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Effects of genotype-environment interactions on genetic correlations

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Abstract. The objective of the work presented here was to investigate the influence of genotype-environment interaction on genetic correlations. In our theoretical models we have considered plant populations consisting of random samples of lines from chromosome-doubled haploids produced from F_1 gametes, highly inbred SSD-lines, and clones of randomly breeding populations grown in two and multiple environments. The results of our theoretical considerations are that if genotype-environment interaction exists, great differences are expected to occur in the estimates of genetic correlation coefficients obtained in different environments. Based on the variance and covariance components for genotype-environment interaction we suggest a new type of correlation coefficient, called genotype-environment correlation, r_{ge}. Our theory has been applied to several series of experiments. Estimates are presented from two series, both of which demonstrate clearly the consequences of genotype-environment interaction on the genetic correlations.

Key words: Genetic correlation – Genotype-environment interaction

Introduction

The characters observed in the individuals of a population can be correlated, negatively or positively. There are three main causes for such correlations, namely pleiotropy, linkage, and environmental effects. In genetic studies the first problem will always be to distinguish between genetic and environmental causes of correlation. The genetic cause of correlation is chiefly pleiotropy, though linkage is a cause of transient correlation, particularly in experimental and breeding populations of cross-fertilizers and in populations derived from crosses between inbred lines. Pleiotropy means that a gene affects two or more characters, so that, if the gene is segregating, it causes simultaneous variation in the characters it affects. For example, the major genes (*V*-*v*) in the two-rowed six-rowed locus of barley affect plant height, tillering capacity, seed number per plant, seed size, and grain yield (Aastveit 1961). The degree of correlation arising from pleiotropy expresses the extent to which two characters are influenced by the same genes. The resulting correlation caused by pleiotropy is the overall or net effect of all the segregating genes that affect both characters. Some genes may increase or decrease both characters, while others increase one and reduce the other. Thus the gene (*v*) for six-rowed ear in barley mentioned above tends to increase the number of seeds per plant but reduces plant height and seed size, as compared to the homologous gene (*V*). Depending on whether the genes tend to increase or reduce both characters or increase one or reduce the other, the correlation will be positive or negative. The observed correlation will be net of all genes affecting two characters. Therefore, even if pleiotropy is present it does not necessarily cause a detectable correlation. The environment is a cause of correlation in so far as two characters are influenced by the same difference of environmental conditions. Also the correlation caused by envionmental differences is the overall effect of all environmental factors that vary; some may tend to cause positive correlations, others negative ones.

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Genetic and environmental correlations can be estimated in various ways. The methods described by Falconer (1989) are based on the estimation of variances and covariances from the breeding values. This means that the estimation is based mainly on additive gene effects, while non-additive gene effects are pooled together with all residual variation expressed by $1 - h_A^2$, where h_A^2 designates the narrow-sense heritability. The fraction $1 - h_A^2$, is treated as pure environmental variation. Such a partitioning may be sufficient to deal adequately with most practical problems in domestic animal genetics, where the environment is standardised to a large extent and the individual genotypes cannot normally be replicated by cloning or by the production of homozygous lines. The situation is quite different in the majority of cultivated plants, where replication of genotypes is easy and the environment normally less standardised. Consequently genotype-environment interaction seems to play a much more important role in plant populations as compared to populations of animals. It was the objective of the present work to investigate the effect of genotype-environment interactions on genetic correlations in different types of genetic plant materials.

Theoretical considerations

In order to be able to estimate effects of genotype-environment interactions on genetic or genotypic correlations one needs populations consisting of genotypes that can be replicated. In self-fertilizing crops, populations consisting of randomly selected chromosome-doubled haploids (DH-lines) or highly inbred SSD-lines from crosses between homozygous lines are suitable. In such lines the genetic causes of variation are purely additive, or else are caused in part by additive–additive interallelic interactions. For populations of clones derived from randomly-selected plants in a cross-fertilizing crop, the genetic variation will be made up of components due to additive gene effects, dominance, and possibly all sorts of interallelic interaction. The same is the case for populations consisting of full-sib or half sib families. It is rather complicated to deal with all sorts of materials. We have, therefore, confined ourselves mainly to populations of homozygous lines and populations of clones from randomly-selected genotypes of open-pollinating diploid populations.

