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Heritabilities, gains from selection and genetic correlations for grain yield of barley grown in two contrasting environments

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Abstract

Heritabilities and variance component estimates were obtained from a set of 15 barley lines and cultivars grown for three consecutive years in two contrasting environments in the high plateaux of Eastern Algeria. Genotype × environment interactions, particularly related to seasonal effects, seriously limited selection for increased barley grain yield. Their effect was to reduce the genetic variance component, heritability estimates and genetic correlation coefficients.

The results indicated that selection in a high-yielding location does not identify genotypes suitable for low-yielding environments, which are more representative of the production conditions of a low-input agriculture. Selection in low-yielding environments appears more efficient.

Keywords: Correlated response; Heritability; *Hordeum vulgare*; Selection; Yield

1. Introduction

After durum wheat, barley is the most important field crop grown in Algeria. It is grown mainly in marginal low-rainfall environments of the high plateaux where rainfall variability within and between years is high. Production varies from year to year, being 0.3 Mt in 1958–59 and 1.2 Mt in 1991/92 (Anonymous, 1993). Absolute yields are among the lowest in the region. Production increases are sought through improved agronomic practices and introduced cultivars. This germplasm is often high yielding in good environments, but fails to give acceptable grain yield under stress conditions (Bouzerzour and Hadj-Sahraoui, 1989). These failures have been used to argue that development of agronomic practices rather than new cultivars, should receive priority to improve subsistence agriculture in the semi-arid conditions of the high plateaux (Anonymous, 1992).

Breeding for low-rainfall environments is difficult and results in slow progress. Performance of breeding material in a range of environments is affected by the environment in which the selection is made (Allen et al., 1978; Fox and Rosielle, 1982; Ceccarelli et al., 1991; Simmonds, 1991). The choice of environment to maximize genetic progress is an important issue. Environmental and genotypic variances have been reported to be greater when growing conditions were favourable, i.e. when yields were high. On the other hand, estimates of heritability and genetic gains have not been associated with grain yield in a consistent way (Allen et al., 1978). Frey (1964) reported no significant differences in mean yield in a given environment between sets of lines selected in two contrasting envi-

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ronments; but heritability estimates were greater in the non-stress environment.

Byth et al. (1969) found that genetic advance in yield of soybean was the same for lines selected in high- and low-yielding environments. Johnson and Frey (1967) used heritability estimates as a criterion for identifying environments in which selection would be most effective. They pointed out that their criterion is valid only if genotype × environment interactions do not nullify gains when the selected genotypes are grown in other environments. They reported also that genotypic and environmental variances increased as yields increased. It has been suggested that heritability estimates are smaller in stress environments, because of increased environmental variance relative to those in non-stress environments. This increases the difficulties in relating phenotype to genotype. Ceccarelli (1987) reported genetic differences observed in the absence of stress are not relevant to selection for high-stress environments.

Selection for grain yield in favourable conditions is inefficient in identifying the highest-yielding genotypes for high-stress environments and favours less stable genotypes. Riggs et al. (1980) reported results for barley grown in different locations. They found that correlation coefficients computed within sites and between seasons did not differ in magnitude from those computed between sites in the same seasons. They concluded that selection between sites would be effective. Hamblin (1992) reported that there are two schools of thought: first that selection in high-yield environments correlated with performance in stress environments; second that selection for stress environments was only effective in those environments. These differing views were reconciled when it was realized that a critical point occurred somewhere in the range 2–3 t/ha. Selection in favourable environments will be effective for low-yielding environments with yields greater than 3 t/ha, otherwise selection for stress environments had to be carried out in those environments.

Plant breeding aims to identify genotypes that have high average yield for a target population of environments. However selection is based on performance in only a small subset of environments. Accurate heritability estimates and expected gains from selection are necessary to develop an optimum selection and evaluation strategy for barley lines adapted for the high plateaux of Algeria. Generally, heritability estimates are

Table 1
The set of genotypes tested and their mean grain yield (g/m^2) averaged over sites and years

Name	Origin	Yield	Name	Origin	Yield
Tichedrett	Algeria	274	Tabaissa	Spain	318
El Dorado	Spain	256	Acsad	Syria	279
Harmal	Syria	293	Barber	France	276
Saida	Algeria	279	Rihane	Syria	277
Jaidor	France	279	Tatiana	Spain	325
Tina	Spain	355	Begonia	Spain	327
Soufara	Syria	339	Gerbel	France	334
Roho/Deli	Syria	304			

obtained from barley genotypes grown at high-yielding sites. Whether these are relevant in contrasting sites is not known. The purpose of this research was to estimate genotypic and environmental variances for seed yield for a set of barley genotypes tested at an Algerian selection site and to determine if these values are applicable at a contrasting site.

