Indian J. Genet., **65**(2): 77-83 (2005)

Estimation of heritability using spatial variability models: The case of lentil (*Lens culinaris* Medikus) trials in Syria

M. Singh, A. Sarker and W. Erskine

International Center for Agricultural Research in the Dry Areas (ICARDA), PO Box 5466, Aleppo, Syria

(Received: August 2004; Revised: March 2005; Accepted: March 2005)

Abstract

Heritability is a key determinant of response to selection and breeding efficiency, and is often estimated using data from field trials involving simple block designs. However, spatial variability patterns that cannot be modeled using a classical block analysis framework have been found to be prevalent in field trials of lentil (*Lens culinaris* Medikus), an important food legume crop worldwide. Therefore, 18 different models, each describing a different spatial pattern, were assessed using lentil yield data from preliminary and advanced yield trials in Syria. More often the best models included linear trends and auto-correlated errors in addition to the classical block effect than those based on block effects alone. For instant, of the 31 preliminary yield trials on seed yield, model based on complete block and first-order autocorrelated errors along rows was found best in eight trials followed by auto-correlated errors in rows and column dimensions in seven trials. Out of the 18 advanced yield trials, randomized complete block was most suitable to describe the field variability in six trials followed by complete blocks with a linear trend along rows in three trials.

These trials evaluated pure lines of two seed sizes, and were conducted using square lattices, in three contrasting West Asian environments. The most appropriate model for a given trial was identified and used to estimate heritability (1) using data from individual trials, and (2) using combined data from multi- environment trials, to incorporate genotype × environment interaction. Average broad-sense heritability over individual trials was found to be 0.47 for seed yield and 0.45 for biomass. Based on individual trials, average heritability estimates were similar for the two seed-size types. However, the presence of genotype × environment interaction reduced the estimates considerably, with an overall average of 0.21 for seed yield and 0.22 for biomass. Higher estimates of heritability were obtained for small-seeded genotypes (0.24 for seed and 0.22 for biomass) than for large-seeded material (0.15 for seed yield and 0.21 for biomass). Preliminary yield trials gave higher estimates of heritability (0.24 for seed yield and 0.29 for biomass) than advanced yield trials (0.16 for seed yield as well as for biomass). This approach can therefore be used to estimate heritability from multi-environment trials with a spectrum of spatial patterns in the experimental fields.

Key words: *Lentil, heritability, field trials, spatial variability*

Introduction

Field trials are conducted to assess the adaptability and the yield potential of various genotypes in contrasting environments. Heritability estimates of various traits help researchers determine a suitable strategy for crop improvement, and are frequently used by breeders to predict response to selection [1-2]. Heritability has mainly been estimated in situations where simple experimental designs were employed, and where simple models were used in data analysis. The precision or standard errors of the heritability estimates, or the confidence intervals for these estimates, have been reported for different situations by various researchers [3-11]. However, these situations are simplistic, as the above classical statistical models are based on the assumption that experimental errors are independent. In field trials, however, experimental plots are fixed in a two-dimensional layout (rows and columns), and thus plot errors are often inter-dependent. The use of a number of models incorporating the dependence of plot errors that arises from the rectangular layout used in field trials has also been reported in the literature [12-13]. In addition, spatial variation is often considerable in variety trials that are conducted in multiple environments (e.g. location and year combinations), to allow genotype × environment interactions to be assessed. Taking proper account of spatial variability will yield a realistic estimate of heritability which will, in turn, provide a more efficient assessment of the expected response to selection.

In this study, we used lentil (*Lens culinaris* Medikus) yield trials to develop a procedure for estimating heritability in situations (such as those described above) where spatial variability occurs. The objectives of this study were (1) to describe the spatial models and procedures for estimation of heritability, (2) to identify, based on a particular criterion, the most appropriate spatial model for each of 49 lentil variety yield trials, (3) to present estimates of heritability for individual and multi-environment trials, and (4) to assess whether the heritability of seed yields differed in relation to the seed size of different lentil lines.

