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Estimating Heritability and Genetic Correlation Between Traits from Generations F_2 and F_3 of Self-fertilizing Species: a Comparison of Three Methods

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Summary. Three methods of estimation of heritability and genetic correlation between traits in the F_2 and F_3 generations of self-fertilizing species were compared. The methods were:

1. Subtracting the estimates of environmental variances and covariances from the corresponding phenotypic estimates in the segregating generation which yields 'broad-sense' heritability and genetic correlation.
2. Analyses of variance and covariance of full-sib families; correlations were calculated from the between-families components and heritability was estimated by using intraclass correlation.
3. Offspring on parent regression for single traits and pairs of traits which yields estimates of heritability and genetic correlation.

Theoretically, the family-analysis method is superior to the two others, because those estimates are less affected by non-additive genetic variance and covariance. Actual estimates for six traits in peanuts and their 15 two-trait combinations were calculated only for the purpose of comparison between the three methods. These estimates seem to be in agreement with conclusions which were drawn from the theoretical considerations.

Key words: Parent-offspring regression – Intraclass correlation – peanuts

Introduction

'Narrow-sense' heritability and additive genetic correlation between traits are easily estimated in a random-mating population. They are established, in the main, by analyses of variance and covariance of half-sib families or by regression of offspring on their parents. In self-fertilizing plants, outcrosses are very rare and half-sib families can be formed only by artificial matings. In many crops, e.g. cereals and legumes, such matings are laborious and not prolific and they are therefore not practical. Thus, different methods are necessary to obtain estimates of additive genetic variances (and covariances between traits) in self-fertilizing crops. Horner et al. (1955) described such a method, which is based on nested analyses of data obtained from offspring of crosses between purebred parents. This method cannot, however, be used before the F_4 or F_5 generation is evaluated, as it requires a large amount of data and pedigree information. On the other hand, it is important for the plant breeder to have estimates for heritability and genetic correlations in earlier segregating generations.

In an attempt to find shorter methods for estimating heritability and genetic correlation three different approaches will be considered and compared in the present study. These approaches will be based on analyses of early generations of a single cross between two purebred plants. The methods will be compared in accordance with the following criteria:

1) Expected bias from the 'narrow sense' heritability and genetic correlation.

2) Actual estimates obtained from data on peanuts and their standard errors.

3) Amount of data and experimental efforts required.

Material and Methods

1 *Material*

The analyses of this study were carried out by using data obtained from a general research project in peanuts (*Arachis hypogaea* L.) concerned with quantitative traits. This project was based on complete two-way (Diallel) and four-way (Double) crosses of four, purebred varieties. The varieties and the experimental procedures have been described elsewhere (Cahaner et al. 1979). As data from generation F_3 of the two-way crosses were not available, the first (DC_1) and second (DC_2) segregating generations of the double cross were used instead of F_2 and F_3. Sixty DC_1 plants were grown in 1974; 15 offspring of each together with 50 plants of each of the four parent varieties, all obtained by self-fertilization, were grown in complete random layout in 1975 under the same experimental procedure as in 1974. Six traits were measured on each plant in both years:

1) Weight of pods per plant (PWP). All pods were weighed after two weeks of air drying.

2) Number of pods per plant (PNP).

3) Mean pod weight (MPW). The mature pods of each plant were counted and weighed, to calculate mean weight.

4) Oven-dry weight of tops per plant (TWP).

5) Number of flowers per plant (NFP). The flowers were counted daily from the first flower until the 45th day after planting.

6) R/R + V ratio on the main ('n') branch (RVN). R and V represent reproductive and vegetative secondary branches, respectively. The R/R + V ratio (Perry 1968; Wynne 1975) described the branching pattern of each plant.

