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M. Singh · S. Ceccarelli · S. Grando

Genotype x environment interaction of crossover type: detecting its presence and estimating the crossover point

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Abstract Genotype-environment interaction (GEI) introduces inconsistency in the relative rating of genotypes across environments and plays a key role in formulating strategies for crop improvement. GEI can be either qualitative (i.e., crossover type) or only quantitative (i.e., non-crossover type). Since the presence of crossover-type interaction has a strong implication for breeding for specific adaptation, it is important to assess the frequency of crossover interactions. This paper presents a test for detecting the presence of crossover-type interaction using the response-environment relationship and enumerates the frequency of crossovers and estimation of the crossover point (CP) on the environment axis, which serves as a cut-off point for the two environments groups where different/specific selections can be made. Sixty-four barley lines with various selection histories were grown in northern Syria and Lebanon giving a total of 21 environments (location-year combinations). Linear regression of the genotypic response on the environmental index represented a satisfactory model, and heterogeneity among regressions was significant. At a 5% level of significance, 38% and 19% of the pairs showed crossover interactions when the error variances were considered heterogeneous and homogeneous, respectively, implying that an appreciable number of crossovers took place in the case of barley lines responding to their environments. The CP of 1.64 t/ha, obtained as the CP of regression lines between the genotype numbers 19 and 31, provided maximum genotype x environment-group interaction. Across all environments, genotype nos. 59 and 12 stood first and second for high yield, respectively. The changes in the ranks of genotypes under the groups of environments can be used for selecting specifically adapted genotypes.

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M. Singh (✉)
International Center for Agricultural Research in the Dry Areas,
P.O. Box 5466, Aleppo, Syria
e-mail: m.singh@cgiar.org
Tel.: +963-21-2213477
Fax: +963-21-2213490

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Introduction

Genotype-environment interaction (GEI) plays a key role in developing strategies for crop improvement. Numerous methods for exploiting GEI have been developed in the literature (Yates and Cochran 1938; Finlay and Wilkinson 1963; Eberhart and Russell 1966; Byth et al. 1976; Gauch 1988; Singh et al. 1996b), among others) and reviewed (Freeman 1973; Lin et al. 1986; Westcott 1986; Kang 1990). In general, the selection of genotypes is based on their evaluation in a number of environments. The relative response of the genotypes varies over the environment, indicating a change in the superiority of one genotype over the others with respect to the environment, including a change in the rank of the genotypes. Selection of genotypes with an objective of yield maximization in the case of rank changes over environments is complicated (Haldane 1947) due to non-separability of response behavior (Gregorius and Namkoong 1986). In clinical trial situations, Peto (1982) distinguished qualitative interaction, where the direction of true treatment (genotype in the present case) differences varies among subsets of patients (environments in the present case) from quantitative interactions where treatment differences vary only in magnitude, but not in direction (i.e., in rank). Gail and Simon (1985) introduced the term crossover interaction for qualitative interaction and non-crossover interaction for quantitative interaction, and provided a test for crossover interaction between clinical treatments and patients. The “crossover” here is different from the crossover term used in genetics (e.g., Sinnot et al. 1958). Baker (1988) applied the tests given by Azzalini and Cox (1984) and Gail and Simon (1985) on spring-wheat data for testing crossover genotype-environment interaction (COGEI). The consequences of COGEI on breeding strategies have been discussed

by Ceccarelli (1996) who used the presence of COGEI as the basis for selecting specific rather than wide adaptation. Baker (1990) compared three models for interaction along with a disease model and observed that the differences in disease resistance of high heritability led to COGEI. However, unlike the situation in clinical trials, in multi-locational variety testing a genotype is described by its response relationship to the environment by measuring the environment by the mean of all genotypes in that environment. In many situations, linear-response relationships have been considered to be satisfactory (Yates and Cochran 1938; Finlay and Wilkinson 1963; Eberhart and Russell 1966).

The methods of Azzalini and Cox (1984) and Gail and Simon (1985) can be used to detect the presence of COGEI for a given pair of genotypes. Methods based on ranks are given by Kendall and Gibbons (1990) and de Kroon and van der Laan (1981). However, these methods do not take into account the form of response relationship and do not provide the estimation of the crossover point (CP), which is important for developing genotypes for specific adaptation. Therefore, the objectives of the study presented here were (1) to obtain a statistical test for the existence of COGEI using the response relationship, based on data from multi-locational trials, and (2) to estimate the crossover point on the environmental mean axis separating the two groups of environments. For any chosen pair of the genotypes, we also provide (3) the confidence interval for the crossover point and the probability of the crossover taking place within the observed environmental boundaries and outside. Although the response relationship has been restricted to the linear form, the methodology can easily be extended to nonlinear forms as well.

