, the latter techniques are preferable (Lin et al., 1986). Multivariate techniques are

in general more effective in explaining GE interactions than linear regression models (Zobel et al., 1988; Nachit et al., 1992a).

Among the multivariate techniques, cluster analysis, based on differences in yield response of genotypes across environments, is the most widely used. Abou-El-Fittouh et al. (1969) applied this technique first for cotton (*Gossypium hirsutum* L.) trials in the USA. A disadvantage of the technique, however, is that the clustering itself gives no insight into the yield response of genotypes across environments. This problem has been overcome by combining the analysis of main effects and interaction into an additive main effects and multiplicative interaction (AMMI) model (Gauch, 1988). In this model, main effects are first accounted for by an analysis of variance, whereafter the interaction is analyzed by a principal component analysis (Gauch, 1988; Gauch and Zobel, 1988). The optimum number of interaction principal component axes (IPCA) to be retained in the model, in order to obtain the most accurate estimation for grain yield, can be determined by either a postdictive or predictive assessment. The postdictive assessment uses an *F*-test to identify the significance of each IPCA. The predictive assessment splits the data set into a part for model construction and a part for model validation and uses the cross validation technique (Wold, 1978; Krzanowski, 1983).

Genotype-by-environment interactions can reduce the progress of a breeding program if the test environment is not representative of the target environment. Differential yield responses of genotypes can be caused by differences in phenology. In a comparison across Mediterranean environments between two barley genotypes with nearly similar heading dates but of different growth type (winter versus spring), van Oosterom et al. (1993) showed that the winter type, which required vernalization, had a lower yield response to both rainfall in winter and frost in spring. This suggests that the winter type has a lower yield in favorable wet environments, but a higher yield stability in unfavorable cold environments. Since the negative effect of late heading on grain yield increases as terminal stress increases (Fischer and Maurer, 1978; Bidinger et al., 1987; Ceccarelli, 1987), HY environments may not be representative of LY ones. Consequently, selection for yield in LY environments can best be done by repeated selection in representative LY environments (Ceccarelli and Grando, 1991).

The objectives of our study were first to assess the relationship between yield response and development for barley in Mediterranean environments, and second to

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Abbreviations: AMMI, additive main effects and multiplicative interaction; E, environment; G, genotype; GE, genotype by environment; HY, high-yielding; IPCA, interaction principal component axis; JLB Jordanian local barleys; LY, low-yielding; RMS PD, root mean square predictive difference. SLB, Syrian local barleys; SS, sum of squares

Table 1. Origin, average grain yield, growth type, and heading date of the genotypes used in the analysis, classified according to the results of the cluster analysis.

Name†	Origin	Grain yield‡ g m ⁻²	Growth type§	Heading date¶
Cluster 1				
Harmal	ICARDA	280.2	S	30.9
WI 2269	Australia	274.8	S	31.3
S BON 96	ICARDA	252.6	S	32.3
ER/Apm	—	272.1	S	34.6
Roho/Mazurka	ICARDA	283.3	S	38.7
WI 2291	Australia	253.8	S	35.6
WI 2291/BgS	Australia	238.6	S	35.5
S BON 29	ICARDA	241.4	S	34.1
A16/2728/Sv Mari	ICARDA	237.7	S	35.9
Jerusalem a barbes lisses/CI10836	ICARDA	230.7	S	37.1
WI 2198	Australia	235.1	S	34.2
Arabi Abiad	North west Syria	231.8	W	36.4
SLB 39-99	South Syria	230.6	W	33.8
SLB 60-02	North west Syria	227.8	W	37.8
JLB 08-89	Jordan	210.6	W	35.4
JLB 08-84	Jordan	206.1	W	34.2
WI 2291/WI 2269	Australia	254.9	S	31.5
Roho	Egypt	261.0	S	34.2
Cluster 2				
Arabi Aswad	East Syria	187.0	W	36.5
SLB 45-16	North east Syria	176.9	W	38.6
SLB 62-68	South west Syria	178.6	W	34.7
SLB 45-38	North east Syria	190.9	W	36.7
SLB 45-65	North east Syria	198.6	W	38.9
SLB 62-99	South west Syria	192.7	W	34.3
JLB 08-06	Jordan	207.4	W	34.6
SLB 39-43	South Syria	205.5	W	35.9
SLB 03-77 (Tadmor)	East Syria	199.8	W	35.7
Cluster 3				
Atem	UK	221.5	S	43.0
BON 27	ICARDA	214.7	S	41.3
S BON 89	ICARDA	203.8	S	40.7
Alger/Union	Algeria/Germany	188.5	S	39.5
WI 2291/EH 70-F3-AC	Australia India	215.7	S	36.6
Kervana/Mazurka	ICARDA	205.5	S	38.4
Swanneck	UK/S. Africa	195.0	S	36.8
Cytris	France	233.4	S	38.7
Cluster 4				
Lignee 131	France	226.1	W	45.1