2 *Definitions*

DC_1, DC_2	First and second generations of Double Cross.
V_{F_3}, $Cov_{F_3}\ (x,y)$	Phenotypic variance of a trait and phenotypic covariance between traits in generation F_3.
$\bar{V}_P$, $\overline{Cov}_P\ (x,y)$	Average variance of a trait and average covariance between pair of traits within purebred parental lines.
V_A, V_D	Additive and dominance variance of a trait in a random breeding population at equilibrium. Generation F_2 is a special case in which gene frequencies are equal, namely $p = q = 1/2$.
$Cov_{A(x,y)}$, $Cov_{D(x,y)}$	Additive and dominance covariance between traits x and y in a random breeding population at equilibrium.
V_E, $Cov_E\ (x,y)$	Environmental variance of a trait and environmental covariance between traits.
$H^2_{F_3}$	True value (parameter) of heritability in generation F_3.
$r_{A(x,y)}$	Additive genetic correlation between traits x and y.
$h^2_{F_3P}$, $h^2_{F_3}$, $h^2_{F_2F_3}$	Estimates of heritability obtained from the three approaches discussed in the text.
r_{F_3P}, r_{F_3}, $r_{F_2F_3}$	Estimates of genetic correlations obtained from the three approaches discussed in the text.
$Cov_{\bar{F}_3,F_2}$	Covariance between individuals of generation F_2 and the means of their progenies in F_3.
$\left.\begin{matrix} b_{\bar{F}_3(x),F_2(y)} \\ b_{\bar{F}_3(y),F_2(x)} \\ b_{\bar{F}_3(x),F_2(x)} \\ b_{\bar{F}_3(y),F_2(y)} \end{matrix}\right\}$	Regression coefficients between F_2 plants and their progeny means in generation F_3; x and y are two quantitative traits. Correlations between the generations are denoted the same, using r instead of b.
σ^2_b, σ^2_w	Components of the variance between and within families in the lowest rank for any given generation.
$\sigma_{b(x,y)}$	Covariance component between the lowest rank families in any given generation; x and y are a pair of quantitative traits.
t	Intraclass correlation in a given generation: $t = \dfrac{\sigma^2_b}{\sigma^2_b + \sigma^2_w}$

3 *Methods*

Three different appraoches of estimating heritability and genetic correlation were considered and utilized. The first method ('F_3P') estimates genetic variance and covariance by subtracting the variances and covariances of non-segregating generations from those of segregating generations. The second method ('F_3') uses intraclass correlation of segregating generations to estimate heritability and genetic correlations. The third method ('F_2F_3') is based on the relationship between two successive segregating generations. A detailed description of the methods will be done in the following:

1) *'F_3P'*: This method is based on information obtained from generation F_3 and the original purebred parental lines. Phenotypic variances of the traits and covariances between traits (V_{F_3} and Cov_{F_3}, respectively) are calculated from observations on plants in F_3. The environmental variances and covariances (V_E and Cov_E) are estimated by the 'mean variances' and 'mean covariances' within the purebred parental varieties ($\bar{V}_P$ and $\overline{Cov}_P$). Heritabilities in this method are threfore given by:

$$h^2_{F_3P} = \frac{V_{F_3} - \bar{V}_P}{V_{F_3}}$$

Similarly, the genetic correlation r_{F_3P} for the pair of traits x and y is:

$$r_{F_3P} = \frac{Cov_{F_3} - \overline{Cov}_P}{\sqrt{[V_{F_{3(x)}} - \bar{V}_{P(x)}]\,[V_{F_{3(y)}} - \bar{V}_{P(y)}]}}$$

2) *'F_3'*: This method is based merely on information obtained from generation F_3 (or DC_2 in the present case). As the data in this generation are composed of full sib families, components of variances and covariances – 'Between families' (σ^2_b) and 'Within families' (σ^2_w) – are obtained through one-way analyses of variance. The heritability estimates in this method are 3/2 times that of the intraclass correlation:

$$h^2_{F_3} = \frac{3}{2}\,\frac{\sigma^2_b}{\sigma^2_b + \sigma^2_w}$$

The standard errors of these estimates of heritability are obtained from the sampling variance of the intraclass correlation (Falconer 1960). Genetic correlations between traits are calculated in this method as:

$$r_{F_3} = \frac{\sigma_{b(x,y)}}{\sigma_{b(x)}\,\sigma_{b(y)}}$$

The standard error of these estimates of the genetic correlation were calculated in accordance with the procedure suggested by Tallis (1959).

3) *'F_2F_3'*: This method is based on information obtained from generations F_2 and F_3 (in our case, DC_1 and DC_2 respectively). The correlation between parent and progeny means ($r_{\bar{F}_3,F_2}$) was preferred to regression in order to estimate heritability. Standard error for $h^2_{F_2F_3}$ is estimated by:

$$\sqrt{(1 - r^2_{\overline{F}_3,F_2})/(n-2)}$$

where n is the average number of plants per family.