Materials and methods

Multi-environment barley trials

Sixty-four lines with various selection histories were grown during four successive cropping seasons (from 1990/1991 to 1993/1994) at six locations (Tel Hadya, Bouider, Breda and Hassake in northern Syria, and Terbol and Kfardan in Lebanon), giving a total of 21 environments (location-year combinations). Planting was usually done in dry soil in the drier sites (Breda, Bouider and Hassake) and after the first rain in all the other sites. In Breda, Bouider and Hassake no fertilizer was applied, whereas in Tel Hadya a standard amount of 40 kg/ha of N as ammonium sulfate and 60 kg/ha of P_2O_5 was applied each year to conform with the cultural practices in the region represented by this location. Plot size was 12 m^2; (eight rows of 7.5 m long with a between-row spacing of 20 cm), of which 7.5 m^2 were harvested (the central six rows for a length of 6.25 m). In each environment the experimental design was a triple lattice. We present the results for grain yield measured per plot and converted to kg/ha for the statistical analysis.

Statistical methods for testing the presence of GEI

We consider a set of multi-environment variety trials to evaluate a set of varieties. Let the trial at the j-th environment be conducted in a randomized complete block design with the same set of v varieties and r_j replication (j=1,2…L). Denote the response variable, say yield, by y and an estimate of performance of i-th variety in the j-th environment by y_{ij} (mean over replicates), with estimated variance s_j^2/r_j where s_j^2 is the residual mean square, an unbiased estimate of the experimental error variance σ^2_j, at the j-th location. In the case of an incomplete block design (such as a triple lattice) used at j-th environment, y_{ij} would be the mean values adjusted for block differences and associated with the standard error ($s_j/r_j^{1/2}$) (j=1,2,…v). Environment mean ($x_j = \sum_{i=1}^{v} y_{ij}/v$), called the environmental index, is considered as a biological measure of the environment j (j=1…L) (Finlay and Wilkinson 1963; Eberhart and Russell 1966). The model used by Yates and Cochran (1938) and Finlay and Wilkinson (1963) for y_{ij} is

$$y_{ij} = \alpha_i + \beta_i x_j + \varepsilon_{ij} \quad (1)$$

where α_i and β_i are the intercept and slope, respectively, of the regression line of the i-th genotype (i.e., sensitivity of the genotype to the environment) (i=1…v). The quantities ε_{ij}'s are random errors normally distributed (which follows from the assumption of plot-wise errors to be normally distributed) with mean zero and variance σ^2_j/r_j. Another measure of the environment is the mean over all genotypes except the genotype in consideration, but this gives different values even for the same environment since it varies with the genotype (Mather and Caligari 1974). The quantities x_j have been considered as values of a non-stochastic regressor, a reasonable assumption if moderately large number of genotypes are used (Finlay and Wilkinson 1963; Eberhart and Russell 1966). Tests concerning β's and α's may depend on the degree of heterogeneity of error variances σ_j^2 (j=1…L). Under homogeneous error variances, GEI was tested by comparing the ratio of GEI mean square to the pooled error mean squares against the F-ratio with appropriate degrees of freedom (df). Under the observed heterogeneous error variances, a weighted analysis of variance was computed, and the GEI sum of squares was compared against χ^2 with (v–1) (L–1) df.

Crossover genotype-environment interaction (COGEI)

Having tested for the presence of GEI, one may like to explain it in terms of functional forms such as linear regressions. A test for homogeneity of regression slopes would test for the non-existence of overall crossover and non-crossover GEI. Non-tenability of the homogeneity of slopes will indicate the existence of overall crossover GEI or of non-crossover GEI. Therefore, we first perform testing of the hypothesis (H_0) for the parallelism of all the regression lines, i.e., H_0: $\beta_1=\beta_2=\ldots=\beta_v$. One way to obtain a test for H_0 is to fit the model (1) on genotype-environment means data (y_{ij}) using terms consisting of an environment mean (x_j) to fit a common slope (df=1), a factor for genotype accounting for intercept differences (df=v–1), and interaction between the genotype and environmental index to provide slope differences (df=v–1). The ratio of mean square due to interaction between genotype and environmental index (df=v–1) to the residual mean square (df=v (L–2)) will provide a test for the equality of slopes. Under parallelism of all response lines, this will follow an F-distribution on v–1 and v (L–2) degrees of freedom. If the error variances are heterogeneous, then a weighted analysis of variance with weights inversely proportional to the variances of the means can be used, in this case the weighted sum of squares due to heterogeneity of slopes (i.e., genotype and environmental index interaction) will follow a χ^2 distribution on v–1 df if the regression lines are parallel. Such a test has been termed as heterogeneity of regressions and used to partition GEI (Perkins and Jinks 1968, 1973; Freeman and Crisp 1979). When heterogeneity of regression lines exists, then of those pairs of regression lines (or equivalently, the pairs of genotypes or entries) which are detected to be heterogeneous (non-parallel regression lines), some pairs of genotypes may exhibit crossover-type interactions while others may indicate non-crossover-type interactions. With v genotypes there are n=v (v–1)/2 pairs. A chosen pair would have either parallel regression lines or show crossover interaction or a non-crossover interaction.

