Estimation of additive genotypic variance with the F_3 of autogamous crops

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The additive genotypic variance, D , estimated with the F_3 of autogamous crops can be taken as an estimate of genotypic variance of its F_∞ -progeny. Two possible ways of estimating D are compared on the basis of their mean square error. For each of the two estimators the F_3 -population design, *i.e.*, the number of lines, the number of plants per line and the number of parent plants, is chosen such that for a given experimental capacity its mean square error is minimal. Subsequently the two estimators are compared for various combinations of F_∞ -heritability, dominance level and experimental size. In by far the most cases the second estimator, D_2 , which takes twice the between F_3 -line genotypic variance as its estimate, outperforms the first estimator, D_1 , which uses both the between and the within F_3 -line genotypic variance. Further it is shown that, when it is necessary to work with plot totals because of low F_∞ -heritability, the performance of D_1 becomes very poor. With respect to the estimator of the dominance component of genotypic variance, H , its very large mean square error and its highly negative correlation with D_1 are demonstrated.

INTRODUCTION

Quantitative genetic theory has developed models that enable the prediction of the F_∞ -progeny (its genotypic mean and variance) of a cross between two pure-breeding lines (*e.g.*, Mather and Jinks, 1971). With the predicted mean and variance, and with a normality assumption, the ability of the cross to produce superior inbred lines can be predicted (Jinks and Pooni, 1976). The necessary parameters have to be estimated in a time and labour extensive way in order to be applicable in a practical breeding programme. One of the few approaches that meet these requirements is the method employing the F_3 -generation. This paper concentrates on the estimation of the F_∞ -variance. In the absence of epistasis and linkage this F_∞ -variance equals the additive genotypic variance D . We will assume that epistasis and linkage are absent, but in the discussion we will comment on these assumptions and try to relax these assumptions.

There are two straightforward methods to estimate the additive genotypic variance D from an F_3 of a cross between two inbred lines. One method

is to estimate the genotypic between line variance (V_{1F3}) and the genotypic within line variance (V_{2F3}), and successively estimate D and H (H is the dominance component of the genotypic variance). Since the genotypic variances are different linear combinations in D and H (*e.g.*, Mather and Jinks, 1971):

$$V_{1F3} = \frac{1}{2} \cdot D + \frac{1}{16} \cdot H \quad \text{and} \quad V_{2F3} = \frac{1}{4} \cdot D + \frac{1}{8} \cdot H,$$

D and H can be estimated from the estimated V_{1F3} and V_{2F3} (defining estimators D_1 and H_1):

$$D_1 \stackrel{\text{def}}{=} \frac{4}{3} \cdot (2 \cdot \hat{V}_{1F3} - \hat{V}_{2F3}), \quad (1)$$

and

$$H_1 \stackrel{\text{def}}{=} \frac{16}{3} \cdot (2 \cdot \hat{V}_{2F3} - \hat{V}_{1F3}). \quad (2)$$

The second method is to estimate only V_{1F3} , and successively estimate D as follows (Jinks and Pooni, 1980) (defining estimator D_2):

$$D_2 \stackrel{\text{def}}{=} 2 \cdot \hat{V}_{1F3}. \quad (3)$$

A disadvantage of D_2 is, in contrast to D_1 , that it is biased if dominance variance is present ($H > 0$):