2. Material and methods

2.1. Field experiments

A set of 15 barley lines and cultivars (Table 1) was evaluated for three years, from 1988/89 to 1990/91, at the Agricultural Experiment Station (1081 m elevation, 36°9′N and 5°21′E) and the Sersour Public Farm (920 m elevation, 35°56′N and 5°32′E) in the Setif region. Although only situated 35 km apart, the two sites represent two entirely different agricultural systems. At Sersour Public Farm (SPF) barley is the only possible rainfed crop, and is produced in a fallow-cereal system. The soil is a Xerothent, or semi-desert brown soil, characterized by a redistribution of lime-rich sandy material at 40–50 cm depth. Crop failures due to harsh environmental conditions are frequent and expected yields are approximately 1 t/ha. At the Agricultural Experiment Station (AES), a range of farming systems are practised, the soil is a typical calciorthid, or brown steppe soil, and expected yields are greater (3–4 t/ha).

Long-term climatological data are given in Table 2. AES had, on average, 100 mm more rainfall, less days of hot wind per year and medium temperature range.

Table 2
Long-term average (1967–1991) climatological data for the Agricultural Experimental Station (AES) and Serour Public Farm (SPF)

Site		Months												
		J	F	M	A	M	J	J	A	S	O	N	D	Total
		Hot wind days												
AES		0.2	0.5	1.8	1.7	1.2	2.4	2.6	1.8	1.6	0.7	0.8	0.0	15.3
SPF		0.0	0.0	0.7	3.6	3.8	5.2	6.6	4.3	3.0	0.2	0.2	0.0	27.6
		Temperatures (°C)												
AES	Max	21.1	24.1	27.1	30.0	35.9	38.2	41.0	40.6	37.6	31.1	27.2	20.6	
	Min	−15.0	−15.2	−6.6	−6.8	−2.8	0.9	7.0	5.4	1.2	−2.3	−4.0	−9.3	
	Mean	4.5	5.6	8.4	11.4	15.5	20.7	24.6	24.3	20.4	14.4	9.2	5.6	
SPF	Max	22.6	25.3	28.1	31.2	37.9	39.7	42.3	44.0	39.2	31.6	27.5	19.6	
	Min	−17.0	−16.3	−8.0	−7.2	−3.4	1.0	8.2	6.1	1.0	−3.2	−5.2	−9.7	
	Mean	5.1	5.9	9.2	12.3	16.1	22.6	26.3	25.6	21.7	15.9	11.3	6.9	
		Rainfall (mm), (days of rain)												
AES		52.0 (2)	38.0 (10)	38.0 (10)	35.0 (9)	44.0 (8)	28.0 (6)	11.0 (3)	17.0 (4)	34.0 (7)	38.0 (8)	43.0 (11)	41.0 (12)	419 (100)
SPF		29.0 (7)	26.0 (5)	30.0 (7)	33.0 (5)	41.0 (5)	14.0 (3)	06.0 (2)	14.0 (3)	30.0 (4)	37.0 (4)	33.0 (5)	33.0 (6)	326 (56)

This is enough to induce large differences in crop production between sites.

The experimental design was a randomized complete block with three replications. Plots were 1.2 m wide × 10 m long. Planting occurred after 10 November of each year, at both sites. Plant populations were approximately 200 plants/m^2 (250 viable seeds were sown per m^2, with an average of 25% seed losses). Trials were kept weed free by applications of 2,4-D at 0.75 l of commercial product per ha, before the jointing stage. Plots were harvested in June.

2.2. Data analysis

Seed yield was estimated from the combine-harvested whole plots. In the statistical analysis, years, locations, blocks and genotypes were considered as random effects. Separate analyses of variance were performed within each site, between sites within year, within site over years and over sites and years.

The error variance (σ_e^2) and genetic variance (σ_g^2) were estimated from a bivariate analysis. Components of variance and their standard errors were also estimated from the combined analyses by setting the mean squares equal to their expectations (Comstock and Moll, 1963; McIntosch, 1983). Heritability estimates, on a mean basis, were determined as

$$h^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_e^2).$$

The genetic correlation between locations (represented here by A and B instead of AES and SPF, for simplicity) within year was calculated as indicated by Falconer (1982) as:

$$r_g = \sigma_{gAB} / (\sigma_{gA}^2 \cdot \sigma_{gB}^2)^{0.5},$$

where r_g is the genetic correlation; σ_{gAB} is the genetic covariance between location A and location B; and σ_{gA}^2, σ_{gB}^2 are genetic variances within location. Standard errors for the genetic correlations were calculated after Falconer (1982) as:

$$\sigma_{r_g} = \frac{1 - r_g^2}{2^{0.5}} \left(\frac{\sigma_{h_A^2} \cdot \sigma_{h_B^2}}{h_A^2 \cdot h_B^2} \right)^{0.5},$$

where $\sigma_{h_A^2}$ and $\sigma_{h_B^2}$ are the standard errors for the heritability estimates for location A and B. The predicted direct response to selection in environment A was computed as: $R = i h_A \sigma_{gA}$ where $i = 2.06$ was the selection coefficient for 5% selection intensity (Allard, 1960). The predicted correlated response of grain yield in location B to selection for high grain yield in location A was computed as: $CR_B = i h_A r_g \sigma_{gB}$ (Falconer, 1982).

3. Results and discussion

There were significant differences between lines for grain yield within site, combined over sites and over years and sites (Table 3). At SPF, mean grain yield

Table 3
Mean grain yield (g m^{-2}), standard errors and range of 15 barley lines averaged over years and locations

Year		Locations		
		SPF	AES	Average
88/89	mean	156±17.7	565±21.1	361±19.7
	range	103–203**	500–657**	103–656**
89/90	mean	163±11.3	529±24.6	346±19.1
	range	69–253**	445–678**	69–678**
90/91	mean	108±13.6	284±18.8	196±17.5
	range	55–172**	204–343**	55–343**
average	mean	142±13.5	459±23.1	301±19.6
	range	55–253**	204–678**	55–678**

**genotypic effect significant at 1% level.

was 1.6 standard deviations smaller than at AES (142 vs 459 g m^{-2}). The genetic and environmental components of variance were significantly correlated ($r=0.747$, $P=0.05$) but showed no significant correlations with trial means ($r=0.261^{ns}$ and $r=0.589^{ns}$ respectively). The heritability estimates from one year's data were large (Table 4). The phenotypic correlation coefficients between locations were not significant. The genetic correlation coefficients were of the same magnitude as their corresponding phenotypic coefficients and were twice their standard error (Table 5). Because only two environments were considered, the departure of the genetic correlation coefficient from unity is a measure of the magnitude of genotype × environment interaction. In the combined analyses, 2-way and 3-way interactions between genotypes, years and locations were highly significant. This indicates that selection based on a single, one-year, site test is not effective. Heritabilities estimated from combined data (sites within year) were low to medium in magnitude and contrasted with the high figures obtained

Table 4
Estimates of components of variance, their standard errors, and heritabilities (h^2) for seed yield of 15 barley lines grown in two contrasting environments

Year. Location	Statistics					
	σ_e^2	σ_g^2	σ_{gy}^2	$\sigma_{gAESSPF}^2$	$\sigma_{gyAESSPF}^2$	h^2
88 SPF	104.8±1.11	924.3±4.9				0.90
89 AES	159.6±1.37	2039.5±7.2				0.93
Combined	65.1±0.86	309.8±6.4		514.3±5.2		0.35
89 SPF	42.9±0.71	3643.1±9.3				0.98
90 AES	201.0±1.5	5229.6±11.3				0.96
Combined	61.1±0.83	1644.7±12.1		1391.5±8.3		0.53
90 SPF	61.6±0.85	1249.6±5.5				0.98
91 AES	118.5±1.18	1524.0±6.2				0.92
Combined	51.6±0.76	773.4±7.2		300.0±4.0		0.68
SPF	30.1±0.47	1634.0±9.8	258.2±3.1			0.85
AES	87.9±0.81	0.0±8.3	950.6±5.9			0.00
Overall	21.8±0.41	435.5±4.5	159.5±5.3	54.9±6.5	224.9±4.1	0.48

σ_e^2 = error variance, σ_g^2 = genetic variance, σ_{gy}^2 = genotype * year interaction, $\sigma_{gAESSPF}^2$ = genotype * location interaction, $\sigma_{gyAESSPF}^2$ = genotype * year * location interaction.

Table 5
Phenotypic (r_p) and genetic (r_g) correlation coefficients, predicted response (R) and predicted correlated response (CR) for barley seed yield

Year	r_p	r_g	R_{AES}	R_{SPF}	CR_{AES}	CR_{SPF}	CR_{AES}/R_{AES}	CR_{SPF}/R_{SPF}
88/89	0.276^{ns}	0.282+0.14	89.7	61.4	25.7	17.0	0.29	0.28
89/90	0.336^{ns}	0.339+0.18	145.9	123.1	49.9	41.3	0.34	0.34
90/91	0.124^{ns}	0.126+0.08	77.1	72.1	10.1	08.8	0.13	0.12

ns: non significant.

from one year's data. The genotype × location variance component ($\sigma^2_{gAESSPF}$) was higher than the σ^2_g component once in 3 years.