Materials and methods

Materials: Forty nine trials (31 preliminary and 18 advanced), comprising lentil genotypes of two seed sizes (32 small-seeded with < 4 g 100^{-1} and 17 large-seeded with > 4 g 100^{-1}), were evaluated over three years (from 1995/96 to 1997/98) at three locations: Breda (35°56′N, 37°10′E, 300 m a.s.l.) and Tel Hadya (36°01′N 36°56′E, 284 m a.s.l.) in Syria, and Terbol (33°49′N, 35°59′E, 950 m a.s.l.), in the Beqqa valley in Lebanon. Average seasonal precipitation (November to May) over this period was 277 mm in Breda (defined as a low-rainfall site), 398 mm in Tel Hadya (a moderate-rainfall site) and 531 mm in Terbol (a high-rainfall site in West Asia). Soils at all three locations are heavy-textured, with a high percentage of clay.

The trials, comprising sets of 25 and 16 genotypes, were conducted in square-lattice designs with two to four replications. In the two-dimensional layouts, the replicates comprised the row containing all the incomplete blocks; the number of columns was equal to the number of genotypes. The genotypes in different sets were different. However, all the genotypes in a given set were used across locations in a particular year. In total, 18 sets of multi-environment trials, and their associated genotype × environment interactions (arising from 2-3 locations), were evaluated within one year.

Plants were harvested from the centre of each plot. In the advanced trials, the area harvested was 4.8 m^2 (2 m × 8 rows × 0.3 m inter-row distance), and in the preliminary trials the area harvested was 3 m^2 (2 m × 5 rows × 0.3 m inter-row distance). Plants were weighed both before and after threshing. Seed and biomass yield per plot was converted to kilograms per hectare (kg/ha) for the purposes of statistical analysis.

Statistical methods

Heritability: Consider a given number (25 in the present case) of pure lines randomly selected from a population with variance σ_g^2 for a certain trait. These lines are evaluated (as was the case in this study) using a complete or an incomplete block design with a rectangular layout in a field at a single location. Using σ_ε^2 to denote the environmental variance, the broad-sense heritability h_b^2 of the trait may be defined as

$$h_b^2 = \sigma_g^2 \Big/ \left(\sigma_g^2 + \sigma_\varepsilon^2 \right)$$

In the case of multi-environment trials, if $\sigma_{G \times E}^2$ denotes the genotype × environment interaction variance, the broad-sense heritability $\left(h_b^2 \right)$ of the trait is defined as

$$h_b^2 = \sigma_g^2 \Big/ \left(\sigma_g^2 + \sigma_{G \times E}^2 + \sigma_\varepsilon^2 \right)$$

The above formulation of heritability is on plot basis for genetic and error variance components [10-11].

Selection of the best model: A range of spatial patterns, in terms of block structures and plot error structures, was gauged using a set of 18 models. These models were used to analyze the seed yields of each of the trials and crops [14-15]. The models describe the components of spatial patterns (Table 1), and were obtained by fitting, in different combinations, the following:

1. block structures (complete blocks or incomplete blocks)
2. trends in the direction of columns (using a linear trend, a linear trend with random cubic smoothing spline (CS), or assuming no trend)
3. three structures for plot errors (first-order auto-regressive (AR) errors in columns, or AR errors in columns as well as in row directions (ARAR), or independence of plot errors (I)).

Let *y*, representing the vector of yields from an experimental design on a rectangular layout, be modeled as $y = \mu + X\tau + Zu + \xi + \varepsilon$

Table 1. Distribution of the best (spatial) models over lentil trials

		Components of spatial pattern						
Sr. No.	Model No.@	Block	Trend	Errors	Seed yield		Biomass	
					PYT	AYT	PYT	AYT
1	1	Complete		I	6	6	1	1
2	2	Complete		AR	8	1	3	1
3	3	Complete		ARAR	7	2	4	1
4	4	Incomplete		I	3	2	1	3
5	5	Incomplete		AR	1	0		
6	6	Incomplete		ARAR	0	0	1	
7	7	Complete	L	I	4	3	1	1
8	8	Complete	L	AR	1	0		
9	9	Complete	L	ARAR	1	1	1	1
10	10	Incomplete	L	I				1
11	13	Complete	LCS	I		2		3
12	15	Complete	LCS	ARAR		1		1
13	16	Incomplete	LCS	I				1
		(total)			31	18	12	14
		(Other than RCB or Lat)*			22	10	10	10

@Model numbers are from Singh *et al.* (2003).