$$E(D_2) = E(2 \cdot \hat{V}_{1F3}) = D + H/8.$$

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Another supposed disadvantage is that the dominance component H cannot be estimated. However, H describes genetic variation that cannot be exploited in autogamous crops, unless one is interested in making hybrid varieties (which we are not in the present study). An advantage of D_2 is that there is no need to estimate the residual (environmental) variance by growing isogenous material (mostly the parents), for this may take up a fairly large proportion of the experimental field. D_2 was introduced by Jinks and Pooni (1980), and they concluded that the D_2 -estimate could be used with the same confidence as the estimate from the (elaborate) triple test cross. However, they did not extend their conclusion beyond their case of two traits in tobacco. The purpose of this paper is to show that in many situations (*i.e.*, combinations of heritability, dominance level and experimental size) D_2 is a better estimator of D than D_1 , *i.e.*, the mean square error of D_2 is smaller than that of D_1 . We make the usual assumptions: (1) the quantitative trait is determined by a large number of independently segregating loci, and hence that the trait will have a normal distribution, (2) the residual error also has a normal distribution, (3) there is no epistasis. We define the F_∞ -heritability: $h^2_{(F_\infty)} = D/(D + E)$.

EXPERIMENTAL DESIGN BASED ON INDIVIDUAL PLANTS

Numerous experimental designs are possible. A standard design is a completely randomized design (a 1-way classification), in which each F_3 -line is represented by the same number of plants and all plants of all lines are randomized. To estimate the residual error usually parent plants are added. The accompanying analysis of variance is given in table 1.

Mean square errors of the estimators

A measure for comparing estimators is the mean square error (MSE). It comprises both the variance and the bias of the estimator. We will derive the mean square error of both estimators (D_1 and D_2). The mean squares of table 1 have chi-square-like distributions:

$$MS \approx \frac{E(MS)}{df} \cdot \chi^2(df).$$

($\chi^2(df)$ is a chi-square random variable with df degrees of freedom.) Since $\text{var}(\chi^2(df)) = 2 \cdot df$, the

Table 1 Analysis of variance of a completely randomized F_3

MS	name	df	$E(MS)$
MSB	between lines	$l - 1$	$E + V_{2F3} + n \cdot V_{1F3}$
MSW	within lines	$l \cdot (n - 1)$	$E + V_{2F3}$
MSI	within parents	$2 \cdot (i - 1)$	E

l , No. of lines; n , No. of plants per line; i , No. of plants per parent.

V_{1F3} , genotypic between line variance; V_{2F3} , genotypic within line variance; E , residual variance.

variance of the mean squares is:

$$\text{var}(MS) = \frac{E^2(MS)}{df^2} \cdot 2 \cdot df = \frac{2 \cdot E^2(MS)}{df}. \quad (4)$$

As a consequence of the experimental design the three mean squares are mutually stochastically independent. The estimators of V_{1F3} and V_{2F3} are:

$$\hat{V}_{1F3} = (MSB - MSW)/n,$$

$$\text{resp. } \hat{V}_{2F3} = MSW - MSI. \quad (5)$$

Combining equations (1), (2) and (3) with (5) results in (simultaneously defining coefficients f_1 up to f_8):

$$D_1 = \frac{8}{3 \cdot n} \cdot MSB + \frac{-8 - 4 \cdot n}{3 \cdot n} \cdot MSW + \frac{4}{3} \cdot MSI$$

$$\stackrel{\text{def}}{=} f_1 \cdot MSB + f_2 \cdot MSW + f_3 \cdot MSI, \quad (6)$$

$$H_1 = \frac{-16}{3 \cdot n} \cdot MSB + \frac{16 + 32 \cdot n}{3 \cdot n} \cdot MSW + \frac{-32}{3} \cdot MSI$$

$$\stackrel{\text{def}}{=} f_4 \cdot MSB + f_5 \cdot MSW + f_6 \cdot MSI, \quad (7)$$

$$D_2 = \frac{2}{n} \cdot MSB + \frac{-2}{n} \cdot MSW$$

$$\stackrel{\text{def}}{=} f_7 \cdot MSB + f_8 \cdot MSW. \quad (8)$$

The variances of the estimators are:

$$\text{var}(D_1) = f_1^2 \cdot \text{var}(MSB) + f_2^2 \cdot \text{var}(MSW) + f_3^2 \cdot \text{var}(MSI), \quad (9)$$

$$\text{var}(H_1) = f_4^2 \cdot \text{var}(MSB) + f_5^2 \cdot \text{var}(MSW) + f_6^2 \cdot \text{var}(MSI), \quad (10)$$

$$\text{var}(D_2) = f_7^2 \cdot \text{var}(MSB) + f_8^2 \cdot \text{var}(MSW). \quad (11)$$

