Theor Appl Genet (1997) 95 : 1044–1048

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Precision of the genotypic correlation estimated from variety trials conducted in incomplete block designs

Received: 9 December 1996 / Accepted: 2 May 1997

Abstract Precise assessment of an association among traits of a crop plant is helpful in developing crop-improvement strategies. Two types of association, genotypic correlation and phenotypic correlation, may be used. An estimate of correlation is required along with a measure of precision in terms of standard error. Methods for the evaluation of the standard errors of genotypic and phenotypic correlations are not available in the literature, and when trials are conducted in incomplete blocks an algebraic evaluation of such correlation is cumbersome. Three methods – simulation, jackknife and bootstrap – have been used to evaluate bias and standard errors of genotypic, phenotypic and environmental correlations. We have evaluated their performance with data on grain yield, days-to-heading, and plant height, in barley genotypes in triple lattices. Simulation and jackknife techniques were found to be closer, compared to bootstrap, and can be recommended for assessing the precision of correlation estimates.

Key words Genotypic and phenotypic correlations · Standard error · Lattice design · Variety trials · Incomplete block design

Introduction

Knowledge of the association among traits of a crop plant aids the effective development of selection criteria for desirable plant types; for example, for constructing indirect selection indices for yield (Hazel 1943). Genotypic and phenotypic correlations between plant traits are often used as measures of association. While estimation of genotypic and phenotypic correlations (GC and PC) is straightforward, an evaluation of their precision in terms of standard errors and a test of significance on them is quite cumbersome. Approximate expressions for variances of such correlations have been obtained by Singh (1988), and Singh and Hinkelmann (1992), where the genotypes were evaluated in randomized complete block designs (see also Singh 1992). In the case of data from parent-offspring, Reeve (1955) and Robertson (1959) use the variance and covariance components of the two characters within and between groups of relatives for obtaining a large sample variance.

Plant breeders evaluate a large number of genotypes in a single trial, often conducted in incomplete blocks (such as square lattices, rectangular lattices or α-designs). The α-designs are being increasingly used by the Germplasm Program at the International Center for Agricultural Research in the Dry Areas (ICARDA) and other international agricultural research centres. There are no methods in the literature for estimating the standard error or the distribution of the genotypic correlation from data from incomplete blocks. Considering the complexity of the expression for genotypic correlation, it is almost impossible to obtain even an algebraic approximation for it. Therefore, we have used three computer-intensive methods to compute the precision of the estimates of genotypic, phenotypic and environmental correlations in terms of their biases and standard errors: (1) a simulation technique, (2) a Jackknife method and (3) a bootstrap method (Efron and Tibshirani 1993). We have used data from two variety trials on barley (*Hordeum vulgare* L. subsp. *vulgare*) to present the estimates of the correlations between grain yield, plant height, and days-to-heading, to illustrate the comparison of the methods.

Communicated by H. C. Becker

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Materials and methods

Genotypic correlation using data from an incomplete block design

Let ρ_g denote the genotypic correlation between traits X and Y in an inbred population of lines. For example, X and Y may be the height and grain-yield of barley genotypes respectively. Let v lines be randomly selected from the population and be evaluated in an incomplete block design with r replications and b blocks per replicate, in a single environment. The responses X_{ijk} and Y_{ijk} from the plot of the i-th genotype in the k-th incomplete block of the j-th replicate on traits X and Y respectively are modelled as:

$$\begin{pmatrix} X_{ijk} \\ Y_{ijk} \end{pmatrix} = \begin{pmatrix} \mu_x \\ \mu_y \end{pmatrix} + \begin{pmatrix} \pi_{jx} \\ \pi_{jy} \end{pmatrix} + \begin{pmatrix} \beta_{jkx} \\ \beta_{jky} \end{pmatrix} + \begin{pmatrix} g_{ix} \\ g_{iy} \end{pmatrix} + \begin{pmatrix} \varepsilon_{ijkx} \\ \varepsilon_{ijky} \end{pmatrix}, \quad (1)$$

where on the two traits X and Y respectively, μ_x and μ_y are general means, π_{jx} and π_{jy} are effects of the j-th replication, β_{jkx} and β_{jky} the effects of the k-th incomplete block of the j-th replications, g_{ix} and g_{iy} the effects of the i-th genotype sampled, and ε_{ijkx} and ε_{ijky} are random errors.