The mean of the covariance between trait (x) measured on parents and trait (y) measured on offspring and vice-versa, was used in this method as an estimate of the genetic covariance between the two traits. The estimate of genetic correlation between traits was obtained from this mean of covariance and the covariance between parents and their offspring means for single traits (Hazel 1943). In practice, the calculation was done using regression coefficient estimates (b):

$$r_{F_2F_3} = \sqrt{\frac{\left[b_{\overline{F}_{3(x)},F_{2(y)}}\right]\left[b_{\overline{F}_{3(y)},F_{2(x)}}\right]}{\left[b_{\overline{F}_{3(x)},F_{2(x)}}\right]\left[b_{\overline{F}_{3(y)},F_{2(y)}}\right]}}$$

The standard error for this estimate of genetic correlation is calculated in accordance with the method of Reeve (1955).

Theoretical Considerations

Table 1 summarizes the genetic and environmental expectations of variance and covariance for parental purebred lines, F_2 and F_3 generations and the inter-generation covariances. These expectations assume an additive-dominance model (Horner et al. 1955; Mather and Jink 1971). The expectations of heritability and genetic correlation estimates obtained by the three procedures are presented in Table 2.

1 *Heritability Estimates*

In this section, the expected values of heritability from the three approaches (each of which is of course approxi-

Table 1. Genetic and environmental expectations of variances and covariances between traits. Items are specified for purebred lines, generations F_2 and F_3 and for covariances between individuals from F_2 and their progeny means in F_3

Generation and description	Variances		Covariances	
	Symbol	Expectation	Symbol	Expectation
Within purebred lines	$\overline{V}_P$	V_E	$\overline{Cov}_P$	$Cov_{E(x,y)}$
F_2				
Total phenotypic	V_{F_2}	$V_A + V_D + V_E$	$Cov_{F_2}(x,y)$	$Cov_{A(x,y)} + Cov_{D(x,y)} + Cov_{E(x,y)}$
F_3				
Between families	σ_b^2	$V_A + \frac{1}{4}V_D$	$\sigma_{b(x,y)}$	$Cov_{A(x,y)} + \frac{1}{4}Cov_{D(x,y)}$
Within families	σ_w^2	$\frac{1}{2}V_A + \frac{1}{2}V_D + V_E$	$\sigma_{w(x,y)}$	$\frac{1}{2}Cov_{A(x,y)} + \frac{1}{2}Cov_{D(x,y)} + Cov_{E(x,y)}$
Total phenotypic	$\sigma_b^2 + \sigma_w^2$	$\frac{3}{2}V_A + \frac{3}{4}V_D + V_E$	$\sigma_{b(x,y)} + \sigma_{w(x,y)}$	$\frac{3}{2}Cov_{A(x,y)} + \frac{3}{4}Cov_{D(x,y)} + Cov_{E(x,y)}$
Covariance between parents (F_2) and their progeny ($\overline{F}_3$)	$Cov_{\overline{F}_3,F_2}$	$V_A + \frac{1}{2}V_D$	$Cov_{\overline{F}_{3(x)},F_{2(y)}}$	$Cov_{A(x,y)} + \frac{1}{2}Cov_{D(x,y)}$

Table 2. Estimating procedures and expectations of heritability and genetic correlation between traits for the three methods (see text and list of definitions)

	Heritability		Genetic Correlation	
Method	Estimating procedure	Expectation	Estimating procedure	Expectation
F_3P	$\frac{V_{F_3} - \overline{V}_P}{V_{F_3}}$	$\frac{\frac{3}{2}V_A + \frac{3}{4}V_D}{\frac{3}{2}V_A + \frac{3}{4}V_D + V_E}$	$\frac{Cov_{F_3(x,y)} - Cov_{(x,y)}}{\sqrt{\left[V_{F_{3(x)}} - \overline{V}_{P(x)}\right]\left[V_{F_{3(y)}} - \overline{V}_{P(y)}\right]}}$	$\frac{\frac{3}{2}Cov_{A(x,y)} + \frac{3}{4}Cov_{D(x,y)}}{\sqrt{\frac{3}{2}V_{A(x)} + \frac{3}{4}V_{D(x)}}\sqrt{\frac{3}{2}V_{A(y)} + \frac{3}{4}V_{D(y)}}}$
F_3	$\frac{3}{2}t = \frac{3}{2}\frac{\sigma_b^2}{\sigma_b^2 + \sigma_w^2}$	$\frac{\frac{3}{2}V_A + \frac{3}{8}V_D}{\frac{3}{2}V_A + \frac{3}{4}V_D + V_E}$	$\frac{\sigma_{b(x,y)}}{\sigma_{b(x)}\sigma_{b(y)}}$	$\frac{Cov_{A(x,y)} + \frac{1}{4}Cov_{D(x,y)}}{\sqrt{V_{A(x)} + \frac{1}{4}V_{D(x)}}\sqrt{V_{A(y)} + \frac{1}{4}V_{D(y)}}}$
F_2F_3	$^*b_{\overline{F}_3,F_2} = \frac{Cov_{\overline{F}_3,F_2}}{V_{F_2}}$	$\frac{V_A + \frac{1}{2}V_D}{V_A + V_D + V_E}$	$\sqrt{\frac{\left[b_{\overline{F}_{3(x)},F_{2(y)}}\right]\left[b_{\overline{F}_{3(y)},F_{2(x)}}\right]}{\left[b_{\overline{F}_{3(x)},F_{2(x)}}\right]\left[b_{\overline{F}_{3(y)},F_{2(y)}}\right]}}$	$\frac{Cov_{A(x,y)} + \frac{1}{2}Cov_{D(x,y)}}{\sqrt{V_{A(x)} + \frac{1}{2}V_{D(x)}}\sqrt{V_{A(y)} + \frac{1}{2}V_{D(y)}}}$