An interaction between a pair of genotypes will be detected as a crossover type if their regression lines are not parallel and intersect within the observed range of the environmental index, and as non-crossover if they intersect outside.

Consider, for example, the pair of regression lines for genotypes i and i' ($i \neq i' = 1,2 \ldots v$). A test for equality of slopes β_i and $\beta_{i'}$ can be obtained by the above method of modeling the two genotypes data by regressing on the terms representing a common slope (df=1), genotypic differences in intercepts (df=1), and in slopes (df=1), and testing the ratio of mean square due to slope differences to the residual mean squares against F-distribution on 1 and 2 (L–2) df. Another way is to compute $t=(\hat{\beta}_i-\hat{\beta}_{i'})/\text{ese}(\hat{\beta}_i-\hat{\beta}_{i'})$ where ese(.) is the estimated standard error of the term in parenthesis; the quantity t will follow t–distribution on df=2(L–2) if no COGEI exists between genotype i and i' and the deviations mean square are homogeneous. Let P_0 be the probability of a random variable with F-distribution on 1 and 2(L–2) degrees of freedom receiving values greater than or equal to the variance ratio for the slope differences under the null hypothesis of equality of slopes. Such a probability is available in the analysis printout (or the P-values or the F-probability values) from the standard statistical packages (e.g., GENSTAT, SAS). The quantity P_0 is generally used to assess the statistical significance of the differences between two slopes or parallelism of the two regression lines when compared with a chosen level of significance (e.g., 0.05). Thus, if P_0 is less than 0.05, we consider that the chances are rare for the two lines to have equal slopes (i.e., they are not parallel). A small P_0 (or equivalently a large $1-P_0$) value implies a high chance for the regression lines to have different slopes (or intersecting lines). A large P_0 would indicate parallelism of the lines. The point of intersection of the regression lines will be called the crossover point (CP). The position of the CP on the environment axis will differentiate crossover-type interaction from the non-crossover type depending on whether the CP falls within the observed environmental index range or beyond it.

Crossover point of GEI from a pair of genotypes

The CP, denoted by x_c, for the pair of genotypes i and i' is the point of intersection of the regression lines projected on the environmental mean axis and refers to the coordinate on environmental mean axis:

$$y_i = \alpha_i + \beta_i x \text{ and } y_{i'} = \alpha_{i'} + \beta_{i'} x$$

for genotypes i and i' respectively. Thus x_c can be obtained by solving

$$\alpha_i + \beta_i x_c = \alpha_{i'} + \beta_{i'} x_c \text{ and therefore,}$$
$$x_c = (\alpha_{i'} - \alpha_i)/(\beta_i - \beta_{i'}).$$

In the context of critical point of weed competition, a similar estimation problem has been addressed by Singh et al. (1996a). An estimate $\hat{x}_c$ of x_c is

$$\hat{x}_c = (\hat{\alpha}_{i'} - \hat{\alpha}_i)/\left(\hat{\beta}_i - \hat{\beta}_{i'}\right)$$

where a cap ^ over a parameter denotes its estimate. An asymptotic standard error (ase) and exact 100(1–α)% confidence interval (L=A–B, U=A+B) for x_c are obtained by using the expressions:

$$\text{ase}(\hat{x}_c) = \{v_{11} + \hat{x}_c^2 v_{22} - 2\hat{x}_c v_{12}\}^{\frac{1}{2}} / \text{abs}(\beta_i - \beta_{i'}) \text{ and}$$

$$A = \left\{\hat{x}_c - t^2 v_{12}\left(\hat{\beta}_i - \hat{\beta}_{i'}\right)^{-2}\right\} / \left\{1 - t^2 v_{22}\left(\hat{\beta}_i - \hat{\beta}_{i'}\right)^{-2}\right\}$$

$$B = t\left(\hat{\beta}_i - \hat{\beta}_{i'}\right)^{-1} \cdot \left[v_{11} + \hat{x}_c^2 v_{22} - 2\hat{x}_c v_{12} - t^2 v_{12}\left(\hat{\beta}_i - \hat{\beta}_{i'}\right)^{-2}\left(v_{11} - v_{12}^2 / v_{22}\right)\right]^{\frac{1}{2}} / \cdot \left[1 - t^2 v_{22}\left(\hat{\beta}_i - \hat{\beta}_{i'}\right)^{-2}\right]$$

$$v_{11} = \hat{\text{Var}}(\hat{\alpha}_i) + \hat{\text{Var}}(\hat{\alpha}_{i'}), v_{12} = -\left(\hat{\text{cov}}(\hat{\alpha}_i, \hat{\beta}_i) + \hat{\text{cov}}(\hat{\alpha}_{i'}, \hat{\beta}_{i'})\right),$$
$$v_{22} = \hat{\text{Var}}(\hat{\beta}_i) + \hat{\text{Var}}(\hat{\beta}_{i'})$$

$t=t_{v,\alpha/2}$ [an upper α/2 probability point of t-distribution on v=2 (L–2) df] approximately. Expressions for variance of ratio of two random variables and confidence intervals for the ratio of two parameters are given in Kendall and Stuart (1969) and Seber (1977, p 180).