The parameter vectors $\begin{pmatrix} \mu_x \\ \mu_y \end{pmatrix}$ and $\begin{pmatrix} \pi_{jx} \\ \pi_{jy} \end{pmatrix}$ are assumed to be fixed. However, on the other quantities follow the following assumptions:

(i) $\begin{pmatrix} \beta_{jkx} \\ \beta_{jky} \end{pmatrix}$ are – bivariate normally distributed with a mean $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ (a vector of zeros) and a variance covariance matrix $\begin{pmatrix} \sigma^2_{\beta x} & \sigma_{\beta xy} \\ \sigma_{\beta xy} & \sigma^2_{\beta y} \end{pmatrix}$ and – independent of $\begin{pmatrix} \beta_{j'k'x} \\ \beta_{j'k'y} \end{pmatrix}$ for $j \neq j'$ or $k \neq k'$ ($j, j' = 1 \ldots r$; $k, k' = 1 \ldots b$).

(ii) $\begin{pmatrix} g_{ix} \\ g_{iy} \end{pmatrix}$ are – bivariate normally distributed with a mean vector $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ and a variance-covariance matrix $\begin{pmatrix} \sigma^2_{gx} & \sigma_{gxy} \\ \sigma_{gxy} & \sigma^2_{gy} \end{pmatrix}$ and – independent of $\begin{pmatrix} g_{i'x} \\ g_{i'y} \end{pmatrix}$ for $i \neq i' = 1 \ldots v$.

(iii) $\begin{pmatrix} \varepsilon_{ijkx} \\ \varepsilon_{ijky} \end{pmatrix}$ are – bivariate normally distributed with a zero mean vector $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ and a variance-covariance matrix $\begin{pmatrix} \sigma^2_{ex} & \sigma_{exy} \\ \sigma_{exy} & \sigma^2_{ey} \end{pmatrix}$ and – independent of $\begin{pmatrix} \varepsilon_{i'j'k'x} \\ \varepsilon_{i'j'k'y} \end{pmatrix}$ for $i \neq i'$, $j \neq j'$, $k \neq k'$.

(iv) The vectors $\begin{pmatrix} \beta_{jkx} \\ \beta_{jky} \end{pmatrix}$, $\begin{pmatrix} g_{ix} \\ g_{iy} \end{pmatrix}$ and $\begin{pmatrix} \varepsilon_{ijkx} \\ \varepsilon_{ijky} \end{pmatrix}$ are independent of each other.

In the above, $i = 1, 2 \ldots v$; $j = 1, 2 \ldots r$; $k = 1, 2, \ldots b$ (Singh and Hinkelmann 1992).

Against the above background, the genotype correlation ρ_g is given by:

$$\rho_g = \sigma_{gxy}/(\sigma_{gx}\,\sigma_{gy})\,. \quad (2)$$

An estimate of ρ_g is obtained in terms of the estimates of the variance and covariance components σ^2_{gx}, σ^2_{gy} and σ_{gxy}. The variance components σ^2_{gx} and σ^2_{gy} can be estimated by using residual (or restricted, known alternatively) maximum-likelihood (REML) method of Patterson and Thompson (1971) on model (1). For this purpose VCOMPONENTS and REML commands of GENSTAT 5 Rel 3 (1993), or Proc MIXED, or Proc VARCOMP of SAS can be used on plot-wise data on each of the two variables X and Y. Let the estimates of σ^2_{gx} and σ^2_{gy} be denoted by $\hat{\sigma}^2_{gx}$ and $\hat{\sigma}^2_{gy}$. In order to estimate the covariance σ_{gxy}, we construct a new variable Z with the plot-wise values

$$Z_{ijk} = X_{ijk} + Y_{ijk}, \quad (3)$$

which can be modelled by

$$Z_{ijk} = \mu_z + \pi_{jz} + \beta_{jkz} + g_{iz} + \varepsilon_{ijkz}\,, \quad (4)$$

where $\mu_z = \mu_x + \mu_y$, $\pi_{jz} = \pi_{jx} + \pi_{jy}$, $\beta_{jkz} = \beta_{jkx} + \beta_{jky}$, $g_{iz} = g_{ix} + g_{iy}$ and $\varepsilon_{ijkz} = \varepsilon_{ijkx} + \varepsilon_{ijky}$, $i = 1, 2 \ldots v$; $j = 1, 2 \ldots r$; $k = 1, 2 \ldots b$.