* Coefficient of correlation can be used instead of regression. Its expectation is given in the text

mate) are compared to the theoretical heritability of generation F_3. As breeders are usually interested in predicting the response to selection in the early generations we shall restrict our comparison to the 'narrow sense' heritability of generation F_3; its expectation is:

$$H^2_{F_3} = \frac{\frac{3}{2} V_A}{\frac{3}{2} V_A + \frac{3}{4} V_D + V_E}$$

(to avoid confusion, this special definition of heritability is denoted by H^2 rather than h^2). A comparison between this formula and the expectations of heritability derived from the three approaches (Table 2, column 3) shows that estimates obtained from these methods are all biased.

Estimates obtained by the first approach ($h^2_{F_3 P}$) can be considered as a measure of the 'broad sense' heritability of generation F_3. These estimates are, therefore, always an overestimate of $H^2_{F_3}$ except the case when non-additive variance is absent. The second approach supplies estimates ($h^2_{F_3}$) of similar nature but with a smaller bias because the non-additive variance in the numerator is half that in the numerator of the previous estimate. In both approaches, the smaller the fraction of non-additive variance, the less is the bias in the estimates.

When considering the third approach, i.e. estimating heritability from relationships between two generations (e.g. between generations F_2 and F_3), one should always take into account the fact that parent-offspring regression is a biased estimate of heritability when the two generations have different means and variances. Such differences, caused by environmental or experimental changes, are common in experiments with plants. In such situations parent-offspring correlation rather than regression is recommended as the measure of heritability in random-mating populations (Frey and Horner 1957; Turner and Young 1969). In our case, when heritability is being estimated as a correlation between plants from generation F_2 and their offspring means in generation F_3 ($r_{\bar{F}_3, F_2}$), the above-mentioned environmental bias may be removed but the formula still gives a biased estimate of $H^2_{F_3}$ as can be seen from its expectation:

$$r_{\bar{F}_3 F_2} = \frac{\mathrm{Cov}_{\bar{F}_3, F_2}}{\sqrt{V_{F_3} V_{F_2}}} = \frac{V_A + \frac{1}{2} V_D}{\sqrt{V_A + \frac{1}{4} V_D + \frac{1}{n} V_E}\ \sqrt{V_A + V_D + V_E}}$$

where n is the number of individuals within families of generation F_3.

This estimate ($h^2_{F_2 F_3}$) can be either an underestimate or an overestimate, depending on the quantitative relationship between the three components of the estimate. The greater V_D the more it is overestimated; the greater V_E the more it is underestimated. Even when non-additive variance is absent, the lack of bias in this correlation as an estimator of $H^2_{F_3}$ is not self-evident and depends on n; when n has a value of 2-3 the correlation is unbiased; when each F_3 family is represented by a single plant (n = 1), it is an underestimate and when there are large numbers of individuals in each family, the correlation is an overestimate of $H^2_{F_3}$.