*Spatial patterns in fields of these many trials showed the presence of linear trends (L), cubic smoothing spline (LCS) and auto-correlated errors (AR: along rows; ARAR along rows and columns), which could not be accounted by the complete blocks or incomplete blocks alone. T indicates that the plot errors were independent [15].

where μ is the general mean, τ is a vector of fixed parameters (used, for example, to represent the effects of fixed trends and genotypes), and u is a vector of effects of replications and blocks within replications and is assumed to be random. X and Z are incidence matrices associated with τ and u respectively [13]. The vector ξ represents spatial variability (for example, the random cubic smoothing spline). Any linear components associated with the cubic smoothing spline would be part of the vector τ. The quantity ε is a random error vector of spatially correlated errors (for example, those following an auto-regressive structure in two dimensions). Modeling data with fixed effects for the genotypes assumed here allows accounting genotypic variation with its full degrees of freedom and, therefore, better estimates the contribution of other factors including spatial errors. Once a spatial pattern has been identified, it can be used for estimating various parameters including heritability.

Each of the models was fitted using the residual maximum likelihood (REML) method and the associated commands in the Genstat software package [16]. The Akaike Information Criterion (AIC), expressed in terms of the quantity 'deviance', was used to select the best model with same set of fixed effects fitted [15]. The main reason for this step was to identify, in each trial, the model that best represented the spatial pattern of the variation in that trial. In order to estimate heritability in each trial, the spatial structure of the best model of the trial was fitted (with the genotype effects treated as random), and the variance components, σ_g^2 and σ_ε^2, were estimated.

Estimation of heritability for an individual trial: For the genotypes (lines) evaluated in a single environment, heritability is estimates using the following expression in terms of the estimate of the genotypic variance component be denoted by $\hat{\sigma}_g^2$ and that of the environmental error variance component by $\hat{\sigma}_\varepsilon^2$.

$$\hat{h}_b^2 = \hat{\sigma}_g^2 \Big/ \left(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2 \right)$$

Standard error of the heritability estimates can be computed by using an approximation for the variance of a ratio of two random variables [17] and estimated variances and covariance of the estimates of the variance components, and is simplified as follows:

$$\hat{se}\left(\hat{h}_b^2\right) = \hat{h}_b^2$$

$$\sqrt{v_{gg}/(\hat{\sigma}_g^2)^2 + (v_{gg} + v_{ee} + 2c_{ge})/(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)^2 - 2(v_{gg} + c_{ge})/(\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2))}$$

where

$$v_{gg} = \hat{var}(\hat{\sigma}_g^2),\ v_{ee} = \hat{var}(\hat{\sigma}_\varepsilon^2),\ c_{ge} = \hat{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2)$$

are the elements in the estimated variance-covariance matrix of the associated variance components estimates.

Estimation of heritability from multi-environment trials: In multi-environment trials, the best model was selected for each individual trial, because the combination of block structure, fertility trends and plot-error structure may have been unique for each trial site. We also introduced a term representing random genotype × environment interaction effects, with its variance component denoted by $\sigma_{G\times E}^2$.

However, it should be noted that the error variance component $\left(\sigma_{\varepsilon_j}^2\right)$ may vary with the environment (j = 1, 2, ... L, where L is the number of environments), and need not necessarily be homogeneous. An estimate of environmental variance could be obtained by calculating the average of the variance components over environments. We computed a weighted average $\bar{\hat{\sigma}}_\varepsilon^2$ using as weights the error degrees of freedom (v_j) associated with the error variance $\sigma_{\varepsilon_j}^2$ in the j-th environment. Thus $\bar{\hat{\sigma}}_\varepsilon^2 = \sum_{j=1}^{L} w_j \hat{\sigma}_{\varepsilon_j}^2$ where

$$w_j = v_j \Big/ \sum_{j=1}^{L} v_j .$$

Statistical software can be used to fit a model combining the data from several environments (where residuals from each environment could follow a different error structure) and to obtain estimates of the variances and covariances of the estimates of the variance components. Using these estimates, one can then obtain the following variance and covariances of the average error variance as:

$$\hat{var}(\bar{\hat{\sigma}}_\varepsilon^2) = \sum_{j=1}^{L} w_j^2\, \hat{var}(\hat{\sigma}_{\varepsilon_j}^2)$$

$$+\ 2 \sum_{j<j'=1}^{L} w_j w_{j'}\, \hat{cov}(\sigma_{\varepsilon_j}^2, \hat{\sigma}_{\varepsilon_j'}^2)$$

$$= \sum_{j=1}^{L} w_j^2 v_{e_j} + 2 \sum_{j<j'=1}^{L} w_j w_{j'} C_{e_j e_{j'}} = v_{\overline{ee}},\ say$$