Pleiotropy in populations of homozygous lines

Let us first consider a population consisting of N lines produced by chromosome doubling of haploid plants (DH-lines) from a cross between two homozygous parents without selection of any kind. Let us further assume that a fairly large population of these lines is grown on plots in a randomised block experiment in each of two or more environments (i.e., E_1 and E_2), with K replications in each environment, and that observations are taken on two characters, X and Y. Each character can then be analysed after the following model:

$$X_{ijk} = m + G_i + E_j + GE_{ij} + r_{k(j)} + f_{ijk}, \quad (1)$$

where m is the general mean, G stands for genotype, E for environment, r for replication and f_{ijk} is an unexplained effect of environment, inaccuracies of measurements etc. The most common differences between environments in plant experiments are associated with different years, different locations, or differences in management. The genetic and environmental effects in model (1) can be specified in more detail. The simplest situation one can think of is that the N lines are different in only one locus with two alleles, *A-a*, and that they are grown in only two environments, E_1 and E_2. If there has been no selection the probability of the two possible genotypes, *AA* and *aa*, will then be equal to 0.5. If the genes in locus *A-a* affect character X as well as character Y, which means that pleiotropy exists, the effects may be specified as shown in Table 1 where it is assumed that $E(X) = E(Y) = 0$. This can be done without loss of generality. In this table d designates the additive gene effect and is defined according to Mather and Jinks (1982), e is the effect of environment, while g takes care of the interaction between d and e. Specified in this way the contribution of the *A-a* locus to the population mean over the two environments is 0. The contribution of the *A-a* locus to the genetic variance based on averages over the two environments will then be d_x^2 and d_y^2 for characters X and Y, respectively, and the contribution to the covariance $d_x d_y$. Based on the averages over the two environments the genetic correlation will therefore be

$$r_g = \frac{d_x d_y}{\sqrt{d_x^2 * d_y^2}}.$$

If the N lines were genetically completely equal, except for the alleles *A-a*, the genetic correlation is expected to be ± 1.0. Estimates of r_g based on N lines would, of course, be influenced by sampling errors of the variances as well as the covariances. The contribution to the variances and covariance of the two environments will similarly be e_x^2, e_y^2 and $e_x e_y$, respectively.

If instead of means over environments the estimates are based on the line means within each environment, the genetic contribution to the variance within environments will be

$$\mathrm{Var}(X)_1 = d_x^2 + 2d_x g_x + g_x^2$$

and (2)

$$\mathrm{Var}(X)_2 = d_x^2 - 2d_x g_x + g_x^2,$$

Table 1. Specification of the effects of locus *A-a* on characters *X* and *Y* in an experiment with *N* homozygous lines grown in two environments, E_1 and E_2

Environment	Frequencies of genotypes $\frac{1}{2}$	$\frac{1}{2}$	
	$AA(d)$	$aa(-d)$	Mean
$e\,(E_1)$	$X = d_x + e_x + g_x$ $Y = d_y + e_y + g_y$	$X = -d_x + e_x - g_y$ $Y = -d_y + e_y - g_y$	e_x e_y
$-e\,(E_2)$	$X = d_x - e_x - g_x$ $Y = d_y - e_y - g_y$	$X = -d_x - e_x + g_x$ $Y = -d_y - e_y + g_y$	$-e_x$ $-e_y$
Mean	d_x d_y	$-d_x$ $-d_y$	0 0

d_x and d_y = additive genetic effects on characters *X* and *Y*, respectively; g_x and g_y are genotype-environmental interactions and $\pm e$ the effects of environments

Table 2. This table illustrates the effect of genotype-environment interaction on genetic correlations, r_g. It is assumed that two homozygous lines differing in only one locus with two alleles and with pleiotropic effects on the characters *X* and *Y* are grown in two environments, E_1 and E_2