The covariance of D_1 with H_1 is:

$$\begin{aligned} \text{cov}(D_1, H_1) &= f_1 \cdot f_4 \cdot \text{var}(MSB) \\ &\quad + f_2 \cdot f_5 \cdot \text{var}(MSW) \\ &\quad + f_3 \cdot f_6 \cdot \text{var}(MSI). \end{aligned} \quad (12)$$

The (usual) definition of the mean square error of a (possibly biased) estimator X of a certain parameter θ is: $MSE(X) = E(X - \theta)^2$. If the bias is δ , i.e., $E(X) = \theta + \delta$, then: $MSE(X) = \text{var}(X) + \delta^2$. Thus, the mean square errors of the three estimators are:

$$MSE(D_1) = \text{var}(D_1), \quad MSE(H_1) = \text{var}(H_1),$$

and

$$MSE(D_2) = \text{var}(D_2) + \frac{1}{64} \cdot H^2.$$

If there is no dominance variance, then D_2 is unbiased and hence its mean square error is equal to its variance. Comparing equation (9) with (11) we can see that in this case the MSE of D_1 will always be larger than the MSE of D_2 :

$$f_1^2 = \frac{64}{9 \cdot n^2} = \frac{7.111}{n^2} > \frac{4}{n^2} = f_7^2,$$

and

$$\begin{aligned} f_2^2 &= \left(\frac{-8 - 4 \cdot n}{3 \cdot n} \right)^2 \\ &= \left(\frac{-2.667}{n} - 1.333 \right)^2 > \left(\frac{-2}{n} \right)^2 = f_8^2. \end{aligned}$$

and additionally the variance of MSI contributes to the variance of D_1 . Furthermore, the experimental size needed for D_1 in this comparison is larger because of the need to estimate the residual variance. Therefore, we conclude that in the absence of dominance it is always better to use D_2 . Of course it is realized that one never knows beforehand the presence or level of the dominance variance (which also applies to epistasis and linkage). Thus subsequently only situations in which dominance is present need to be studied.

We define the scale independent parameter, the coefficient of error (CE) of estimator X of θ : $CE(X) = \sqrt{MSE(X)}/\theta$. For an unbiased estimator the coefficient of error equals the coefficient of variation.

Optimum allocation of the experimental size

Equations (9) and (11) show that, at a given experimental size k , the variance of D_1 and D_2 depends on the design of the F_3 -population and, additionally for D_1 , on the proportion of the experimental size that is assigned to parent plants. In order to make a fair comparison between the two estimators we need to find the design, in which

the number of lines (l), the number of plants per line (n), and the number of plants per parent (i) are optimal, i.e., the design in which l , n and i are chosen such that the MSE , and consequently the variance, of the estimator is minimal. In practice, of course, the maximum number of seeds produced per F_2 -plant may be smaller than the optimum number of plants per line, in which case one will have to settle for a sub-optimal situation.

The variance of D_2 can be minimized for a given F_3 -population size $k = l \cdot n$ by substitution of l by k/n in an elaborated form (using equations (4) and (8)) of equation (11). The variance of D_2 becomes a function in n (as far as the allocation of the experimental size is concerned), and using the first derivative of this function ($\delta \text{var}(D_2)/\delta n$), the optimum number of plants per line for a given F_2 -population size k , and given magnitudes of variance components (V_{1F3} , V_{2F3} and E) can be found:

$$n_{\text{opt}} = \frac{(1+k) \cdot (E + V_{2F3}) + k \cdot V_{1F3}}{2 \cdot (E + V_{2F3}) + k \cdot V_{1F3}}$$