† SLB = Syrian local barleys; JLB = Jordanian local barleys.

‡ Grand mean grain yield: 224.0 g m⁻².

§ S = spring type; W = winter type.

¶ Days from 1 March to heading. Average days to heading: 36.4.

determine whether or not HY environments are representative of LY ones.

MATERIALS AND METHODS

Plant Material and Environments

Thirty-six two-rowed genotypes of barley were grown in 14 environments (location-by-year combinations), nine in Syria and five in western North Africa. Details of the genotypes are given in Table 1. The genotypes referred to as Syrian or Jordanian local barleys (SLB and JLB) are pure lines extracted from landraces. Arabi Abiad and Arabi Aswad, however, two barley landraces widely grown in Syria, are mixtures. The word genotypes is thus used for convenience and does not imply homozygosity of all material used.

In Syria, experiments were carried out at three locations: Tel Hadya, Breda, and Bouider (Table 2), ranging in mean annual rainfall from 327 mm at Tel Hadya to 262 mm at Breda and 219 mm at Bouider. The North African environments in this study in general had higher amounts of rainfall, especially in March and April (Table 2). Although frost occurs, winters in North Africa tend to be milder than in Syria. Latitudes of

the sites used in Morocco were comparable to those of south Syria.

The experimental design was a randomized complete block with three replications. Plots were 2.4 m wide (12 rows, 20 cm apart) and 5 m long. Emergence dates ranged from early November to late January. Grain yield was obtained from a hand-harvested sample of 0.8 m²; for environment Khroub 1989, combine-harvested yields were used. Average grain yields ranged from 7 g m⁻² at Bouider 1989 to 513 g m⁻² at Khroub 1989. The low yields at Tel Hadya and Bouider in 1989 were due to the combination of a late emergence and a very dry spring; plants were mainly growing on stored moisture.

Classification of Genotypes and Environments

A cluster analysis of grain yield data was used to group genotypes. The similarity between two genotypes was expressed as the squared euclidean distance. The clustering method employed was the average linkage method, which estimates the distance between two clusters as the average distance between pairs of genotypes, one in each cluster. To adjust for differences in yield level between environments, data for each environment were standardized to a mean of zero and a standard deviation of one (Fox and Rosielle, 1982). A large distance between the last few clustering steps was an indicator of truncation of the clustering. Environments were grouped similarly, using the same set of standardized data.

Genotype-by-Environment Interaction

To analyze the GE interaction, the AMMI model was used (Gauch, 1988; Nachit et al., 1992a). The equation of this model is:

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_{n=1}^N \lambda_n \gamma_{gn} \delta_{en} + \theta_{ge} + \epsilon_{ger}$$

where Y_{ge} is the yield of genotype g in environment e ; μ is the grand mean yield; α_g is the genotype mean deviation; β_e is the environment mean deviation; λ_n is the eigenvalue of the n^{th} principal component; γ_{gn} and δ_{en} are the genotype and environment scores for the n^{th} principal component; θ_{ge} is the residual and ϵ_{ger} is the random error, which is the difference between the Y_{ge} treatment mean and the single observation for replicate r (Gauch, 1988; Zobel et al., 1988). The additive part of the AMMI model (μ , α_g , β_e) is estimated from an analysis of variance and the multiplicative part (λ_n , γ_{gn} , and δ_{en}) from a principal component analysis (PCA). If most of the GE interaction sum of squares (SS) can be captured in the first N PCA axes, a reduced AMMI model, incorporating only the first N axes, can be used. The interaction between any genotype and environment can be estimated by multiplying the score for the interaction principal component axis (IPCA) of a genotype ($\lambda_n^{0.5} \times \gamma_{gn}$) by an environment IPCA score ($\lambda_n^{0.5} \times \delta_{en}$).