Inclusion probabilities of COGEI within the observed environment range

Let the observed environment range be denoted by (E_L, E_U) where $E_L=\min(x_1,\ldots,x_L)$ and $E_U=\max(x_1 \ldots x_L)$. We further assume that the boundary values E_L and E_U on the environmental mean axis are known constants given by the minimum and maximum values of the environmental indices, respectively. If $\hat{x}_c$ lies within (E_L, E_U), there is crossover interaction, and if it falls outside (but not at infinity) then non-crossover interaction. It would be worthwhile to know the probability of observing a crossover-or non-crossover-type interaction and to identify the genotypes whose relative ranks do not necessarily change within the observed environment but may do so beyond it. This information is of significance to explore the GEI after including some more relevant environments. Thus, it would be useful to know how often COGEI takes place within an observed range of the environment. We need to evaluate the coverage or inclusion probability (PrInc), γ, computed from the distribution of the estimator $\hat{x}_c$ of x_c. Given a pair of genotypes i and i' (with different slopes), we can order them such that $\hat{\beta}_i - \hat{\beta}_{i'} > 0$:

$$\gamma = \text{Prob}[E_L \le \hat{x}_c \le E_U] = \text{Prob}[\hat{x}_c \le E_U] - \text{Prob}[\hat{x}_c \le E_L]$$

$$\text{Now, Prob}[\hat{x}_c \le E_U] = \text{Prob}\left[(\hat{\alpha}_{i'} - \hat{\alpha}_i) - E_U\left(\hat{\beta}_i - \hat{\beta}_{i'}\right) \le 0\right]$$

$$= [\text{Prob}(\hat{\alpha}_{i'} - \hat{\alpha}_i) - E_U\left(\hat{\beta}_i - \hat{\beta}_{i'}\right) - \{\alpha_i - \alpha_{i'} - E_U(\beta_i - \beta_{i'})\}$$
$$\le -\{\alpha_i - \alpha_{i'} - E_U(\beta_i - \beta_{i'})\}]$$
$$= \text{Prob}[\frac{(\hat{\alpha}_{i'} - \hat{\alpha}_i) - E_U\left(\hat{\beta}_i - \hat{\beta}_{i'}\right) - \{\alpha_i - \alpha_{i'} - E_U(\beta_i - \beta_{i'})\}}{\text{SENumerator}}$$
$$\le \frac{-\{\alpha_i - \alpha_{i'} - E_U(\beta_i - \beta_{i'})\}}{\text{SENumerator}}]$$

where SENumerator=$\{v_{11}+v_{22}E^2_U-2v_{12}E_U\}^{\frac{1}{2}}$; an estimate of standard error of the numerator, $\hat{\alpha}_{i'}-\hat{\alpha}_i-E_U\,(\hat{\beta}_i-\hat{\beta}_{i'})$; a normal random variable with mean $\{\alpha_i-\alpha_{i'}-E_U(\beta_i-\beta_{i'})\}$ and variance as a function of variances and covariances of the estimates of intercepts ($\hat{\alpha}_i$, $\hat{\alpha}_{i'}$) and slopes ($\hat{\beta}_i$, $\hat{\beta}_{i'}$). Thus, Prob[$\hat{x}_c \le E_U$]=Prob[$t \le T$] which, after replacing T by T_U, can be estimated as $G_\eta\,(T_U)$. Here, $G_\eta(t)$ is a distribution function of t-distribution on η df, $T_U=-\{\hat{\alpha}_{i'}-\hat{\alpha}_i-(\hat{\beta}_i-\hat{\beta}_{i'})E_U\}/\{v_{11}+v_{22}E^2_U-2v_{12}E_U\}^{\frac{1}{2}}$, and η is pooled degrees of freedom of the residuals from regressions for the i-th and the i'-th genotypes. Applying the above approach for obtaining Prob[$\hat{x}_c \le E_L$], we can estimate γ by $G_\eta(T_U)-G_\eta(T_L)$, where $T_L=-\{\hat{\alpha}_{i'}-\hat{\alpha}_i-(\hat{\beta}_i-\hat{\beta}_{i'})E_L\}/\{v_{11}+v_{22}E^2_L-2v_{12}E_L\}^{\frac{1}{2}}$. The probability of crossover interaction (PrCOI) between genotypes i and i' is=(1 – probability of that the F-distributed random variable exceeds the observed variance ratio for slope differences)×probability that their CP lies within (E_L, E_U)]=$(1-P_0)\gamma$. The probability that the two genotypes posses a non-crossover type-interaction (PrNonCOI) is=$(1-P_0)(1-\gamma)$. Thus, any given pair of genotypes is classified in one of the three groups: (1) genotypes' regression lines are parallel and can be assessed with probability P_0, (2) genotypes showing crossover-type interaction [with probability $(1-P_0)\gamma$], and (3) genotypes showing non-crossover-type interaction [with $(1-P_0)(1-\gamma)$]. The three probabilities add to unity. The above probabilities can be computed when error variances are homogeneous or heterogeneous.