and hence $l_{\text{opt}} = k/n_{\text{opt}}$. Since n and l are integer numbers, we have to evaluate $\text{var}(D_2)$ at the smaller and the larger integer numbers next to n_{opt} ; consequently the product $l_{\text{opt}} \cdot n_{\text{opt}}$ may sometimes not be exactly equal to k . The constraints on account of the ANOVA are: $1 \geq 2$ and $n \geq 2$. Fig. 1 presents the optimum number of plants for a few situations. It shows that n_{opt} depends chiefly on the F_{∞} -heritability and for medium to low F_{∞} -heritability also on the experimental size. There is very little influence of the dominance level.

The minimization of $\text{var}(D_1)$ is somewhat less straightforward, because the experimental size is a function of three parameters: $k = l \cdot n + 2 \cdot i$. However, l and n appear only in the first part of (the elaborated form of) equation (9) [$f_1^2 \cdot \text{var}(MSB) + f_2^2 \cdot \text{var}(MSW)$], and i appears only in the last part [$f_3^2 \cdot \text{var}(MSI)$]. For a given number of F_3 -plants $c = l \cdot n$ we can obtain the optimum number of plants per line by minimizing this first part of equation (9) in a manner similar to the minimization of $\text{var}(D_2)$. This results in:

$$n_{\text{opt}} = \frac{(2+3 \cdot c) \cdot (E + V_{2F3}) + 2 \cdot c \cdot V_{1F3}}{5 \cdot (E + V_{2F3}) + 2 \cdot c \cdot V_{1F3}},$$

and hence $l_{\text{opt}} = c/n_{\text{opt}}$. Since $i = (k - c)/2$, we can now rewrite equation (9) by taking the minimum of the first part plus the second part, in which i is substituted by $(k - c)/2$. The resulting equation for $\text{var}(D_1)$ depends solely on c (as far as the alloca-

Figure 1 Optimum number of plants per line (n_{opt}) for D_2 for various F_{∞} -heritabilities, two experimental sizes (k) and two dominance levels.

tion of the experimental size is concerned):

$$\text{var}(D_1) =$$

$$\begin{aligned} & \frac{64 \cdot (E + V_{2F3} + c \cdot V_{1F3}) \cdot (5 \cdot (E + V_{2F3}) + 2 \cdot V_{1F3})^2}{9 \cdot ((2 + 3 \cdot c) \cdot (E + V_{2F3}) + 2 \cdot c \cdot V_{1F3}) \cdot (c - 1)} \\ & + \frac{96 \cdot ((4 + c) \cdot (E + V_{2F3}) + 2 \cdot c \cdot V_{1F3})^2 \cdot (E + V_{2F3})}{9 \cdot ((2 + 3 \cdot c) \cdot (E + V_{2F3}) + 2 \cdot c \cdot V_{1F3}) \cdot (c - 1) \cdot c} \\ & + \frac{32 \cdot E^2}{9 \cdot (k - c - 2)}. \end{aligned}$$

The first derivative of this function in c , $\delta \text{var}(D_1) / \delta c$, could not be solved to find a solution for c . Therefore, the behaviour of $\text{var}(D_1)$ was studied numerically; it appeared that a unique minimum exists (at $c = c_{\text{opt}}$) for $1 < c < k - 2$. Fig. 2 shows the optimum fraction of the total experimental size taken up by the F_3 (c_{opt}/k). It depends mainly on the F_{∞} -heritability, it varies only slightly with the experimental size. For situations without

dominance ($H = 0$) up to a high dominance level ($D = 2 \cdot H$) the fraction deviates, for the same value of k , not more than 0.02 from the fractions presented in fig. 2 (with $H = \frac{1}{2} \cdot D$). Since l , n and i are integer numbers, $\text{var}(D_1)$ must be evaluated at the smaller and larger integer numbers next to $i_{\text{opt}} = (k - c_{\text{opt}})/2$ and next to n_{opt} . The constraints on account of the ANOVA are: $l \geq 2$, $n \geq 2$ and $i \geq 2$.