The genotypic variability of variable Z, denoted by σ^2_{gx}, is expressed as:

$$\sigma^2_{gz} = \mathrm{Var}(g_{iz}) = \mathrm{Var}(g_{ix} + g_{iy})$$

or

$$\sigma^2_{gz} = \sigma^2_{gx} + \sigma^2_{gy} + 2\sigma_{gxy}\,. \quad (5)$$

Thus, the covariance component σ_{gxy} can be written in terms of variance components as

$$\sigma_{gxy} = (\sigma^2_{gz} - \sigma^2_{gx} - \sigma^2_{gy})/2. \quad (6)$$

We now apply REML on Z_{ijk} s values of Z to obtain an estimate $\hat{\sigma}^2_{gz}$ of σ^2_{gz}. Substituting the estimates of the three variance components in (6) we get an estimate $\hat{\sigma}_{gxy}$ where

$$\hat{\sigma}_{gxy} = (\hat{\sigma}^2_{gz} - \hat{\sigma}^2_{gx} - \hat{\sigma}^2_{gy})/2\,.$$

Substituting the estimates of σ^2_{gx}, σ^2_{gy} and σ_{gxy} in (2) we obtain an estimate $\hat{\rho}_g$ where

$$\hat{\rho}_g = \hat{\sigma}_{gxy}/(\hat{\sigma}^2_{gx}\,\hat{\sigma}^2_{gy})^{1/2}. \quad (7)$$

Phenotypic and environmental correlations

Phenotypic variances and covariances are given by:

$$\sigma^2_{px} = \sigma^2_{gx} + \sigma^2_{ex},\ \sigma^2_{py} = \sigma^2_{gy} + \sigma^2_{ey}$$

$$\sigma_{pxy} = \sigma_{gxy} + \sigma_{exy}\,. \quad (8)$$

The phenotypic correlation (ρ_p) and the environmental correlation (ρ_e) between the traits X and Y are expressed as:

$$\rho_p = \sigma_{pxy}/(\sigma_{px}\,\sigma_{py}) \quad (9)$$

$$\rho_e = \sigma_{exy}/(\sigma_{ex}\,\sigma_{ey}). \quad (10)$$

GENSTAT 5 and the SAS procedure will also provide a value of the estimate of the experimental error variances σ^2_{ex} and σ^2_{ey} (for example, setting the option SGIMA2 to a scalar will hold the value of σ^2_{ex} or σ^2_{ey} in that scalar). The covariance σ_{exy} can be obtained from the variance component of σ^2_{ez} of model (4) and σ^2_{ex} and σ^2_{ey} using

$$\sigma_{exy} = (\sigma^2_{ez} - \sigma^2_{ex} - \sigma^2_{ey})/2\,. \quad (11)$$

Thus ρ_e can be estimated using (10). Since the phenotypic variance and covariance components are expressible in terms of the estimates of the genotypic and environmental variance and covariance components, an estimate of ρ_p can be obtained using (8) and (9). An exact measure, or even an approximation, of the variance of $\hat{\rho}_g$ in terms of the joint moments of $\hat{\sigma}^2_{gx}$, $\hat{\sigma}^2_{gy}$ and $\hat{\sigma}_{gxy}$ would be cumbersome. Therefore, computer-intensive methods were sought. Three alternative ways to compute the precision in terms of the standard error of $\hat{\rho}_g$ are given in the following.