Both postdictive and predictive assessments were used to analyze the GE interaction. In the postdictive assessment, those IPCAs which were not significant were pooled into the residual. In the predictive assessment, two random replications for each GE combination ($36 \times 14 \times 2 = 1008$ observations) were used for construction of the model and one replication (504 observations) for validation. The optimum number of IPCAs to be retained in the model was identified by the cross-validation technique (Wold, 1978; Krzanowski, 1983; Nachit et al., 1992a). The root mean square predictive difference (RMS PD) was used as the criterion for predictive success; the RMS PD is the square root of the squared difference between the predicted values and validation observations, summed over all genotypes and environments and divided by the number of validation observations (Nachit et al., 1992a). The AMMI model with the lowest RMS PD value has the best predictive value.

Table 2. Latitude, mean barley grain yield, precipitation, and classification of 14 Mediterranean environments.

Year	Site	Latitude	Grain yield	Precipitation†		Cluster
				O-A	M-A	
	Syria		gm⁻²	mm		
1985-1986	Tel Hadya (TH6)	36°01	331	287.5	48.1	A
	Breda (BR6)	35°56	134	207.9	34.0	B
	Bouider (BO6)	35°40	133	177.8‡	42.0	B
1986-1987	Tel Hadya (TH7)	36°01	246	340.3	76.1	B
	Breda (BR7)	35°56	148	244.6	64.6	B
1987-1988	Tel Hadya (TH8)	36°01	296	495.2	122.0	A
	Bouider (BO8)	35°40	273	376.0	66.4	A
1988-1989	Tel Hadya (TH9)	36°01	89	219.5	17.8	B
	Bouider (BO9)	35°40	7	184.0	26.7	B
	Morocco					
1987-1988	Annoceur (AN8)	33°50	200	462.3	64.0	A
1988-1989	Annoceur (AN9)	33°50	286	364.7	193.3	A
	Jemaa Shiam (JS9)	32°40	226	408.0‡	133.0	A
	Sidi El Aidi (SA9)	33°10	254	406.4	134.0	A
	Algeria					
1988-1989	Khroub (KH9)	36°25	513	326.8	99.7	A

† O-A, October-April; M-A, March-April.

‡ Excluding October.

The average RMS PD value of 25 validation runs was used; use of 100 validation runs did not change the results.

Environmental Contributions to the Genotype-by-Environment Interaction

If the GE interaction is significant, individual environments must have a different pattern of contributions to the classification of genotypes. To assess whether or not HY environments discriminate well between genotypes with a good or poor performance in LY environments, environmental contributions to the major fusion points in the genotype clustering were calculated. This contribution was calculated as the squared difference in each environment between the mean standardized yields of the two groups clustered (Shorter et al., 1977).

RESULTS

Genotype and Environment Classification

The classification of genotypes was truncated at the four-group level (Fig. 1) and the differences between clusters explained 63.0% of the genotypes SS (Table 3). The first cluster contained 18 genotypes (Table 1). All but two of them had an above-average grain yield and, with two exceptions, headed earlier than average. Apart from five landraces, these genotypes were spring types. Cluster 2 contained nine landraces; all of them were winter types with a below-average mean grain yield and heading close to the average. The third cluster included eight spring types, characterized by a below average mean grain yield (except genotype Cytris) and late heading. The fourth cluster contained only Lignee 131, a winter type with late heading but an average grain yield close to the grand mean.

The classification of environments was truncated at the two group level (Fig. 2); this division explained 51.4% of the SS for environments (Table 3). The two clusters had significantly different average grain yields ($P < 0.001$ for a t -test), despite standardization of the data. Environments with yield levels of 200 g m⁻² and above were grouped in cluster A and those with yield levels below 200 g m⁻² in cluster B. An exception was Tel Hayda

1987 (average yield of 246 g m⁻²), which was clustered with the LY environments.