$$\hat{cov}(\bar{\hat{\sigma}}_\varepsilon^2, \hat{\sigma}_g^2) = \sum_{j=1}^{L} w_j\, \hat{cov}(\hat{\sigma}_{\varepsilon_j}^2, \hat{\sigma}_g^2)$$

$$= \sum_{j=1}^{L} w_j C_{ge_j} = v_{g\bar{e}}, \text{ say};$$

$$\widehat{cov}(\overline{\hat{\sigma}}^2_{\varepsilon}, \hat{\sigma}^2_{G \times E}) = \sum_{j=1}^{L} w_j \widehat{cov}(\hat{\sigma}^2_{\varepsilon_j}, \hat{\sigma}^2_{G \times E})$$

$$= \sum_{j=1}^{L} w_j \; c_{G \times E e_j} = v_{G \times E \bar{e}}, \text{ say}.$$

Thus, for multi-location situation, the estimate of heritability and its standard error are given as:

$$\hat{h}^2_b = \hat{\sigma}^2_g / (\hat{\sigma}^2_g + \hat{\sigma}^2_{G \times E} + \hat{\sigma}^2_{\varepsilon})$$

$$\widehat{se}(\hat{h}^2_b) = \hat{h}^2_b$$

$$[v_{gg}/(\hat{\sigma}^2_g)^2 + \{v_{gg} + v_{G \times E\, G \times E} + v_{\overline{ee}}$$

$$+ 2(c_{g\, G \times E} + c_{g\bar{e}} + c_{G \times E \bar{e}})\}/$$

$$(\hat{\sigma}^2_g + \hat{\sigma}^2_{G \times E} + \overline{\hat{\sigma}}^2_{\varepsilon})^2$$

$$-2(v_{gg} + c_{g\, G \times E} + c_{g\bar{e}}) /$$

$$(\hat{\sigma}^2_g(\hat{\sigma}^2_g + \hat{\sigma}^2_{G \times E} + \overline{\hat{\sigma}}^2_{\varepsilon}))]^{1/2}$$

where

$$v_{gg} = \widehat{var}(\hat{\sigma}^2_g),\; v_{G \times E\;\; G \times E} = \widehat{var}(\hat{\sigma}^2_{G \times E}),$$

$$c_{g\, G \times E} = \widehat{cov}(\hat{\sigma}^2_g, \hat{\sigma}^2_{G \times E}),\;\; v_{ejej} = \widehat{var}(\hat{\sigma}^2_{\varepsilon_j})$$

$$c_{e_j e_{j'}} = \widehat{cov}(\sigma^2_{\varepsilon_j}, \hat{\sigma}^2_{\varepsilon_{j'}}),\; c_{gej} = \widehat{cov}(\sigma^2_{\varepsilon_j}, \hat{\sigma}^2_g),$$

$$c_{G \times E e_j} = \widehat{cov}(\hat{\sigma}\varepsilon_j^2, \hat{\sigma}^2_{G \times E}) \text{ for}$$

$$j = 1, 2, ..., L.$$

We used Genstat statistical package for the required computations.

Results and discussion

Based on the set of 49 trials, the distribution of the best model (i.e. the model with the lowest AICD value) is presented in Table 1. These were used to compute heritability of seed yield and biomass from (1) the individual trials, and (2) the multi-environment trials for the same set of genotypes. Measurements of biomass were also made in 26 of the 49 trials in which seed yield was measured. As judged by the AIC criterion, the incomplete blocks were effective in six trials for seed yield and in seven trials for biomass (i.e., the lattice model was indeed the best model for accounting for variability in those trials). But, in 31 trials for seed yield and 17 for biomass, we observed that linear trends along rows and correlations among the plot errors replaced the effect of incomplete blocks. Spatial patterns varied over the fields. For example, for the fields under preliminary yield trials, spatial pattern of seed yield described by autocorrelated errors along rows was most prevalent followed by autocorrelation along columns in addition. For seed yield in advanced yield trials, randomized complete blocks were found most suitable in six trials followed by complete blocks with linear trend along rows in three trials.