Simulated distribution of $\hat{\rho}_g$

In a simulation study, independent values of $\hat{\rho}_g$ are generated from the population with parameters equal to their corresponding

estimates in model (1). We generated the following vectors of values of $\begin{pmatrix} x' \\ y' \end{pmatrix}$ for the plot corresponding to the i-th genotype in the k-th block of the j-th replicate:

$$x' = \beta'_{jkx} + g'_{ix} + \varepsilon'_x \tag{12}$$

$$y' = \beta'_{jky} + g''_{iy} + \varepsilon''_y$$

$$\beta'_{jkx} = l_{bx}\mu_{bx}$$

$$\beta'_{jky} = l_{by}\mu_{by}$$

$$g'_{ix} = l_{gx}\mu_{gx}$$

$$g''_{iy} = l_{gy}(\hat{\rho}_g\mu_{gx} + \sqrt{1-\hat{\rho}_g^2}\,\mu_{gy})$$

$$\varepsilon''_y = \hat{\rho}_e\varepsilon'_x + \sqrt{1-\hat{\rho}_e^2}\,\varepsilon'_y\,.$$

The quantities μ_{bx}, μ_{by}, μ_{gx}, μ_{gy}, ε'_x and ε'_y are independent standard normal variate values, and can be generated by using functions NED() and URAND() of GENSTAT 5 or the procedure GRANDOM of its library. Further quantities l_{bx}, l_{by}, l_{gx} and l_{gy} are the square root of the variance ratios gives by:

$$l_{bx}^2 = \hat{\sigma}_{\beta x}^2/\hat{\sigma}_{ex}^2,\ l_{by}^2 = \hat{\sigma}_{\beta y}^2/\hat{\sigma}_{ey}^2$$

$$l_{gx}^2 = \hat{\sigma}_{gx}^2/\hat{\sigma}_{ex}^2, \quad \text{and} \quad l_{gy}^2 = \hat{\sigma}_{gy}^2/\hat{\sigma}_{ey}^2\,.$$

The variance component estimates can be obtained by setting the variance component VCOMPONENTS parameter of the VKEEP directive (GENSTAT 5) and retrieving them in scalar structures identifying $\hat{\sigma}_{\beta x}^2$ and $\hat{\sigma}_{\beta y}^2$ respectively.

Since the estimates of correlation's ρ_g, ρ_p or ρ_e are invariant with respect to the units of measurements of the traits X and Y, we have set $\hat{\sigma}_{ex}^2 = \hat{\sigma}_{ey}^2 = 1$ (unity). Also, since they do not depend on fixed parameters such as μ_x, μ_y, π_{jx} and π_{jy}, we have set each of them to zero. These settings do not provide any loss of generality but make the computer program for the simulation simpler. The distribution of $\hat{\rho}_g$ depends, for a given experimental design, only on the values of the constants l_{bx}, l_{by}, l_{gx}, l_{gy}, $\hat{\rho}_e$ and $\hat{\rho}_g$ chosen. The values of (x', y') were obtained for each plot following (12) and were analysed to estimate the genotypic correlation (7). This gives the first simulation-run value which we shall denote by $r_g^{(1)}$, for the estimate of ρ_g. We performed $N = 200$ independent simulation runs, each time beginning at (12) and computing an estimate of ρ_g. This process generated a set of N independent values: $[r_g^{(l)};\ l = 1, 2, \ldots N]$ representing a simulated distribution of $\hat{\rho}_g$. The standard error of $\hat{\rho}_g$ is the standard deviation of the distribution $[r_g^{(l)};\ l = 1, 2, \ldots N]$ and is given by:

$$se_{sim}(\hat{\rho}_g) = \sum_{i=1} [r_g^{(l)} - \bar{r}_g]^2/N,$$

where $\bar{r}_g = \sum_{l=1}^{N} r_g^{(l)}/N$.

An estimate of bias is:

$$Bias_{sim} = \bar{r}_g - \hat{\rho}_g.$$

The N values $[r_g^{(l)};\ l = 1, 2, \ldots N]$ can also be used to obtain the shape of the distribution of $\hat{\rho}_g$ in terms of skewness and kurtosis, as well as the probability points giving critical points for tests of significance on ρ_g. However, in order to compute probability points, N should be large, probably exceeding 1000. The simulation of probability points may require considerable computing time if the size of the experiment is even moderately large. In the above process, we obtained negative estimates of variance components. We replaced them by zero. The covariance-component estimates may lead to estimates of correlation going beyond $(-1, 1)$. In that case, correlation was set within the boundary values (-1 or $+1$). Corresponding to each simulation run, the values of $\hat{\rho}_p$ and $\hat{\rho}_e$ were also generated following the steps given in equations (8)–(11).