Genotype-by-Environment Interaction

In the AMMI model, IPCA1 explained 50.4% of the interaction SS (Table 4). In the postdictive assessment, the first five IPCAs were significant (Table 4). The model captured 98.1% of the treatments SS, using 263 degrees of freedom (df): 35 for genotypes, 13 for environments and 215 for IPCA1 to IPCA5. In the predictive assessment, AMMI1, the model including only the first IPCA, had the lowest value for RMS PD and was hence most predictive (Table 5). This model accounted for 92.2% of the treatments SS using 95 df; the remaining 7.8% of the treatments SS was non-interpretable random variation (noise). The full AMMI model needed 3.8 replications in order to be as effective as the AMMI1 model based on two replications. AMMI1 thus had a replication benefit of 1.8, equal to 881 observations (plots) com-

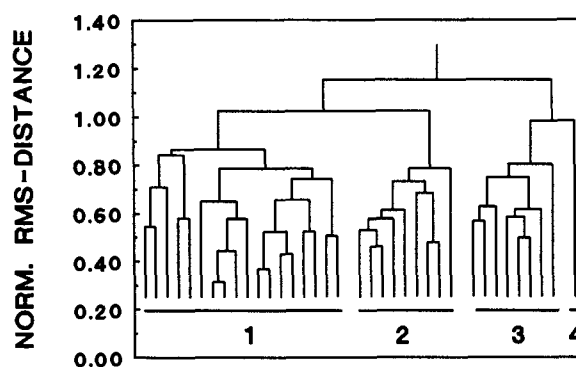


Fig. 1. Dendrogram from average linkage cluster analysis of standardized grain yield of 36 two-rowed barley genotypes grown in 14 Mediterranean environments. Distances between clusters are expressed as root mean square (RMS) distances. Values below each cluster represent the cluster number. The order of genotypes from the left to the right corresponds with the order in Table 1.

Table 3. Analysis of variance plus the partitioning of the sum of squares into among- and within-group components for grain yield of 36 two-rowed barley genotypes across 14 environments in Syria and North Africa.

Source	df	SS	MS
Total	1511	30728338	20336**
Treatments	503	26583859	52851**
Genotypes (G)	35	1249076	35868**
Among clusters (C _g)	3	786914	262304**
Within clusters (G(C _g))	32	462161	14443**
Environments (E)	13	21158336	1627564**
Among clusters (C _e)	1	10878246	10878246**
Within clusters (E(C _e))	12	10280090	856674**
G × E	455	4176447	9179**
Rep(env)	28	488050	17430**
Error	980	3656505	3731

** indicates significance at $P < 0.01$.

pared with the full model. Results will therefore focus on the AMMI1 model.

A biplot of the AMMI1 model is given in Fig. 3. For both genotypes and environments, clusters in the biplot were well separated, except for the separation of Cluster 3 from Cluster 4. Environments of Cluster A consistently had lower values for IPCA1 than Cluster B environments. The landraces of Cluster 2 had a positive interaction with all the environments of Cluster B (similar sign for IPCA1). Their interaction with Cluster A environments was negative or close to zero, except with Tel Hadya 1986. Genotypes of Clusters 3 and 4 had average grain yields comparable to those of Cluster 2, but an opposite response pattern, with a negative interaction with LY environments and a positive interaction with HY environments. Genotypes of Cluster 1 had a wide range in response patterns; however, the highest yielding genotypes had, with two exceptions, a low interaction with environments, as their value for IPCA1 was close to zero.