	$d_x = d_y = 1$ $g_x = g_y = 0$	$d_x = d_y$ $= g_x = g_y = 1$	$d_x = d_y = 1$ $g_x = g_y = 0.5$	$d_x = d_y = g_x = 1$ $g_y = 0$	$d_x = d_y = 1$ $g_x = 1,\ g_y = -1$
Over environments	1.0	1.0	1.0	1.0	1.0
Within E_1	1.0	1.0	1.0	1.0	0.0
Within E_2	1.0	0.0	1.0	0.0	0.0
Average over E_1 and E_2	1.0	0.5	1.0	0.5	0.0

for environment E_1 and E_2 respectively. The genetic contribution to the variance of *Y* will similarly be

$$\mathrm{Var}(Y)_e = d_y^2 \pm 2d_y g_y + g_y^2,$$

and the genetic contribution to the covariances:

$$\mathrm{Cov}(X, Y)_1 = d_x d_y + d_x g_y + d_y g_x + g_x g_y$$

$$\mathrm{Cov}(X, Y)_2 = d_x d_y - d_x g_y - d_y g_x + g_x g_y. \quad (3)$$

Genotype-environment interaction will clearly influence the variances as well as the covariances. Table 2 gives an example of the effect of such interaction on the genetic correlations for some selected values of d_x, d_y, g_x, and g_y.

If the estimates of variances and covariances are based on all data within and over environments, the following results are obtained:

$$\mathrm{Var}(X) = d_x^2 + g_x^2 + e_x^2 + f^2 \text{ (unexplained)} \quad (4)$$

$$\mathrm{Var}(Y) = d_y^2 + g_y^2 + e_y^2 + f^2 \text{ (unexplained)} \quad (5)$$

$$\mathrm{Cov}(X, Y) = d_x d_y + g_x g_y + e_x e_y + f_x f_y \text{ (unexplained)} \quad (6)$$

The four different components can be estimated by means of an analysis of variance, provided that replications within environments have been used. And as soon as the components are estimated, four types of correlation may be estimated, namely (1) the pure additive genetic correlation, $r_{g(A)}$, which is equal to

$$r_{g(A)} = \frac{d_x d_y}{\sqrt{d_x^2 * d_y^2}},$$

(2) the pure environmental,

$$r_e = \frac{e_x e_y}{\sqrt{e_x^2 * e_y^2}},$$

(3) the genotype-environment correlation,

$$r_{ge} = \frac{g_x g_y}{\sqrt{g_x^2 * g_y^2}}$$

(4) and a correlation based on the residual covariance and variance components.

$$r_{res} = \frac{f_x f_y}{\sqrt{f_x^2 * f_y^2}}.$$

If the variances and covariances are estimated over many environments (j) the following results are obtained:

$$\mathrm{Var}(X) = \sum_j d_x^2 + \sum_j g_{xj}^2 + \sum_j e_{xj}^2 + \sum_j f_{xj}^2$$

$$\mathrm{Var}(Y) = \sum_j d_y^2 + \sum_j g_{yj}^2 + \sum_j e_{yj}^2 + \sum_j f_{yj}^2$$

$$\mathrm{Cov}(X, Y) = \sum_j d_x d_y + \sum_j g_{yj} g_{xj} + \sum_j e_{xj} e_{yj} + \sum_j f_{xj} f_{yj}.$$

The different components can be estimated as mentioned above, and thereby also the different types of correlations.

So far we have considered only one locus with pleiotropic effects of the genes. For typical quantitative characters each character will be influenced by the genes at many loci. The pleiotropic effects may for some loci be positive, for others negative or independent. What we are able to measure in experiments are the sum effects over loci.

Linkage in populations of homozygous lines

The principal difference between genetic correlations caused by pleiotropy and linkage is that the correlation in the latter case can be broken or even change sign. The reason for this difference is, of course, that in the case of pleiotropy two or more characters are governed by the same genes, while in the case of linkage two or more characters are governed by different genes. But since these genes are located more or less close on the same chromosome, the genotypes in the population may deviate from a random distribution and thereby cause correlations. Table 3 gives a specification of the genes in two linked loci, *A-a* and *B-b*, which govern two different characters X and Y.

We suppose that a random sample of homozygous lines of a diploid species have been produced by chromosome doubling of F_1-haploids from a cross between homozygous parents, and grown in a replicated randomised block experiment in two different environments. Let p designate the recombination frequency ($p+q=1$). We assume that locus *A-a* governs character X, while locus *B-b* governs character Y. Table 3 specifies the effects and frequencies.