For each individual trial, both the estimate of heritability and the precision of that estimate (in terms of its standard error) were calculated (Table 2). When evaluated over different sites in the same year, substantial variation was observed in the heritability estimates calculated for the same material. The heritability estimates given in Table 2 were further summarized by trial type and seed type (details not presented). Of the 49 trials in which seed yield was recorded, the following two were not included in the summaries, because no genotypic variability in seed yield was found: a preliminary yield trial (PYT; 1998 at Tel Hadya) and an advanced yield trial (AYT; 1996 at Terbol). On average, the heritability of seed yield was 0.46 (maximum 0.79) in the 17 advanced yield trials, and 0.48 (maximum 0.80) in the 30 preliminary yield trials. With regard to biomass, the average heritability was 0.48 (maximum 0.80) in the 14 advanced trials and 0.41 (maximum 0.62) in the 12 preliminary trials where biomass was recorded. In the case of both seed yield and biomass, heritability estimates of less than 0.20 were found in two AYTs and three PYTs (although these were not necessarily the same trials in either case; Table 2).

Averaged across all the trials (AYT and PYT; Table 2), the estimates of heritability for grain yield and biomass were very similar: 0.47 for grain yield and 0.45 for biomass. Summarizing results in terms of seed size, the average heritability for seed yield for small-seeded material (32 trials) was 0.47 (maximum 0.80) and for large-seeded material (15 trials) 0.49 (maximum 0.77). Also in terms of seed size, the average heritability for biomass for small-seeded material was 0.45 (maximum 0.69); for large-seeded material it was 0.49 (maximum 0.77). With regard to trial type: for seed yield, the average heritability was 0.46 (maximum 0.79) based on 17 AYTs and 0.48 (maximum 0.80) based on 30 PYTs. For biomass, the averages (and maximum values) were 0.48 (0.80) from 14 AYTs and 0.41 (0.62) from 12 PYTs, over both the seed-size categories.

Heritability estimates were lower for small-seeded material than they were for large-seeded material (0.48

Table 2. Estimates of heritability (h_b^2) of seed yield and biomass (± standard error), for individual trials

Year	Seed type[a]	Seed yield				Biomass			
		Breda	Tel Hadya	Terbol	Average	Breda	Tel Hadya	Terbol	Average
(a) Preliminary yield trials									
1996	S1	0.59±0.13	0.37±0.10	0.80±0.072	0.59		0.58±0.094	0.57±0.14	0.58
	S2	0.29±0.17	0.35±0.12		0.32				
	S3	0.49±0.14	0.25±0.10		0.37		0.14±0.064		0.14
1997	S1	0.54±0.17	0.18±0.091	0.46±0.14	0.39	0.62±0.12	0.18±0.091	0.50±0.14	0.43
1998	S1	0.74±0.069	0.54±0.098	0.71±0.075	0.66				
	S2	0.065±0.095	0.026±0.076	0.55±0.097	0.21				
	S3		0.65±0.085	0.46±0.11	0.56				
	S4	0.75±0.074	0.61±0.092	0.57±0.14	0.64				
	S5	0.41±0.15	0.59±0.11		0.50				
1996	L1		0.29±0.091	0.63±0.097	0.46		0.01±0.059	0.40±0.13	0.21
	L2		0.34±0.11		0.34		0.54±0.099		0.54
	L3		0.64±0.097		0.64		0.33±0.11		0.33
1997	L1	-	0.52±0.11	0.51±0.13	0.52		0.44±0.12	0.57±0.13	0.51
1998	L	-	(+)	0.51±0.17	0.51				
(b) Advanced yield trials									
1996	S	0.7610.071		0.79±0.067	0.78	0.51±0.12			0.51
	S1		0.37±0.10		0.37		0.55±0.096		0.55
1997	S1	0.27±0.10	0.50±0.12	0.46±0.12	0.41	0.37±0.14	0.42±0.13	0.15±0.13	0.31
	S2	0.19±0.14	0.086±0.13	0.56±0.12	0.28	0.63±0.11	0.69±0.092	0.43±0.14	0.58
1996	L	0.68±0.095	0.28±0.13	(+)	0.48	0.80±0.06	0.64±0.094	0.04±0.15	0.49
1997	L	0.40±0.13	0.32±0.13	0.34±0.11	0.35	0.55±0.12	0.48±0.13	0.44±0.11	0.49
1998	L	0.72±0.10	0.77±0.088	0.35±0.17	0.61				

[a]:S, S1-S5: sets of trials with small-seeds with red cotyledons; L, L1-L3: sets of trials with large seeds with yellow cotyledons. (+) indicates trials with no genotypic variability.

compared with 0.49 in PYTs, and 0.44 compared with 0.48 in AYTs for grain yield; and 0.47 compared with 0.49 for biomass in AYTs). The only exception to this was the case of biomass in PYTs, where the trend was reversed (0.43 and 0.38 for small-seeded and large-seeded material, respectively).