Crossover point of COGEI based on all genotypes

The approach presented above for estimating the crossover point of COGEI is applicable for a given pair of genotypes. Such a point may vary with the genotype pair. However, one may be interested in obtaining a single critical point to partition the environments into two groups (consisting of low-yielding and high-yielding environments) but based on all the genotypes. Such a point can be estimated as the value of the environmental index where there is least variability between genotypic responses (v>2). If we consider

$$y_i = \hat{\alpha}_i + \hat{\beta}_i x$$

as the estimated response relationship for the i-th genotype, then the variability between the predicted responses of genotypes at a general point x on the environmental mean axis is a quadratic function in x.

$$\Sigma(y-\bar{y})^2 = \Sigma(\hat{\alpha}_i-\bar{\alpha})^2 + x^2\Sigma\left(\hat{\beta}_i-\bar{\beta}\right)^2 + 2x\Sigma(\hat{\alpha}_i-\bar{\alpha})\left(\hat{\beta}_i-\bar{\beta}\right)$$

where '–' bar denotes the mean of the associated quantities over all the genotypes. This function attains minimum value when $x=\hat{x}_{co}$, where

$$\hat{x}_{co} = -\Sigma(\hat{\alpha}_i-\bar{\alpha})\left(\hat{\beta}_i-\bar{\beta}\right) / \Sigma\left(\hat{\beta}_i-\bar{\beta}\right)^2.$$

Thus, $\hat{x}_{co}$ partitions the environments in two groups—one consisting of the environments with means less than $\hat{x}_{co}$ and the other with environment means greater than this value. In each group of the environments, the variability in the predicted response of the genotypes increases with the distance of the environment mean (index) from $\hat{x}_{co}$.

Genotypic evaluation for specific adaptation

Using an estimate $\hat{x}_c$ or $\hat{x}_{co}$ of x_c one can group the environments into E_L=(environments where environmental index $\leq\hat{x}_c$) and E_U=(environments where environmental index $>x_c$). We examined the effect of the grouping on GEI and evaluated the genotypes in terms of their means and slopes of the regression line for each group of the environments.

Results and discussion

Individual trials were analyzed and significant genotypic variability ($0.001\leq P\leq 0.01$) was observed. Experimental error variances were found to be heterogeneous ($P\leq 0.001$) over the environments using Bartlett's test. Lattices were found to be more efficient than the randomized complete block design (RCBD) in 19 of the 21 trials with the percentage efficiency over RCBD reaching up to 192% (see Table 1). In the majority of multi-environment trials, the experimental errors are heterogeneous, but in the literature, results by and large have been presented ignoring the heterogeneity. We, therefore, cover here both the situations – heterogeneous errors and assumed homogeneous errors – to provide a comparison and assessment of the effect of ignoring the heterogeneity on the results. GEI (using an F-test under assumed homogeneity and a chi-square test under observed heterogeneity of error variances) was found to be significant (P<0.001).

For individual genotypes, yield response to the environments was modeled as linear regression on the environmental index. The percentage variance accounted for varied in the range 92–99% over the genotypes in the case of assumed homogeneity of error variances and in the range 91–99% in the case of heterogeneous errors. Using a linear regression model for all the genotypes, we found heterogeneity of regressions to be statistically significant with P<0.001 (further results from the regression analysis not included here).

To evaluate the pairs of genotypes which contributed to the COGEI, we compared all possible pairs (2016 in total) for parallelism of slopes, and the number of pairs found significantly different in slopes at overall probability levels of significance of 10%, 5%, 1% and 0.1%

Table 1 Ranges of the values of the probability of exceeding the observed variance ratio, coefficient of variation (cv), of plot errors, efficiency of lattices over randomized complete block design (RCBD), environment means and error mean square (EMS), and distribution of efficiency of lattices and coefficient of variation from analyses of the individual trials

Range	Minimum	Maximum
Probability[a]	<0.001	<0.01
Plot CV%	6.1	38
Eff% (RCB)[b]	100	192
Environmental mean (t/ha)	0.35	4.86
EMS[c] (*df*=105)	0.006508	0.2207

Efficiency of the lattice over RCBD(%)

Range	100–105	105–110	110–120	120–150	150+
Number of environments	5	4	2	6	4
%	(24)	(19)	(10)	(28)	(19)
Cum. %	(24)	(43)	(53)	(81)	(100)

Coefficient of variation of CV%

Range	0–5	5–10	10–15	15–20	20–30	30+
Number of environments	0	4	10	4	2	1
%	(0)	(19)	(48)	(19)	(10)	(4)
Cum. %	(0)	(19)	(67)	(86)	(96)	(100)

[a] Probability is the probability of exceeding the observed variance ratio under the null genotypic difference (probability values were <0.001 except for environments 5 and 9 where they were in the range 0.001–0.01)
[b] Eff% is the efficiency of the lattice over RCBD (%)
[c] EMS, Error mean square (t/ha)^2