The variances of characters X and Y become

$$\mathrm{Var}(X) = d_a^2 + e_X^2 + g_a^2 + f_X^2 \text{ (unexplained)} \quad (7)$$

and

$$\mathrm{Var}(Y) = d_b^2 + e_Y^2 + g_b^2 + f_Y^2 \text{ (unexplained)}. \quad (8)$$

The covariance between the characters X and Y becomes

$$\mathrm{Cov}(X,Y) = (q-p)\, d_a d_b + (q-p)\, g_a g_b = e_X e_Y = f_X f_Y \text{ (unexplained)}. \quad (9)$$

These equations show that as long as each character is governed by only one locus, the covariance is affected by linkage, but not the variances. In this case we have assumed that linkage in the parents was in the coupling phase. If it had been in the repulsion phase, p and q would have to be interchanged. Equation (9) shows that the additive genetic component of the covariance, as well as the genotype-environment interaction component, are both linear functions of the recombination frequency, p. If $p=q=0.5$ these components will become zero, which means that there is no linkage, combination is free. If, on the other hand, $p=0$, there will be no recombination and Eq. (9) becomes equal to Eq. (6). If two loci are so closely linked that p is equal to zero, the two loci will have the same effect as pleiotropy associated with one locus. From Eq. (9) we can see that linkage in the coupling phase will give positive genetic correlations, while linkage in the repulsion phase will give negative correlations. If two characters are each governed by many linked loci, coupling and repulsion linkage can more or less counter balance each other.

Extension to J environments and the side conditions $\sum e_{xj} = \sum g_{xj} = 0$, gives the following variances and covariances:

$$\mathrm{Var}(X) = \sum_j d_a^2 + \sum_j g_{aj}^2 + \sum_j e_{xj}^2 + \sum_j f_{xj}^2$$

$$\mathrm{Var}(Y) = \sum_j d_b^2 + \sum_j g_{bj}^2 + \sum_j e_{yj}^2 + \sum_j f_{yj}^2$$

$$\mathrm{Cov}(X,Y) = (q-p)\sum_j d_x d_y + (q-p)\sum_j g_{xj} g_{yj} + \sum_j e_{xj} e_{yj} + \sum_j f_{xj} f_{yj}.$$

If each character is governed by more than two loci,

Table 3. Specification of the effects of the four homozygous genotypes in a two-locus model by cultivation in two environments, E_1 and E_2

Environment (effect)	Genotype (frequency)				
	AABB ($q/2$)	*AAbb* ($p/2$)	*aaBB* ($p/2$)	*aabb* ($q/2$)	Mean
E_1 (e)	$X = d_a + e_a + g_a$	$X = d_a + e_a + g_a$	$X = -d_a + e_a - g_a$	$X = -d_a + e_a - g_a$	e_a
	$Y = d_b + e_b + g_b$	$Y = -d_b + e_b - g_b$	$Y = d_b + e_b + g_b$	$Y = -d_b + e_b - g_b$	e_b
E_2 ($-e$)	$X = d_a - e_a - g_a$	$X = d_a - e_a - g_a$	$X = -d_a - e_a + g_a$	$X = -d_a - e_a + g_a$	$-e_a$
	$Y = d_b - e_b - g_b$	$Y = -d_b - e_b + g_b$	$Y = d_b - e_b - g_b$	$Y = -d_b - e_b + g_b$	$-e_b$
Mean	d_a	d_a	$-d_a$	$-d_a$	0
	d_b	$-d_b$	d_b	$-d_b$	0

some of them linked, and if interallelic interaction is present, the model becomes much more complicated.

The variances of each character can be influenced by interallelic interaction as well as by linkage, and the genes in each locus may have its own interaction with the environments. As a simple example we may assume that character X is governed by a locus A-a which is linked to locus B-b with a recombination frequency p. Character Y is governed by locus B-b and in addition also by locus C-c. Interallelic interaction (i) exists between loci B-b and C-c.