Environmental Contributions to the Genotype-by-Environment Interaction

Environments of Cluster B (LY environments) had a high contribution to the separation of genotype Clusters 1 and 2 from Clusters 3 and 4 (Table 6). This was due to the low grain yield of genotypes of Clusters 3 and 4

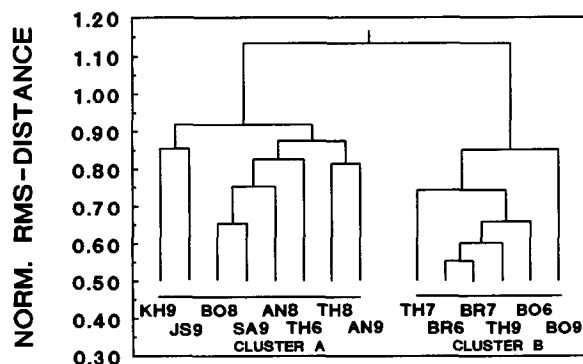


Fig. 2. Dendrogram from average linkage cluster analysis of standardized barley grain yield of 14 environments in Syria and North Africa. Yield level of each environment is given in Table 2. Distances between clusters are expressed as root mean square (RMS) distances.

Table 4. Partitioning of the genotype-by-environment interaction for grain yield of 36 barley genotypes, grown in 14 Mediterranean environments, by the postdictive AMMI model.

Source	df	SS	MS
Treatments	503	26583859	52851**
Genotypes (G)	35	1249076	35868**
Environments (E)	13	21158336	1627564**
GE interaction	455	4176447	9179**
IPCA1	47	2105759	44803**
IPCA2	45	602238	13383**
IPCA3	43	411031	9559**
IPCA4	41	331427	8084**
IPCA5	39	226174	5799*
Residual	240	499816	2083
Rep (env)	28	488050	17430**
Error	980	3656505	3731

*, ** indicates significance at $P < 0.05$ and $P < 0.01$, respectively.

in these environments. Environments of Cluster A (HY environments) had a low contribution to this separation, indicating that they did not discriminate well between genotypes with high or low yields in LY environments. The HY environments, however, discriminated genotype Cluster 1 from Cluster 2, due to the low yield potential of Cluster 2 genotypes. In general, they also separated Cluster 3 better from Cluster 4 than did LY environments.

DISCUSSION

The classification of genotypes was related to heading date and growth type: late heading genotypes were grouped in Clusters 3 and 4, whereas most winter types were grouped in Clusters 2 and 4. Early heading spring types were thus grouped in Cluster 1, medium early heading winter types in Cluster 2, late heading spring types in Cluster 3, and late heading winter types in Cluster 4. Different combinations of growth type and earliness are associated with differences in apical development pattern (Van Oosterom and Acevedo, 1992). The classification of genotypes therefore strongly suggests that development pattern has a marked effect on yield response across environments. An association between morpho-physiological traits and components of the GE interaction in the Mediterranean region has also been reported for durum wheat (*Triticum turgidum* L. var. *durum*) (Nachit et al., 1992b).

The five landraces that were grouped in Cluster 1 all had a high average grain yield compared with the other landraces (Table 1). This was due to a better performance in HY environments than the other landraces. The landrace with the highest average yield in these environ-

Table 5. Average root mean square predictive difference (RMS PD) for seven AMMI models, based on 25 validation runs and used for the predictive AMMI model.

Model	RMS PD
AMMI0	g/m ² 76.56
AMMI1†	72.20
AMMI2	73.47
AMMI3	74.87
AMMI4	75.54
AMMI5	76.04
AMMI Full model	78.54

† Model selected by the predictive assessment.

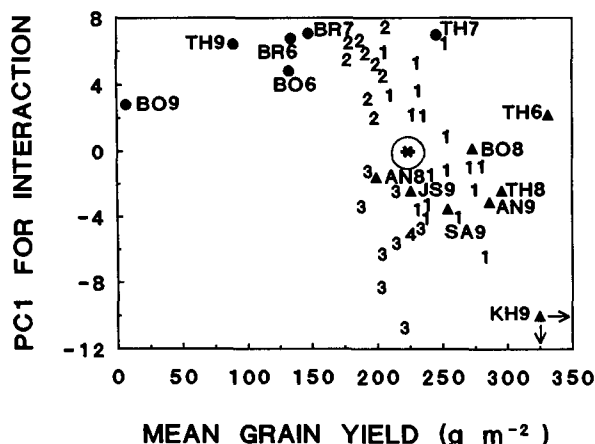


Fig. 3. Biplot of the AMMI model for 36 two-rowed barley genotypes, grown in 14 environments in Syria and North Africa. Genotypes are represented by values indicating the cluster in which they are grouped (Fig. 1). Environments are represented by a solid triangle (Cluster A) and a solid circle (Cluster B). The environment in the lower right corner is Khroub 1988/89, which fell outside the range of the figure. Encircled star represents grand mean yield.