Finally, in using the second method ($h^2_{F_3}$) (which appears to be the least biased), we have suggested multiplying the intraclass correlation (t) by the factor of $\frac{3}{2}$ (see Table 2) as t has an upper limit of $\frac{2}{3}$. Using this kind of argument, one can generalize this case by expressing the expected value of heritability as a function of intraclass correlation in any given generation g:

$$h^2_{F_g} = [2 - (1/2)^{g-2}]t$$

2 Estimates of Genetic Correlation Between Traits

The additive genetic correlation between quantitative traits x and y will be designated as $r_{A(x,y)}$ and its expectation is:

$$r_{A(x,y)} = \frac{\mathrm{Cov}_{A(x,y)}}{\sqrt{V_{A(x)} V_{A(y)}}}$$

The estimating procedures and expectations of genetic correlation following the three approaches are summarized in Table 2 (Column 4).

Comparing expectations of the three estimates to that of $r_{A(x,y)}$ reveals that these estimates contain some non-additive genetic variances and covariances (see last column in Table 2). These non-additive factors can cause serious bias by reducing the absolute value of the estimate; this source of bias is most significant when the two kinds of covariances (additive and non-additive) have opposite signs and when there are non-additive variances.

On the other hand, when the two covariances have the same sign and the non-additive variances are of the same magnitude as the non-additive covariances, the bias is reduced. In all cases, the extent of underestimation depends on the portion of the non-additive variances and covariances in the correlation estimates. The genetic correlation between two traits, estimated by the second method (r_{F_3}) is thus the least biased of the three approaches (see expectations of the genetic correlations in Table 2).

Analyses of Data and Discussion

1 Estimates of Heritability

In analyzing data from three generations – parents, DC_1 and DC_2 (Double Crosses), estimates for heritability and genetic correlation were obtained from the three methods

Table 3. Estimates of heritability, genetic correlation (lower off-diagonal), and phenotypic and environmental correlations (upper and lower figures, respectively, in each cell of the upper off-diagonal). The estimates were calculated for six traits of peanuts, using the three methods detailed in the text and in Tables 1 and 2. Standard errors of estimates, obtained by two of the methods, are also given

			Correlation Estimates					
Trait	Method	Heritability estimates	PWP	PNP	MPW	TWP	NFP	RVN
PWP	F_3P	0.837		0.832	0.409	0.382	0.153	–0.095
	F_3	0.601 ± 0.075		0.733	0.403	0.218	0.254	0.012
	F_2F_3	0.665 ± 0.098						
PNP	F_3P	0.897	0.851		–0.024	0.485	0.101	–0.104
	F_3	0.532 ± 0.073	0.842 ± 0.249		–0.010	0.346	0.222	–0.063
	F_2F_3	0.613 ± 0.104	0.834 ± 0.096					
MPW	F_3P	0.758	0.413	–0.027		–0.152	0.096	–0.030
	F_3	0.628 ± 0.076	0.503 ± 0.179	0.017 ± 0.145		0.083	0.169	–0.017
	F_2F_3	0.803 ± 0.078	0.349 ± 0.237	–0.134 ± 0.290				
TWP	F_3P	0.878	0.409	0.502	–0.169		–0.208	–0.333
	F_3	0.610 ± 0.076	0.434 ± 0.169	0.637 ± 0.200	–0.277 ± 0.153		0.140	0.346
	F_2F_3	0.627 ± 0.102	0.349 ± 0.270	0.604 ± 0.226	–0.381 ± 0.273			
NFP	F_3P	0.560	0.123	0.075	0.062	–0.322		0.642
	F_3	0.551 ± 0.174	0.138 ± 0.148	0.006 ± 0.146	0.187 ± 0.149	–0.307 ± 0.157		0.110
	F_2F_3	0.481 ± 0.115	0.009 ± 0.352	–0.116 ± 0.371	0.140 ± 0.317	–0.610 ± 0.336		
RVN	F_3P	0.877	–0.112	–0.124	–0.033	–0.423	0.877	
	F_3	0.840 ± 0.242	–0.170 ± 0.147	–0.233 ± 0.152	–0.037 ± 0.143	–0.460 ± 0.172	0.840 ± 0.242	
	F_2F_3	0.800 ± 0.167	–o.393 ± 0.284	–0.387 ± 0.292	–0.190 ± 0.269	–0.499 ± 0.247	0.800 ± 0.167	