Comparing D_2 with D_2

Now that we have established ways to obtain optimum population designs for any situation (within the boundaries of the current experimental design), both for D_1 and D_2 , we can compare the two estimators. Above it has already been stated that for situations with no dominance ($H = 0$) D_2 is always better than D_1 . For situations with dominance the ratio of the CE 's of D_1 and D_2

Figure 2 Optimum fraction of the total experimental size taken up by the F_3 (c_{opt}/k) for D_1 for various F_{∞} -heritabilities, two experimental sizes (k) and dominance level $H = \frac{1}{2} \cdot D$.

depends as well on the ratio of the variances of the two estimators as on the dominance level. The variance of D_2 is always smaller than that of D_1 . However, at very large experimental sizes and/or at high F_{∞} -heritabilities the difference between the variances of D_1 and D_2 will be small, and hence the CE of D_1 will eventually become smaller than the CE of D_2 because of the contribution of the dominance level to the CE of D_2 . We computed the CE 's of D_1 and D_2 for all combinations of seven F_{∞} -heritability values ($h^2_{(F_{\infty})} = 0.05, 0.10, 0.25, 0.50, 0.75, 0.90, 0.95$), six experimental sizes ($k = 50, 100, 200, 400, 800, 1600$), and four dominance levels ($H = 0, \frac{1}{2} \cdot D, D, 2 \cdot D$). The ratio $CE(D_1)/CE(D_2)$ varied from 0.54 (at $h^2_{(F_{\infty})} = 0.95, k = 1600, H = 2 \cdot D$) up to as large as 4.59 (at $h^2_{(F_{\infty})} = 0.05, k = 800, H = 0$). Fig. 3 shows that the relative performance of D_1 increases with the F_{∞} -heritability level and the experimental size, but that D_1 only outperforms D_2 at a high dominance level combined with a large experimental size and a medium to high F_{∞} -heritability level. Of all

the 168 studied combinations only 11 combinations showed a D_1 outperforming D_2 , of which 9 were situations with extreme overdominance ($H = 2 \cdot D$).

H_1

The optimum allocation of the experimental size with respect to H_1 can be determined in a very similar way as applied to D_1 . This optimum is different from the optimum with respect to D_1 . This can already be seen at the optimum number of plants per line for a given F_3 -population size ($c = l \cdot n$):

$$n_{opt} = \frac{(1 + 3 \cdot c) \cdot (E + V_{2F3}) + c \cdot V_{1F3}}{4 \cdot (E + V_{2F3}) + c \cdot V_{1F3}}$$

We determined the optima for H_1 numerically for all previously mentioned 168 combinations of F_{∞} -heritability, experimental size and dominance level, and subsequently evaluated the mean square

Figure 3 Ratio of the coefficients of error of D_1 and D_2 , (a), for various F_{∞} -heritabilities, three dominance levels and experimental size $k=100$; (b), for various F_{∞} -heritabilities, three dominance levels and experimental size $k=1600$; (c), for various experimental sizes (k) three dominance levels and F_{∞} -heritability of 0.75.

errors at these optima. The optimum number of parent plants and the optimum number of plants per line were higher than for D_1 . In effect this means that H_1 needs a more accurate estimate of V_{2F3} . The CE is in many of these cases rather high, e.g., at a $h^2_{(F\infty)} = 0.25$ for $k = 1600$ with $H = 2 \cdot D$ $CE = 1.4$ up to as large as $CE = 32.0$ for $k = 50$ with $H = \frac{1}{2} \cdot D$.