Using the same principles as above and two environments:

$$\mathrm{Var}(X) = d_a^2 + g_a^2 + e_X^2 + f_X^2 \text{ (unexplained)}$$

$$\mathrm{Var}(Y) = d_b^2 + d_c^2 + i_{bc}^2 + g_b^2 + g_c^2 + e_Y^2 + f_Y^2 \text{ (unexplained)}$$

$$\mathrm{Cov}(X,Y) = (q-p)d_a d_b + (q-p)g_a g_b + e_X e_Y + f_X f_Y \text{ (unexplained).}$$

The pure additive genetic correlation will in this case be:

$$r_g = \frac{(q-p)d_a d_b}{\sqrt{[d_a^2 * (d_b^2 + d_c^2 + i_{bc}^2)]}}.$$

Since it is assumed that the population in this case consists of homozygous lines, i_{bc} designates the additive–additive interaction, which is fixable by selection (Mather and Jinks 1982). If the lines are a random sample from a population consisting of highly-inbred SSD-lines, instead of DH-lines from an F_1-hybrid between two homozygous lines, the disequilibrium frequencies caused by linkage (cf. Eq. 9) will be different, as pointed out by Jinks et al. (1985).

Clones, families and sub-populations

In diploid cross-fertilizing species there are three genotypes for each locus with two alleles. And, in a panmictic population the frequencies of the three genotypes is expected to be in a Hardy–Weinberg equilibrium. For combinations of genotypes such a population will approach linkage equilibrium if the matings are random; the same applies for loci on the same chromosome. This implies, as pointed out by Falconer (1989), that in old natural populations genetic correlations should be due to pleiotropy and not caused by linkage. If a set of clones produced from randomly-selected plants in a population of the type mentioned above are grown in a randomised block experiment in two environments, the genetic and environmental effects on two characters governed by a locus with two alleles, say A-a, may be specified as shown in Table 4. In this table u and v stand for the frequencies of the alleles A and a, respectively ($u + v = 1$), while h_X and h_Y take care of dominance and are defined in accordance with Mather and Jinks (1982).

The total variances of the characters X and Y will be

$$\mathrm{Var}(X) = 2uv[d_x + (v-u)h_x]^2 + 4u^2v^2h_X^2 + g_X^2 + e_X^2 + f_X \text{ (unexplained),} \quad (10)$$

$$\mathrm{Var}(Y) = 2uv[d_Y + (v-u)h_Y]^2 + 4u^2v^2h_Y^2 + g_Y^2 + e_Y^2 + f_Y \text{ (unexplained)} \quad (11)$$

and the covariance between X and Y

$$\mathrm{Cov}(X,Y) = 2uv\Big[d_X d_Y + (v-u)d_Y h_X + (v-u)d_X h_Y + (v-u)^2 h_X h_Y\Big] + 4u^2v^2 h_X h_Y + g_X g_Y + e_X e_Y + f_X f_Y \text{ (unexplained).} \quad (12)$$

From Eqs. (10), (11) and (12) it can be seen that, if there is no dominance, the contribution of this locus to the genetic correlation between characters X and Y will be independent of gene frequency. If, on the other hand, the degree of dominance is equal for the characters X and Y, the contribution to the correlation coefficient will to a large extent depend on gene frequency. Figure 1 shows r_g as a function of gene frequency (u) for the case where $d_x = h_x = 1$, $d_y = 1$ and $h_y = 0.0$, 0.25, 0.50 and 0.75. The formulas given by Eqs. (10), (11) and (12) can be extended to more than two environments as shown for the other situations discussed previously.

Table 4. Specification of genetic and environmental effects on characters X and Y in a one-locus model of a heterozygous diploid population