When data are analysed per site over years (y), most of the observed variability at AES is included in the genotype × year component (σ^2_{gy}) which nullified the genotypic variance component (σ^2_g) and heritability estimates. Yield at SPF appeared less variable over years, since the σ^2_{gy} component is smaller than σ^2_g component. Plant breeding work is located at AES on the assumption that under these conditions, there is more efficient control of environmental variation, better expression of genetic differences and hence higher heritability. The results presented above question these assumptions. The relative efficiency of indirect versus direct selection (CR/R) at AES and SPF ranged from 0.12 to 0.34 (Table 5), indicating the inefficiency of indirect selection at either site. The performance and rank of the five highest-yielding lines selected in AES and SPF in 88/89 are shown in Table 6. Selections made at AES had relative mean grain yield ranging from 0.89 to 1.00 (relative yield is defined as mean of selected lines over site mean). Relative means of selections made at SPF ranged from 1.00 to 1.29 (Table 6). This indicated that SPF selections maintained their grain yield advantage under low-yielding conditions and were able to give, under favourable growing conditions (AES), a grain yield mean at least equal to the site mean. This was not the case for AES selections. This location behaved as a high-yielding site some years and as an intermediate-yielding site in others, while SPF behaved as a stable, low-yielding site in all years.

Breeders cannot select and test their breeding material in all environments where the future cultivars will be grown. The ideal selection site must meet two requirements. First, genetic differences found in that site should also be expressed in the target environment, and second, the response to selection obtained in the selection site should be maintained to some extent in the target environment. Suitability of selection sites differing in environmental conditions was assessed by estimation of heritabilities and genetic correlations among the alternative locations, based on identical genetic entities grown in both environments. The results suggest little benefit in selecting in one location with the objective of yield improvement in the contrasting environment. This applies even if the heritability levels, on a mean basis, were similar but the genetic correlations between locations were relatively small. Because genotype × environment (G × E) interactions are important in the High Plateaux region of Algeria, extensive variety testing over years and sites is needed to identify genotypes with specific adaptation to the region. Hamblin (1992) stated that when grain yield levels were beyond the 2–3 t/ha range, alternating selection cycles in low- and in high-yielding conditions was ineffective.

Simmonds (1991) suggested that if adaptation to two contrasting environments is the breeding objective, it would be better to divide the program into two parts, rather than use intermediate sites or shuttle breeding. The general conclusion from several studies is that adaptation to an environment is best achieved by selecting in that environment (Rosielle and Hamblin, 1981;

Table 6
Performance (m, g m^{-2}) and rank (r) of the five best selected lines

Varieties	Selection site 88/89		Testing sites 89/90				90/91			
	AES		SPF		AES		SPF		AES	
	m	r	m	r	m	r	m	r	m	r
Soufara	657	1	247	2	468	11	140	4	343	1
Rihane	626	2	117	12	472	10	88	9	232	14
Barber	610	3	84	13	452	14	69	10	299	6
Harmal	596	4	165	8	499	8	99	7	204	15
Roho/D	586	5	163	9	460	12	146	3	268	9
m.sel (a)	615		155		470		108		269	
m.site (b)	565		163		530		108		294	
a/b[a]	1.08		0.95		0.89		1.00		0.95	
	SPF		SPF		AES		SPF		AES	
	m	r	m	r	m	r	m	r	m	r
Begonia	201	1	171	7	579	5	139	5	329	5
Roho/d	200	2	163	9	460	12	146	3	268	9
Harmal	191	3	165	8	499	8	99	7	204	15
Tina	184	4	253	1	631	2	172	1	338	5
Soufara	184	5	247	2	468	11	140	4	343	1
m.sel (a)	192		200		528		139		296	
m.site (b)	155		163		530		108		284	
a/b	1.23		1.23		1.00		1.29		1.04	

[a] a = selected lines mean, b = site mean, a/b = relative yield.

Simmonds, 1991; Ceccarelli et al., 1992). When it is imperative to increase yield in a high-stress environment, selection for tolerance is worthwhile, but it should be recognized that this decreases yield under high-yielding conditions (Rosielle and Hamblin, 1981).

As stress conditions are common in the High Plateaux regions of Algeria, a desirable approach is to choose testing sites representative of the production conditions (low-input agriculture) and to accept a relative yield decrease in non-stress environments, as this minimizes the risk to small-scale, low-input farmers.

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