ments was Arabi Abiad, which is widely grown by farmers in the more favorable environments of northern Syria. Among the four other landraces grouped in Cluster 1 were SLB 60-02, collected from an area with good fertility and high expected yield (Weltzien and Fischbeck, 1988; Weltzien, 1989), one landrace from southern Syria, and two Jordanian landraces. Compared with Syrian landraces, those from Jordan have a more rapid development early in the season and earlier heading (Van Oosterom and Acevedo, 1992). They thus resemble early heading spring types of Cluster 1 more than the Syrian landraces.

The classification of environments was related to mean grain yield and the value of IPCA1; IPCA1 by turn depended on the amount of rainfall and the temperature in each environment. The environments of Cluster A all had high seasonal or spring rainfall (Table 2). This increases grain yield and may lengthen the growing season, which is especially beneficial for late heading genotypes of Clusters 3 and 4. A temperature effect explained the grouping of Tel Hadya 1987 in Cluster B. Based on grain yield, this environment was expected to be grouped in Cluster A. However, in 1986–1987, a period with below-zero minimum temperatures occurred in spring. Such low temperatures late in the season reduced yields of early heading spring types (Cluster 1) more than that of medium early heading winter types of Cluster 2 (Van Oosterom et al., 1993). This is supported by the high value for IPCA1 of both 1987 environments (Fig. 3), which indicates a positive interaction of genotypes of Cluster 2 with environments experiencing late frost. Yau et al. (1991) found, for standardized grain yields of bread wheat (*Triticum aestivum* L.) in Mediterranean environments, a classification of environments that was determined by moisture supply and winter temperatures. Results of Nachit et al. (1992c) for durum wheat in Mediterranean environments show that environmental variables like precipitation and temperature are associated with environmental mean grain yield and environmental score for IPCA1. Our results corroborate

Table 6. Contribution of each environment to the three major fusions in the cluster analysis for genotypes. Contributions are expressed as squared difference between the mean standardized yields of the two groups of genotypes clustered.

Environment	Grain yield g m^{-2}	Fusion		
		1†	2‡	3§
Cluster A				
Khroub 1989	513	1.270	1.376	0.004
Tel Hadya 1986	331	0.885	1.316	3.698
Tel Hadya 1988	296	0.095	1.199	2.415
Annoceur 1989	286	0.301	1.073	2.554
Bouider 1988	273	0.356	2.611	1.447
Sidi El Aidi 1989	254	0.038	3.419	1.997
Jemaa Shiam 1989	226	0.023	0.760	7.054
Annoceur 1988	200	0.003	2.176	0.001
Cluster B				
Tel Hadya 1987	246	2.170	0.364	0.046
Breda 1987	148	3.698	0.010	0.001
Breda 1986	134	3.056	0.015	1.042
Bouider 1986	133	2.307	0.099	0.524
Tel Hadya 1989	89	2.641	0.017	0.019
Bouider 1989	7	1.893	0.945	0.071

† Separation of Clusters 1 and 2 from Clusters 3 and 4.

‡ Separation of Cluster 1 from Cluster 2.

§ Separation of Cluster 3 from Cluster 4.

their conclusion that the AMMI model is a useful tool for interpreting the effects of rainfall and temperature on the GE interaction.

The question of whether or not selection for yield under stress has to be done under stress conditions is highly controversial. Pfeiffer (1988) suggested that high yield potential and a response to input can be combined with drought tolerance in bread wheat. He argued that because genetic advance in non-stress conditions may be higher than in stress conditions, initial selection is preferably done under nonstress conditions. Recently, Braun et al. (1992) concluded that irrigated, HY environments have the highest screening ability for selection of widely adapted spring bread wheat cultivars. Nachit and Ouassou (1988) and Nachit (1989) suggested for durum wheat, grown in Mediterranean environments where LY and HY seasons are alternating, a simultaneous selection in LY and HY environments, to combine yield potential with stress tolerance. Tel Hadya, the wettest Syrian site included in this study, is grouped in both environmental clusters and represents such environments. Ceccarelli (1987) and Ceccarelli and Grando (1989, 1991) concluded for barley in Mediterranean environments that if LY areas are the target environment, selection in LY environments is most cost efficient.