Heritability estimates were calculated for each of the 18 sets of genotypes tested in different locations in the same year (i.e., the 18 sets of multi-environment trials), as described above. Using the location-specific best spatial model for the yield variable, the heritability estimated in the presence of genotype x environment interaction is presented in Table 3. However, two sets for seed yield and one set for biomass were excluded from further summaries, because the material showed no (or a negative estimate of) genotypic variability. For seed yield, the average heritability estimate for 6 sets of multi-environment AYTs was 0.16 (maximum 0.57), while that from 10 sets of PYTs was 0.24 (maximum 0.37). For biomass, the average heritability estimate from 4 sets of AYTs was 0.16 (maximum 0.32), while that from 3 sets of PYTs was 0.29 (maximum 0.35). In terms of the average heritability over trial types, higher estimates were obtained for small-seeded material than for large-seeded material (0.24 and 0.15 for seed yield, and 0.22 and 0.21 for biomass). In the AYTs, the average heritability estimate for small-seeded material was greater than that of the large-seeded material. By contrast, however, the reverse trend was observed in the PYTs: the mean value for large-seeded material was the greater. The above trends (for average heritability over trial types) were observed for both the traits: seed yield and biomass. In two sets of multi-environment trials, the heritability estimates were low (less than 0.05) and the genotype x environment interaction variance components were large. Therefore, genetic improvement through selection based on the means calculated for these diverse sites would not be worthwhile in the case of the materials used in these sets. Thus, breeding for the enhancement of these genotypes should be undertaken at specific sites.

This study therefore describes an approach in which heritability is estimated from a more general perspective from the field data [18]. Since spatial variability in field trials is a reality, this approach is a more realistic and useful way of estimating heritability from field trials and hence genetic gain in response to selection. The average heritability found here for individual trials was 0.47 (maximum 0.80) for seed yield and 0.45 (maximum 0.80) for biomass. In a single

Table 3. Heritability estimates for seed yield and biomass (± standard error), for multi-environment trials, involving genotype × location interaction

	Seed yield			Biomass	
Seed type[a]	1996	1997	1998	1996	1997
(a) Preliminary yield trials					
S1	0.35±0.093	0.16±0.059	0.27±0.09	0.35±0.128	0.19±0.055
S2	0.17±0.110		0±0		
S3	0.12±0.057		0.18±0.122		
S4			0.21±0.079		
S5			0.30±0.116		
L			0±0		
L1	0.24±0.100	0.37±0.115		0±0	0.32±0.121
(b) Advanced yield trials					
S	0.57±0.110				
S1		0.14±0.073			0.03±0.045
S2		0.12±0.067			0.32±0.097
L	0.10±0.064	0.05±0.053	0.01±0.098	0.30±0.103	0.01±0.063

[a] S, S1-S5: sets of trials with small-seeds with red cotyledons; L, L1-L3: sets of trials with large seeds with yellow cotyledons.

experiment conducted using a set of 22 lentil genotypes, an estimate of 0.69 for seed yield was reported [19], which falls within the range of the estimates obtained in the present study.

The heritability estimates obtained in this study varied with seed size. In the presence of genotype × environment interaction, small-seeded genotypes, on average, gave higher heritability estimates (0.24 for seed yield and 0.22 for biomass) than large-seeded genotypes (0.15 for seed yield and 0.21 for biomass). This can be explained by the fact that large-seeded genotypes are more influenced by photoperiod and are more vulnerable to environmental fluctuations, especially variation in rainfall.

We observed higher average heritabilities in PYTs (0.24 for seed yield and 0.29 for biomass) than in AYTs (0.16 for seed yield and biomass), based on data in Table 3. This trend was unlikely to be due to differences in the genetic material used in the two types of trial, because the genetic composition of the F_7 and F_8 generations used in the PYTs and AYTs, respectively, was probably very similar. The trend was more likely to have resulted from differences in experimental error: such error would be lower in the PYTs, because the plots used were smaller than those used in AYTs. In advanced yield trials, seed yield and biomass showed the same level of heritability. This implies that both the traits are equally affected by edapho-climatic factors.