Table 2 Number of pairs of genotypes with significant differences in slopes when errors are homogeneous/heterogeneous

Probability level of significance						
Overall	Comparison-wise					
	Error variances					
	Homogeneous			Heterogeneous		
α	α	a	b	α	a	b
10%	616	11	11	1168	405	400
5%	452	4	3	1032	367	366
1%	226	0	0	802	293	290
0.1%	72	0	0	582	212	212

The comparison-wise probability level from an overall (experimentwise) probability level α is computed as: $a=1-(1-\alpha)^{1/(v(v-1)/2)}$ and $b=\alpha/(v(v-1)/2)$ (Fisher'significant difference test). For example, at 10% overall level, comparison wise probability levels: a=0.0000523 and b=0.10/2016=0.0000496

are given in Table 2. The number of genotype pairs (1) intersecting within and outside the observed range (E_L, E_U), (2) representing crossover and non-crossover interaction, and parallel lines at 1%, 5%, and 10% levels of significance for parallelism of the slopes, and (3) showing their distribution based on various set values of the inclusion probabilities (less than 0.01, 0.05, and 0.1, between 0.1–0.9, and more than 0.9, 0.95 and 0.99) and at the above levels of significance are presented in Table 3.

About 50% of the pairs intersect within the observed range of environmental indices (Table 3-1). At level $P \leq 0.01$ under homogeneous error variances, there were 206 pairs of genotypes with crossover (CO) types and 20 pairs of non-crossover (NCO) types, giving 226 pairs. At the 5% level of significande (100*1564/2016=) 78% of the pairs showed parallel lines, 19% crossover interaction and the remaining 3% non-crossover interaction when the errors were assumed to be homogeneous, while 49% of the pairs had parallel lines, 38% crossover interaction and 13% the non-crossover type in the case of heterogeneous errors (Table 3-2). At the 10% level of significance, the above percentages are, respectively 25, 5, 70 for homogeneous errors and 42, 16, and 42 for heterogeneous errors. This indicated that an appreciable number of crossovers take place in the case of barley lines grown in different environments. Further, the distribution of pairs representing crossovers are considerably higher than non-crossover types at various inclusion probability levels exceeding 90% and at all the levels of significance for parallelism as exhibited in Table 3-3. For example, of the 226 pairs, 133, 75 and 20 have a probability of a crossover interaction (PrCOI) greater than 0.90, between 0.1–0.9, and less than 0.1, respectively. At the 5% level of significance, the percentage of pairs with heterogeneous slopes exhibiting crossover with a confidence of 90% or more [inclusion probability $(1-P_0)\gamma \geq 0.90$] is 196/452×100 (≈43%) and for the non-crossover, 62/452×100 (=14%) under homogeneous errors; under heterogeneous errors, these percentages are 52% and 26%, respectively. Other values of Table 3-3 can be viewed similarly.

The number of pairs with significant slope differences (Tables 2 and 4) varied and were large when level of significance per pair (i.e., comparisonwise error rate) was set even at 0.1% (Table 2). Since we are screening all possible pairs (or making multiple comparisons), the probability level per pair would be $a=1-(1-\alpha)^{1/(v(v-1)/2)}$ given that α is an overall probability level (i.e., the experimentwise error rate) for comparing v genotypes, which further simplifies to $b=\alpha/[v(v-1)/2]$ as in the case for the Fisher significant difference test (Preece 1982). At an overall probability level α=0.05, there were 3 and 4 pairs of genotypes with significantly different slopes using a and b probability levels, respectively. There were 11 pairs of genotypes with significant pairwise COGEI at α=0.10.

We present the crossover point (CP) given by $\hat{x}_c$ and their 95% confidence intervals and the inclusion probabilities in Table 4. The two upper confidence limits based on the exact and asymptotic results are reasonably close, while lower limits vary considerably. The lower limits from the exact expression also go beyond the observed range in seven cases. Further, a close examination of the confidence limits (Table 4) indicates that the lower limit for CP is less than E_L, the lowest environmental index. Ignoring such cases, we considered the CPs (in t/ha) 1.54 (genotype pair 17, 31), 1.57 (genotype pair 19, 27), and 1.64 (genotype pair 19, 31) for grouping the environments. The CP based on all genotypes (i.e., given by $\hat{x}_{co}$) was 1.36 t/ha on the environmental mean axis. The partitioning of GxE interaction was done to assess the amount of interaction between genotype and environment groups by forming two groups of environments: low-yielding environments, E_L=(environments with mean ≤CP), and high-yielding environments, E_H=(environments with mean >CP). The partitioning of GxE interactions for these groupings was carried out, and their mean squares were compared (results not presented here) for various values of CP given in Table 4. The CP of 1.64 t/ha provided maximum genotype×environment-group interaction. This indicates the possibility of more effective grouping based on pair-wise crossover compared with that based on minimum variability between genotypes over the environments. Therefore, we present the performance of the top 5 lines, for each of the two groups of environments created by the two CP values in Table 5, for CP=1.64 t/ha (based on the genotypes pair) and CP=1.36 t/ha (based on overall genotypes), respectively.