Barley is mainly grown in the Mediterranean region in dry environments. Although timing and intensity of the biotic stresses are variable, low yields are predictable. Average grain yields are below 100 g m^{-2} (Somel et al., 1984), well within the yield range of environmental Cluster B. Yau et al. (1991) found for bread wheat environments in the Mediterranean region a grouping into irrigated, high rainfall and rainfed, low rainfall environments, suggesting that in that region irrigated experiments do not represent rainfed, low rainfall environments. A highly significant correlation between environmental mean grain yield and environmental score for IPCA1 has been reported for durum wheat in this region (Nachit et al., 1992c). This indicates that HY and LY environments have contrasting effects on the GE in-

teraction. Ceccarelli et al. (1992) concluded for barley in Mediterranean environments that yield selection in HY environments at best has no correlated response in LY environments. Our results for barley support the view that in the Mediterranean region yield selection in HY environments is of little relevance for LY environments.

Medium early heading winter types of barley had a positive interaction with LY environments and may thus represent an ideotype, well-adapted to these environments. Their negative interaction with HY environments represents their low yield potential. This is of minor importance for regions where favorable seasons are rare and farmers are interested in yield stability rather than in yield potential. It emphasizes, however, that yield selection has to be performed in representative, LY environments.

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REFERENCES

- Abou-El-Fittouh, H.A., J.O. Rawlings, and P.A. Miller. 1969. Classification of environments to control genotype by environment interactions with an application to cotton. *Crop Sci.* 9:135-140.
- Bidinger, F.R., V. Mahalakshmi, and G.D.P. Rao. 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. I. Factors affecting yields under stress. *Austr. J. Agric. Res.* 38:37-48.
- Braun, H.-J., W.H. Pfeiffer, and W.G. Pollmer. 1992. Environments for selecting widely adapted spring wheat. *Crop Sci.* 32:1420-1427.
- Ceccarelli, S. 1987. Yield potential and drought tolerance of segregating populations of barley in contrasting environments. *Euphytica* 36:265-273.
- Ceccarelli, S., E. Acevedo, and S. Grando. 1991. Breeding for yield stability in unpredictable environments: single traits, interaction between traits, and architecture of genotypes. *Euphytica* 56:169-186.
- Ceccarelli, S., and S. Grando. 1989. Efficiency of empirical selection under stress conditions in barley. *J. Genet. Breed.* 43:25-31.
- Ceccarelli, S., and S. Grando. 1991. Environment of selection and type of germplasm in barley for low-yielding conditions. *Euphytica* 57:207-219.
- Ceccarelli, S., S. Grando, and J. Hamblin. 1992. Relationship between barley grain yield measured in low- and high-yielding environments. *Euphytica* 64:49-58.
- Eberhart, S.A., and W.A. Russell. 1966. Stability parameters for comparing varieties. *Crop Sci.* 6:36-40.
- Finlay, K.E., and G.N. Wilkinson. 1963. The analysis of adaptation in a plant-breeding programme. *Austr. J. Agric. Res.* 14:742-754.
- Fischer, R.A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. *Austr. J. Agric. Res.* 29:897-912.
- Fox, P.N., and A.A. Rosielle. 1982. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. *Euphytica* 31:645-656.
- Gauch, Jr., H.G. 1988. Model selection and validation for yield trials with interaction. *Biometrics* 44:705-715.
- Gauch, Jr., H.G., and R.W. Zobel. 1988. Predictive and post-dictive success of statistical analyses of yield trials. *Theor. Appl. Genet.* 76:1-10.