considered. The heritability estimates of the six traits are shown in the first column of Table 3. Two of the three estimates ($h^2_{F_3}$ and $h^2_{F_2F_3}$) of each trait are followed by their standard errors. The relative values of the three estimates vary from trait to trait, but there are some similarities among them. Estimates of $h^2_{F_3P}$ were the largest in five of the six traits, and in all cases larger than the estimates of $h^2_{F_3}$. Considering the standard error of $h^2_{F_3}$, these differences are significant for all traits except NFP. The heritabilities estimated from parent-offspring relation ($h^2_{F_2F_3}$) were slightly and insignificantly larger than $h^2_{F_3}$ in the traits PWP, PNP, TWP and RVN. For MPW, $h^2_{F_2F_3}$ was significantly larger than both $h^2_{F_3}$ and $h^2_{F_3P}$. NFP is the only trait for which $h^2_{F_2F_3}$ was smaller than $h^2_{F_3}$, but the difference was insignificant. In general, it seems that $h^2_{F_3}$ gives the smallest heritability estimate and is probably the closest to the 'narrow sense' heritability – $H^2_{F_3}$. This is in agreement with its expectation since it contained the smallest portion of non-additive variance in the numerator (i.e. 3/8 V_D compared to 1/2 V_D in $h^2_{F_2F_3}$ and 3/4 V_D in $h^2_{F_3P}$) (Table 3). In practice, data from only one generation are needed to calculate $h^2_{F_3}$ which means a possible saving in experimental efforts.

The genetic and statistical reliability of $h^2_{F_3}$ and the experimental advantages of this intraclass correlation approach make it superior to the other two methods in estimating heritability in the F_3 generation. This method can also be used in later generations, where $h^2_{F_g}$ is becoming a better estimate of 'narrow sense' heritability, as the non-additive variance is progressively reduced. Indeed, when data from only one segregating generation are available, this approach is the only one that can be used.

It should be re-emphasized that heritability has meaning only when it is related to the specific genetic population structure from which it was estimated and to the environmental conditions in which the plants were grown. In this study we have further restricted our consideration to one defined population characterized by the genetic structure of generation F_3 resulting from a cross between two purebred lines and followed by two generations of selfing. By making this distinction between different estimates of heritability as a function of the generations from which it was derived, the greatest weakness of heritability has been illustrated. This weakness is especially important when self-fertilizing populations are considered and quantitative genetics techniques are used in the breeding program. Finally, we should make it clear that when dealing with estimates of heritability in segregating generations of self-fertilizing species, no attempt was made to estimate heritability between the founder parents (Hill and Smith 1977). Such an estimate would, of course, have been meaningless. We have concentrated on heterogeneous populations as a temporary phase between the purebred parents and the new variety.

2 *Estimates of Genetic Correlations Between Traits*

The three estimates of genetic correlation actually obtained for each pair of traits are shown in Table 3. Standard errors (S.E.) of two of the three estimates are also presented. Most estimates of r_{F_3} had S.E. values around 0.15, with exceptional values around 0.25 for highly correlated traits like PWP x PNP and NFP x RVN. With the exception of these two pairs, the S.E. of $r_{F_2F_3}$ were larger. Despite these S.E. values, estimates of genetic correlation obtained by the three different methods were very similar for most of the pairs of traits, even when phenotypic and environmental correlations were quite different (Table 3). The similar estimates were obtained despite the fact that the portions of non-additive genetic variances and covariances in the three estimates differed. It demonstrates that estimates of genetic correlation, unlike heritability, are not necessarily biased by non-additive effects. However, since these effects can bias the estimate, it still seems that r_{F_3} is the best approach for estimating genetic correlation, as it contains the smallest portion of non-additive effects.

Conclusions

Estimates of true 'narrow sense' heritability and additive genetic correlation between traits cannot be obtained from generations F_2 and F_3 resulting from selfing of a cross between purebred lines. Among three methods considered, the estimates obtained by using variance and covariance components between and within selfed families were found to be the most reliable. Furthermore, this method is also more economical in experimental efforts since data from only one segregating generation, as early as F_3, are sufficient to provide the required estimates.

The actual estimates of heritability and genetic correlation were calculated in this paper only for the purpose of demonstrating the three methods and comparison between them. The figures themselves have limited meaning as they were based on data from only one population and one environment. Nevertheless, each one of the three methods can be used irrespective of the number of locations and years, while the exogenous effects can be removed by appropriate statistical procedures.

Heritability of a trait in generation F_g ($g \geqslant 3$) is estimated by the intraclass correlation as:

$$h^2_{F_g} = [2 - (1/2)^{g-2}]\ \frac{\sigma^2_b}{\sigma^2_b + \sigma^2_w}$$

Genetic correlation between a pair of traits, in any generation, can be estimated as:

$$r_{F_{g(xy)}} = \frac{\sigma_{b(xy)}}{\sigma_{b(x)}\ \sigma_{b(y)}}$$

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