Across all environments, genotype nos. 59 and 12 stood first and second for yield. When CP=1.64 t/ha was taken to generate 2 environment groups, no 59 remained the highest yielding genotype in the high-yielding environment group but yielded very low (rank=49) in the low-yielding environment group. The first position in the low-yielding environment group was acquired by genotype no. 18, while genotype no. 12 ranked 6. Rank

Table 3 Number of pairs intersecting within and beyond the observed environment, parallel lines, and distribution of crossover (CO) and non-crossover (NCO) points

(1) Number of pairs of lines intersecting:

Error variances	Environment index intervals (t/ha}			
	(0.353, 4.856)	≤0.353	≥4.856	Total
Homogeneous	1137	601	278	2016
Heterogeneous	1117	633	266	2016

(2) Number of pairs of crossover, non-crossover, and parallel lines:

Level of significance	Error variances					
	Homogeneous			Heterogeneous		
	CO	NCO	Parallel	CO	NCO	Parallel
0.01	206	20	1790	613	189	1214
0.05	390	62	1564	760	272	984
0.10	510	106	1400	842	326	848

(3) Distribution of number of pairs of (intersecting) lines for crossover and non-crossover:

Level of significance	Inclusion probabilities (PrInc[a], PrCOI[b], and PrNonC[c]) are							
	Greater than				Less than			Between
		0.90	0.95	0.99	0.01	0.05	0.10	0.1–0.9
When the error variances are homogeneous:								
0.01	PrInc	133	106	49	20	20	20	73
	PrCOI	131	102	41	20	20	20	75
	PrNonC	20	20	20	49	106	133	73
	(Total number of pairs=226)							
0.05	PrInc	210	158	61	62	62	62	180
	PrCOI	196	131	41	62	62	62	194
	PrNonC	62	62	20	62	159	212	178
	(Total number of pairs=452)							
0.10	PrInc	238	176	63	106	106	106	272
	PrCOI	208	131	41	106	106	106	302
	PrNonC	106	62	20	64	178	243	267
	(Total number of pairs=616)							
When the error variances are heterogeneous:								
0.01	PrInc	484	438	274	189	189	189	129
	PrCOI	484	436	271	189	189	189	129
	PrNonC	189	189	189	274	438	484	129
	(Total number of pairs=802)							
0.05	PrInc	563	458	274	272	272	272	197
	PrCOI	537	443	271	272	272	272	223
	PrNonC	272	272	189	274	458	564	196
	(Total number of pairs=1032)							
0.10	PrInc	567	458	274	326	326	326	275
	PrCOI	537	443	271	326	326	326	305
	PrNonC	326	272	189	274	458	570	272
	(Total number of pairs=1168)							

[a] PrInc=γ=Prob[$x_L \le \hat{x}_c \le x_u$] =probability of inclusion
[b] PrCOI=(1–P_o) γ=probability of a crossover interaction
[c] PrNonC=(1–P_0)(1–γ); P_0=Prob (of exceeding the observed variance ratio for slope differences under the null hypothesis)=FProb (in the accumulated ANOVA table from GENSTAT)

changes can be seen for the value CP=1.36 t/ha (Table 5).

Compared to the attempts made for testing GxE interactions, less effort has gone into examining crossover-type interaction. In fact, in our opinion many scientists think that crossover-type interaction does not exist in many crops. The existence of crossover interaction in lentil and barley has been highlighted by Ceccarelli et al. (1994). Because crossover interaction plays a very decisive role in deciding on an appropriate breeding strategy in relation to specific versus wide adaptation, it is very important to ascertain just how frequent this type of interaction is. This study, conducted in the absence of major disease or insect problems, reveals a high frequency of crossover interactions. Boron toxicity may be another cause leading to the crossover interaction (Yau et al. 1995).

It is pertinent to emphasize on the computation of PrCOI. The expression (1–P_0) γ gives the probability of observing COI while accounting for the degree of heterogeneity of the slopes of the regression lines in terms of P_0. The PrCOI will have a value of γ as a special case

Table 4 The 11 pairs of genotypes selected with significant pairwise COGEI (overall proabability level=0.10), estimates of intercepts and slopes, estimates of CP (t/ha), 95% confidence intervals (exact and asymptotic) of CP, and inclusion probability (PrInc=γ) of the CP within the observed environment range (in the case of homogeneous error variances)