Environment	u^2 *AA*	$2uv$ *Aa*	v^2 *aa*	Mean
$E_1(e)$	$X = d_x + e_x + g_x$	$h_x + e_x + g_x$	$-d_x + e_x - g_x$	$(u-v)d_x + 2uvh_x + e_x + (u-v)g_x + 2uvg_x$
	$Y = d_y + e_y + g_y$	$h_y + e_y + g_y$	$-d_y + e_y - g_y$	$(u-v)d_y + 2uvh_y + e_y + (u-v)g_y + 2uvg_y$
$E_2(-e)$	$X = d_x - e_x - g_x$	$h_x - e_x - g_x$	$-d_x - e_x + g_x$	$(u-v)d_x + 2uvh_x - e_x - (u-v)g_x - 2uvg_x$
	$Y = d_y - e_y - g_y$	$h_y - e_y - g_y$	$-d_y - e_y + g_y$	$(u-v)d_y + 2uvh_y - e_y - (u-v)g_y - 2uvg_y$
Mean X	d_x	h_x	$-d_x$	$(u-v)d_x + 2uvh_x$
Y	d_y	h_y	$-d_y$	$(u-v)d_y + 2uvh_y$

For highly inbred lines, DH-lines, and clones produced from individual plants of an outcrossing population mating at random, variances, covariances and genetic correlations can be based on individual replicated genotypes grown in different environments. As soon as we come to various kinds of families, such as half sib or full sib families, this is no longer possible. All sorts of families are to be regarded as sub-populations, since they are highly genetically heterogeneous. Within the families the genetic effects are the same as in homozygous lines and clones. The gene frequencies do, however, vary, and the family means will be a function of gene frequencies. Provided that the number of individuals within each family is not too low, the family or sub-population means for various characters can be treated as genetic units and subjected to analyses like other genetic parameters for the variation and covariation of different characters.

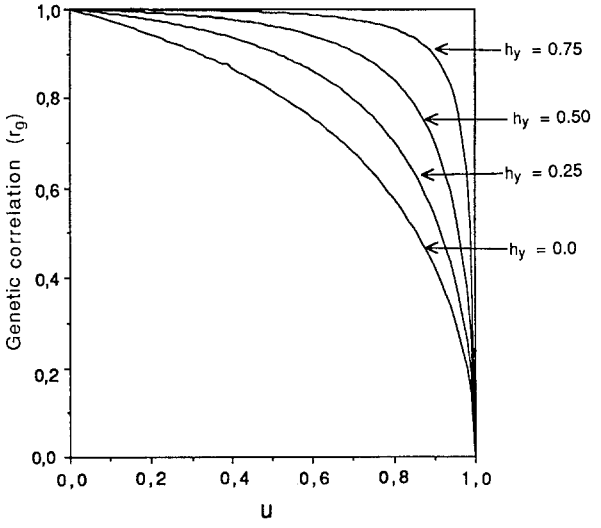

Fig. 1. The genetic correlation (r_g) between characters X and Y as a function of gene frequency in a randomly breeding population. Assumptions: $d_x = d_y = h_x = 1$ and $h_y = 0.0$, 0.25, 0.50, and 0.75

Experimental illustration

The different correlation coefficients described in the previous section have been estimated on data from several series of experiments. Only the results from two series are briefly presented in what follows:

Series 1

Three hundred and ninety four chromosome-doubled haploids (DH-lines) produced by the bulbosum method from F_1 plants after a cross between two nearly homozygous lines were grown in two complete blocks at one place (Ås) in each of 3 years (1987–1989). The experimental design was a special type of incomplete block in which the lines were grouped in sub-blocks of 20 plus two control lines. In the first year each plot consisted of one single row, 1 meter long with 25 handsown seeds, and the rows were set 20 cm apart. In the other two years the plots were machine sown, and the plot size was 3.0 m^2.

Series 2

Five hundred lines, randomly selected among the progenies of F_6 individuals from a bulk population derived from a cross between two nearly homozygous varieties of spring wheat, were grown in two complete blocks at one place (Ås) in each of 2 years (1980 and 1981). The experimental design was the same as in series 1. In the first year the plots consisted of one row, 1 m long with 25 handsown seeds and the rows set 20 cm apart. In the other year the plots were machine sown, and the plot size was 0.9 m^2.

Rates of fertilizer common in practical growing were applied in both series.