- Hadjichristodoulou, A. 1982. The effects of annual precipitation and its distribution on grain yield of dryland cereals. *J. Agric. Sci. (Camb.)* 99:261-270.
- Kempton, R.A. 1984. The use of biplots in interpreting variety by environment interactions. *J. Agric. Sci. (Camb.)* 103:123-135.
- Krzanowski, W.J. 1983. Cross-validated choice in principal component analysis - some sampling results. *J. Stat. Computation and Simulation* 18:299-314.
- Lin, C.S., M.R. Binns, and L.P. Lefkovitch. 1986. Stability analysis: where do we stand? *Crop Sci.* 26:894-900.
- Nachit, M.M. 1989. Moisture stress tolerance and yield stability in durum wheat (*Triticum durum* L. var. *durum*) under Mediterranean dryland conditions. Abstract 23-2. In *Science for plant breeding*. Book of poster abstracts part II, poster groups 16-33. XII EUCARPIA Congress, Göttingen, Germany. 27 Feb. - 4 Mar. 1989. Th. Mann Publishers, Gelsenkirchen, Germany.
- Nachit, M.M., G. Nachit, H. Ketata, H.G. Gauch, Jr., and R.W. Zobel. 1992a. Use of AMMI and linear regression models to analyze genotype-environment interaction in durum wheat. *Theor. Appl. Genet.* 83:597-601.
- Nachit, M.M., and A. Ouassou. 1988. Association of yield potential, drought tolerance and stability of yield in *Triticum durum* L. var. *durum*. p. 867-870. In *Proceedings of the Intl Wheat Genetics Symposium, 7th*, Cambridge, UK. 10-13 July 1988. Inst. of Plant Science Research, Cambridge, UK.
- Nachit, M.M., M.E. Sorrells, R.W. Zobel, H.G. Gauch, R.A. Fischer, and W.R. Coffman. 1992b. Association of morphophysiological traits with grain yield and components of genotype-environment interaction in durum wheat. I. *J. Genet. Breed.* 46:41-49.
- Nachit, M.M., M.E. Sorrells, R.W. Zobel, H.G. Gauch, R.A. Fischer, and W.R. Coffman. 1992c. Association of environmental variables with sites' mean grain yield and components of genotype-environment interaction in durum wheat. II. *J. Genet. Breed.* 46:50-55.
- Pfeiffer, W.H. 1988. Drought tolerance in bread wheat - Analysis of yield improvement over the years in CIMMYT germplasm. p. 274-278. In A.R. Klatt (ed.) *Wheat production constraints in tropical environments*. CIMMYT, Mexico DF, Mexico.
- Shorter, R., D.E. Byth, and V.E. Mungomery. 1977. Genotype \times environment interactions and environmental adaptation. II. Assessment of environmental contributions. *Aust. J. Agric. Res.* 28:223-235.
- Somel, K., A. Mazid, and M. Hallajian. 1984. Survey of barley producers; northern Syria 1981/1982. vol. III, Descriptive statistics. ICARDA Research Report no. 12, Aleppo, Syria.
- Van Oosterom, E.J., and E. Acevedo. 1992. Adaptation of barley (*Hordeum vulgare* L.) to harsh Mediterranean environments. II. Apical development, leaf, and tiller appearance. *Euphytica* 62:15-27.
- Van Oosterom, E.J., S. Ceccarelli, and J.M. Peacock. 1993. Yield response of barley to rainfall and temperature in Mediterranean environments. *J. Agric. Sci., (Camb.)* in press.
- Weltzien, E. 1989. Differentiation among barley landrace population from the Near East. *Euphytica* 43:29-39.
- Weltzien, E., and G. Fischbeck. 1988. Genotypic variability and productivity of local barley landraces under marginal growing conditions in Syria. p. 511-522. In E.E. Whitehead et al. (ed.) *Arid lands: Today and tomorrow*. Proc. Intl Research and Development Conference, Tucson, AZ. 20-25 October 1985. Westview/Cress, Boulder, CO.
- Wold, S. 1978. Cross-validated estimation of the number of components in factor and principal components models. *Technometrics* 20:397-405.
- Yau, S.K., G. Ortiz-Ferrara, and J.P. Srivastava. 1991. Classification of bread wheat-growing environments based on differential yield responses. *Crop Sci.* 31:571-576.
- Zobel, R.W., M.J. Wright, and H.G. Gauch Jr. 1988. Statistical analysis of a yield trial. *Agron. J.* 80:388-393.