Jackknife estimates (Efron and Tibshirani 1993)

In (7) we obtained an estimate $\hat{\rho}_g$ of ρ_g using data from all plots $[(x_{ijk}, y_{ijk}),\ i = 1, 2, \ldots v;\ j = 1, 2, \ldots r;\ k = 1, 2 \ldots b)]$. The jackknife method considers the estimation of the parameter of interest using the set of plots by leaving out one observation at a time and generating a series of estimates (called jackknife replications). If the plots are indexed, using observations (x_{ijk}, y_{ijk}) of all plots except the l-th plot (say), and denote the estimate of ρ_g by $\hat{\rho}_{g(l)}$. Taking $l = 1, 2, \ldots n$ in turn, we get n jackknife estimates. The jackknife estimates of bias and standard error of $\hat{\rho}_g$ are:

$$\hat{bias}_{jack} = (n-1)[\hat{\rho}_{g(.)} - \hat{\rho}_g]$$

$$\hat{se}_{jack} = \left[(n-1)\sum_{l=1}^{n}(\hat{\rho}_{g(l)} - \hat{\rho}_g)^2/n\right]^{1/2},$$

where $\hat{\rho}_{g(.)} = \sum_{l=1}^{n} \hat{\rho}_{g(l)}/n$.

Bootstrap method (Efron and Tibshirani 1993)

The bootstrap method is based on generating a large number B of independent samples (called bootstrap samples) from the set of all n plot values of traits X and Y. Each bootstrap sample is obtained by sampling with replacement n times from the whole set of n plots. Using the data of each such sample and (7), we calculate the value of the estimate, say $\hat{\rho}_g^b$ from the b-th bootstrap sample b = 1, 2, ... B. The quantity $\hat{\rho}_g^b$ is also called a bootstrap replication of $\hat{\rho}_g$. Thus each bootstrap sample will give a bootstrap replication of $\hat{\rho}_g$. The bias of the bootstrap estimate is:

$$\hat{bias}_{boot} = \hat{\rho}_g^* - \hat{\rho}_g$$

and the standard error

$$\hat{se}_{boot} = \left[\sum_{b=1}^{B}(\hat{\rho}_g^b - \hat{\rho}_g^*)^2/(B-1)\right]^{1/2},$$

where $\hat{\rho}_g^* = \sum_{b=1}^{B}(\hat{\rho}_g^b)/B$. A typical range for bootstrap replications (which is the same as number of bootstrap samples B) is 50 to 200. We took $B = 200$.

Bootstrap bias and the standard error of ρ_p and ρ_e can be obtained following the lines of computation used for ρ_g.

Experimental material

The barley (*H. vulgare* L. subsp. *vulgare*) project at ICARDA has been conducting several trials in incomplete block designs. We report the results for two trials conducted in triple lattices with 64 genotypes at Terbol and Kfardan in Lebanon in the 1993/4 growing season. The plot size was 12 m^2 and the harvested area 7.5 m^2. We present the correlation of grain yield (kg/ha) with plant height (cm) and days-to-heading.

Results and discussion

Table 1 presents the estimates of mean and variance components (σ_g^2, σ_p^2, σ_e^2) for the three traits in the two trials. In both trials incomplete blocks were very effective in controlling the error variability in grain yield and plant height. However, as would be expected, incomplete blocks were less effective in the case of days-to-heading. The genotypic variability in the population of lines was significant ($P < 0.01$) at both locations. The

Table 1 Mean, variance and covariance components for traits at Terbol and Kfardan

Location	Trait	Mean	Variance-covariance components			
				GY	*PH*	*DH*
			σ^2_β			
				σ^2_g and σ_{gxy}		
Terbol	GY	3415	30 334	78 363	457.9	705.4
	PH	45.58	3.51		22.18	– nw
	DH	135.8	0.18			16.38
				σ^2_e and σ_{exy}		
	GY			212 944	773.2	– 226.2
	PH				21.15	– nw
	DH					– 2.61
				σ^2_g and σ_{gxy}		
Kfardan	GY	1969	98 206	53 257	– 16.06	96.56
	PH	47.84	17.04		8.42	– nw
	DH	131.0	0.467			40.584
				σ^2_e and σ_{exy}		
	GY			81 511	324.5	– 63.93
	PH				23.38	– nw
	DH					2.201