The presence of genotype × environment interactions substantially lowered the estimates of heritability in all cases, as would be expected as a result of the denominator (the interaction variance component) being large. The average heritability over all 49 trials in which seed yield was recorded, was 0.47 when calculated for individual trials, but was 0.21 when genotype × environment interactions were included. Estimates were similar for biomass. Similar findings on the effect of genotype × environment interactions were reported for barley trials conducted at four contrasting sites in Syria [11].

In recent years, plant breeders have frequently used complex spatial models in variety evaluation, but have used these models far less often when estimating various genetic parameters. The approach presented here illustrates an example of estimation of heritability from individual field trials each having a unique spatial variability.

Acknowledgements

The authors would like to thank Dr. S. Ceccarelli, Dr. R.S. Malhotra and an anonymous reviewer for their constructive suggestions, which considerably improved this manuscript. Thanks are also due to Dr S.E. Williams and Dr J.C. Weale of SCRIPTORIA Academic English Editing Services for editing the final draft of this document.

References

1. **Nyquist W. E.** 1991. Estimation of heritability and prediction of response in plant populations. CRC Crit. Rev. Plant Sci., **10**: 235-322.
2. **Ceccarelli S.** 1989. Wide adaptation: How wide? Euphytica, **40**: 197-205.
3. **Graybill F. A., Martin F. and Godfrey G.** 1956. Confidence intervals for variance ratios specifying genetic heritability. Biometrics, **12**: 99-109.
4. **Bogyo T. P. and Becker W. A.** 1963. Exact confidence intervals for heritability estimated from parental halfsib correlations. Biometrics, **19**: 494-496.
5. **Broemeling L. D.** 1969. Confidence intervals for measures of heritability. Biometrics **25**: 424-427.

6. **Falconer D. S.** 1982. Introduction to quantitative genetics. Longman Inc., New York.

7. **Knapp S. J., Stroup W. W. and Ross W. M.** 1985. Exact confidence intervals for heritability on a progeny mean basis. Crop Sci., **25**: 192-194.

8. **Rao A. R. and Prabhakaran V. T.** 2001. A bootstrap method of estimating heritability from varietal trial data. Indian J. Genet. Pl. Breed., **61**: 87-91.

9. **Bridges Jr. W. C., Knapp S. J. and Cornelius P. L.** 1991. Standard errors and confidence interval estimators for expected selection response. Crop Sci., **31**: 253-255.7.

10. **Singh M., Ceccarelli S. and Hamblin J.** 1993. Estimation of heritability from varietal trial data. Theor. Appl. Genet., **86**: 437-441.

11. **Singh M. and Ceccarelli S.** 1995. Estimation of heritability using variety trials data from incomplete blocks. Theor. Appl. Genet., **90**: 142-145.

12. **Cullis B. R. and Gleeson A. C.** 1991. Spatial analysis of field experiments - an extension to two dimensions. Biometrics, **47**: 1449-1460.

13. **Gilmour A. R., Cullis B. R. and Verbyla A. P.** 1997. Accounting for natural and extraneous variation in the analysis of field experiments. J. Agric. Biol. Env. Stat., **2**: 269-293.

14. **Sarker A., Singh M. and Erskine W.** 2001. Efficiency of spatial methods in yield trials in lentil (*Lens culinaris* ssp. *culinaris*). J. Agric. Sci., (Cambridge) **137**: 427-438.

15. **Singh M., Malhotra R. S., Ceccarelli S., Sarker A., Grando S. and Erskine W.** 2003. Spatial variability models to improve dryland field trials. Exp. Agric., **39**: 151-160.

16. **Payne R. W.** 2000. The Guide to Genstat. Part 2: Statistics. Lawes Agricultural Trust (Rothamsted Experimental Station), Harpenden.

17. **Kendall M. G. and Stuart A.** 1969. Advanced theory of statistics, Vol I. Charles Griffin and Co., London.

18. **Smith S. E., Kuehl R. O., Ray I. M., Hui R. and Soleri D.** 1998. Evaluation of simple methods for estimating broad-sense heritability in stands of randomly planted genotypes. Crop Sci., **38**: 1125-1129.

19. **Erskine W. and Goodrich W. J.** 1988. Lodging in lentil and its relationship with other characters. Can. J. Plant. Sci., **68**: 929-934.