Pair of genotypes (i, j)		$\hat{\alpha}$	$\hat{\beta}$	CP($\hat{x}_c$)	Exact		Asymptotic		
					Lower[a]	Upper[a]	Lower	Upper	PrInc
i	j			t ha^{-1}					
17	–	0.214 ±0.132	0.81 ±0.05						
	31	−0.207 ±0.081	1.082 ±0.031	1.54 ±0.326	0.61	2.11	0.90	2.17	0.988
	32	−0.022 ±0.072	1.070 ±0.027	0.90 ±0.417	–[b]	1.57	0.09	1.71	0.856
	48	−0.077 ±0.079	1.081 ±0.03	1.07 ±0.384	–	1.69	0.32	1.82	0.919
19	–	0.216 ±0.106	0.82 ±0.04						
	27	−0.190 ±0.100	1.084 ±0.038	1.57 ±0.320	0.67	2.14	0.94	2.19	0.990
	31	−0.207 ±0.082	1.082 ±0.031	1.64 ±0.289	0.87	2.17	1.08	2.21	0.996
	32	−0.022 ±0.072	1.070 ±0.027	0.97 ±0.368	–	1.57	0.25	1.69	0.905
	34	−0.023 ±0.084	1.064 ±0.032	1.00 ±0.395	–	1.64	0.23	1.77	0.897
	39	−0.003 ±0.081	1.067 ±0.031	0.90 ±0.399	–	1.54	0.12	1.69	0.867
	48	−0.077 ±0.079	1.081 ±0.03	1.14 ±0.340	0.15	1.71	0.48	1.81	0.954
	52	−0.070 ±0.103	1.087 ±0.039	1.09 ±0.380	–	1.71	0.35	1.84	0.926
	59	−0.103 ±0.136	1.127 ±0.052	1.06 ±0.390	–	1.69	0.29	1.82	0.913

[a] Low, Lower confidence limit; upper, upper confidence limit; $\hat{\alpha}$=estimate of intercept; $\hat{\beta}$=estimate of slope
[b] –, indicates lower limit was less than the observed minimum value

Table 5 Performance of 5 high yielding genotypes under environments with mean yields less than or greater than the CP

Environments									
All				E_L[a]			E_H[b]		
Rank	Mean	Genotype	Slope	Mean	Genotype	Slope	Mean	Genotype	Slope
CP($\hat{x}_c$)=1.64 t ha^{-1}									
	(t ha^{-1})			(t ha^{-1})			(t ha^{-1})		
1	2.48	59	1.13	1.29	18	1.13	3.57	59	1.03
2	2.46	12	1.00	1.26	15	1.01	3.47	32	0.98
3	2.45	2	1.05	1.23	55	1.20	3.45	39	1.01
4	2.45	4	1.02	1.23	9	0.98	3.44	14	1.11
5	2.45	51	1.04	1.22	63	1.15	3.45	51	0.96
CP($\hat{x}_{co}$)=1.36 t ha^{-1}									
1	2.48	59	1.13	1.02	12	1.00	3.16	59	1.12
2	2.46	12	1.00	1.00	15	1.05	3.11	51	0.97
3	2.45	2	1.05	0.98	18	1.11	3.10	4	0.94
4	2.45	4	1.02	0.98	56	0.98	3.08	39	1.07
5	2.45	51	1.04	0.96	9	1.01	3.08	49	0.96

[a] E_L, Set of environments with mean yields less than the CP
[b] E_H, Set of environments with mean yields greater than the CP

when P_0=0 and, in that situation, the observed F-value will lie at infinity, implying that the two lines are extremely heterogeneous for the slope.

The estimation of the crossover point (CP) at the low value of $\hat{x}_{co}$=1.36 or $\hat{x}_c$=1.64 t/ha indicates that one of the reasons why crossover interactions are not always detected is the narrow range of environments often used to test the genotypic responses. While this may be justified in the case of crops mostly grown in favorable environments, it is certainly not true for crops, such as barley, which in developing countries are grown predominantly at yield levels below the CP.

It may be noted that $\hat{x}_{co}$ provides a crossover point which can be used to divide the environment range and is based on response behavior information from all the genotypes. It does not necessarily indicate a common

crossover point for all the genotypes unless the regression lines of all the genotypes must intersect at one point. In such cases, genotype responses have been explained by using shifted multiplicative models (Cornelius et al. 1992), which are more restrictive than the model of Finley and Wilkinson (1963).

The changes in the ranks of entries when evaluated in various groups of environments can be used for recommending the environmental domains of specifically adapted genotypes. The method used for identifying the two groups of the environments for specific adaptation is most appealing when the environments are locations. However, the environments are characterized by weather parameters such as rainfall, temperature, and prevalence of disease distribution in addition to the soil parameters. If the weather parameters could be forecast, one may be in a position to switch to the material adapted for the specific environment in that year at a chosen location.

The datasets analyzed here can provide an opportunity for exploiting GEI using other applied analytical methods, such as the additive main-effects and multiplicative interaction model (Gauch 1988), use of climatic factors in explaining the GEI, and evaluation of the riskiness of production and the optimal allocation of land resources to various genotypes for selection in heterogeneous environments. In the case under study, we found that linear regression is adequate for all the genotypes (percentage variance accounted for exceeded 90%) but that this method for evaluating crossover interaction would not be applicable where the fits are rather poor. In those cases, other forms of relationship as well as those along the lines of the concept of separability (Gregorius and Namkoong 1986) would require evaluation.

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