The estimates of the genetic correlations from the two series are presented in Table 5. In order to obtain information about the precision of the standard devi-

Table 5. Genetic correlations, r_g, within and over years between grain yield (X_1), straw length (X_2) and heading time (X_3). The genotype × year correlations, r_{ge} are presented at the bottom

Year	Barley (series 1)			Wheat (series 2)		
	X_1/X_2	X_1/X_3	X_2/X_3	X_1/X_2	X_1/X_3	X_2/X_3
1	0.66±0.05 (0.55, 0.76)	0.22±0.07 (0.09, 0.36)	0.12±0.05 (0.03, 0.23)	0.03±0.06 (−0.07, 0.12)	0.03±0.08 (−0.09, 0.15)	0.66±0.05 (0.57, 0.74)
2	0.09±0.09 (−0.10, 0.26)	0.77±0.09 (0.62, 0.98)	0.15±0.06 (0.04, 0.27)	0.24±0.05 (0.16, 0.32)	0.61±0.05 (0.53, 0.70)	0.38±0.06 (0.26, 0.47)
3	0.37±0.06 (0.25, 0.48)	0.04±0.08 (−0.12, 0.19)	−0.65±0.04 (−0.73, −0.57)			
Over years	0.34±0.07 (0.20, 0.47)	0.80±0.11 (0.58, 1.0)	−0.38±0.07 (−0.53, −0.24)	0.12±0.06 (0.04, 0.21)	0.24±0.13 (0.03, 0.45)	0.73±0.18 (0.53, 1.0)
r_{ge}	0.30±0.50 (−0.13, 1.0)	−0.42±0.08 (−0.46, −0.27)	−0.74±0.78 (−1.0, −0.18)	0.35±0.011 (0.19, 0.53)	0.32±0.20 (0.12, 0.57)	0.89±0.08 (0.56, 0.81)

± = standard errors
( ) = 95% bias-corrected confidence intervals based on bootstrapping

ations of the correlation coefficients, we have estimated the standard deviations by use of bootstrapping as indicated by Aastveit (1990a, 1990b). Bias-corrected 95%-confidence intervals are also estimated by the use of bootstrapping. Table 5 shows that the correlation coefficients differ considerably over years. Many of the correlations are significant when estimated over years. Three of the genotype × year correlations (r_{ge}) are highly significant.

Discussion

The problem taken up in the present paper is the influence of genotype-environment interaction on genetic correlations. In our theoretical considerations we have worked with models applicable to populations consisting of DH-lines, SSD-lines, and clones from crossfertilizing plants grown in more than one environment. In the literature one can often see that the term genetic or genotypic correlation is used even if the population consists of genotypes non-randomly selected from the same or different populations. Our models are based on random samples within populations, and we suggest that the term *genetic correlation* should be restricted to cases where the sample upon which a correlation is based is a random sample from a clearly-specified population. For the genetic correlation within such a population we suggest the designation r_g if it is based on all genetic effects and $g(A)$ if it is based on only additive genetic effects. If the correlation in based on a non-random sample of genotypes from one or more populations, we suggest the term, *genotypic correlation* ($r_{genot.}$).

For correlations based on family means, or other sorts of sub-population means, we suggest the term genotypic correlation of family means (r_{gm}). Our main concern here, however, is the correlation which is caused by the genotype-environmental components of the covariance between the characters X and Y and the corresponding variances. We designate this correlation r_{ge} and define it as

$$r_{ge} = \frac{\mathrm{Cov}(X, Y)_{ge}}{\sqrt{\mathrm{Var}(X)_{ge}\ \mathrm{Var}(Y)_{ge}}},$$

where the *ge* refers to the genotype-environment components of variances and covariance, respectively. The experimental results presented from series 1 and 2 show that the genotype × year correlation can be highly significant in a positive or negative direction, and comparable in size to the correlations within years. The biological importance of genotype-environment correlations is not always easy to understand. If such a correlation between two characters, say X and Y, is caused by common genes, i.e., pleiotropy, then, relatively speaking, the correlation expresses different environmental modification effects of the same genes on the two characters. If, on the other hand, a significant genotype-environment correlation is caused by linkage disequilibrium, it means that the two characters are governed by different gene systems where the effects are differently modified by the environmental factors under investigation. Differential environmental modifications of the effects of genes common to two or more characters, or of the effects of different gene systems, may be an advantage in the process of adaptation to variable environments. In breeding, however, such modifications cause a lot of unpredictable reactions. Breeding for stability of two or more important characters would be expected to reduce the interactions and thereby the genotype-environment correlations.

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