[a] GY = grain yield, kg/ha. PH = plant height, cm. DH = days to heading. – nw: not worked out

Table 2 Estimates of correlation of plant height (PH) and day-to-heading (DH) with grain yield, bias and standard errors estimated from simulation (Sim), jacknife (Jack) and bootstrap (Boot) methods

Location	Correlation with GY			Bias			Standard errors		
	Trait	Estimate		Sim	Jack	Boot	Sim	Jack	Boot
Terbol	PH	$\hat{\rho}_g$	0.347	– 0.005	0.000	0.000	0.197	0.192	0.105
		$\hat{\rho}_p$	0.346	0.003	0.000	0.005	0.077	0.064	0.064
		$\hat{\rho}_e$	0.364	0.005	0.000	– 0.001	0.077	0.107	0.121
	DH	$\hat{\rho}_g$	0.623	0.001	0.000	– 0.251	0.145	0.175	0.101
		$\hat{\rho}_p$	0.204	– 0.008	0.000	0.014	0.085	0.079	0.066
		$\hat{\rho}_e$	0.304	0.003	0.000	– 0.069	0.097	0.128	0.140
Kfardan	PH	$\hat{\rho}_g$	– 0.091	0.011	– 0.191	– 0.167	0.237	0.339	0.150
		$\hat{\rho}_p$	0.136	0.005	0.000	0.005	0.080	0.083	0.080
		$\hat{\rho}_e$	0.248	– 0.005	0.000	0.001	0.083	0.146	0.141
	DH	$\hat{\rho}_g$	0.066	0.003	0.000	– 0.044	0.170	0.140	0.080
		$\hat{\rho}_p$	0.014	0.002	0.019	– 0.007	0.100	0.077	0.068
		$\hat{\rho}_e$	– 0.151	0.002	– 0.191	0.020	0.096	0.175	0.150

mean yield at Terbol (534 mm rainfall) was higher than that at Kfardan (475 mm rainfall). Kfardan also experienced terminal heat stress.

The estimate of genotypic, phenotypic and environmental correlations, together with their biases and standard errors obtained by simulation, jackknife and bootstrap methods are given in Table 2. There were contrasting values of the genotypic correlations between grain yield and plant height over the two locations. At Terbol it was significant ($P < 0.05$) when assessed against the estimate of standard error obtained from the bootstrap method, while the standard errors obtained from the simulation and jackknife methods were large enough to declare the correlation statistically insignificant. The genotypic correlation grain yield and days-to-heading was statistically significant at Terbol, but not at Kfardan, when assessed against the standard errors obtained by each of the methods.

The phenotypic correlations of grain yield with plant height and days-to-heading were significant at Terbol but not at Kfardan. The contrasting associations in the above variable may be due to the high genotype × environment interaction likely to be contributed by the climatic differences between the two locations.

The biases are reasonably small in the simulation method. Except where the value of correlation was low, jackknife gave a low bias. The biases of the bootstrap and simulation methods are comparable except for one case of genotypic correlation and in 3 of the 12 correlations presented. The bootstrap method resulted in a large bias (-0.251) in the estimation of genotypic correlations, except for the correlation between grain yield and plant height at Terbol. The standard errors resulting from simulation are closer to the jackknife method than to the bootstrap. Bootstrap standard errors are lower than those obtained under the jackknife method, except for two cases of environmental correlations at Terbol. The standard errors for the estimate of a given correlation show considerable variation in magnitude over locations.

Although the illustrations and comparisons of methods are based on only four data sets, we believe that a wider range of situations are covered by them. Therefore, the jackknife or simulation approach can be recommended for the calculation of standard errors of the estimates of genotypic and phenotypic correlations.

Acknowledgements The authors are grateful to the two referees for their suggestions for improving the presentation of this paper.

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