For all 168 combinations, for which the allocation of the experimental size was optimized for D_1 (!), we also computed the correlations of H_1 with D_1 (using equations (9), (10) and (12)). These were found to be highly negative: ranging from -0.83 to -0.95 . Graphical demonstrations of these highly negative correlations can be found in Van Ooijen (1986) and in Shaw (1987).

EXPERIMENTAL DESIGN BASED ON PLOT TOTALS

Sometimes the F_{∞} -heritability of a certain trait is so low that the experimental size, necessary for an accurate estimate of D , expands too much to be able to score each individual plant. In that case the experimental design will be based on plot

totals (or plot means). A corresponding standard design is also a completely randomized design, but now based on plot totals (or plot means). The accompanying analysis of variance is presented in table 2.

Working with plot totals instead of with individual plants means loss of information on genotypic within line variance. As plot size increases there will hardly be any information left on genotypic within line variance. For example, the mean of 2 plots of 100 plants of the same line will hardly differ genotypically, instead most of the difference will be of environmental origin (residual variance). Thus V_{2F3} will be come hard to estimate, its estimator will have a very large variance, and as a result the CE of D_1 will increase. For example, doubling the experimental size by taking a plot of two plants instead of just one plant resulted in an increase (!) in the CE of D_1 for all studied combinations (mentioned above) with an F_{∞} -heritability of up to 0.75; only the studied combinations with an F_{∞} -heritability of 0.90 or 0.95 showed a slight decrease in the CE of D_1 . (Rem.: for these calculations E was split into E_w and E_b by using the empirical law of

Table 2 Analysis of variance of a completely randomized design of plots of F_3 -lines, based on plot totals

MS	name	df	$E(\text{MS})$
MSB	between lines	$l-1$	$n \cdot E_w + n^2 \cdot E_b + n \cdot V_{2F_3} + p \cdot n^2 \cdot V_{1F_3}$
MSW	within lines	$l \cdot (p-1)$	$n \cdot E_w + n^2 \cdot E_b + n \cdot V_{2F_3}$
MSI	within parents	$2 \cdot (i-1)$	$n \cdot E_w + n^2 \cdot E_b$

l , No. of lines; n , No. of plants per plot; p , No. of plots per line; i , No. of plots per parent. V_{1F_3} , genotypic between line variance; V_{2F_3} , genotypic within line variance; E_w residual within plot variance; E_b , residual between plot variance.

H. F. Smith (1938) with a coefficient of heterogeneity $b = 0.5$).

In contrast with this is the effect on D_2 . D_2 does not need an estimate of V_{2F_3} , it only depends on the accuracy of the estimator of V_{1F_3} , which is even raised by increasing plot size. Theoretically there will, of course, be an optimum allocation of experimental size regarding plot size, number of plots and number of lines. However, for many crops plot size will primarily be dictated by agricultural practice, such as the number of seeds produced per plant and the capacity of the harvesting equipment. Therefore it is not attempted in this paper to determine a way of obtaining the optimum allocation of such an experiment.

DISCUSSION

It will be clear that estimator D_2 is more accurate than D_1 in many cases. When it is necessary to use plot totals because of low F_∞ -heritability, the performance of D_1 becomes very inaccurate. When working with individual plants the accuracy of D_1 can only be better than that of D_2 in combinations with a high dominance level, a higher F_∞ -heritability, and/or a large experimental size. In practice there need be no doubt about D_2 when $H < D$, $h^2_{(F_\infty)} < 0.75$, and $n < 400$. For any situation it will be possible to approximate the mean square errors of both estimators once the variance components have been (roughly) estimated in a pilot experiment. The experimenter can decide on which estimator to use, thereby also considering the available experimental capacity and the desired accuracy.

The results may be extended to other experimental designs, such as a complete block design. These designs mostly aim at reducing the residual error. Therefore, we expect to find similar results. Of course it would be best to consider the mean square errors of both estimators for any specific desired design.

Linkage and epistasis may bias both estimators. Depending on the magnitude of the linkage and epistasis parameters, D_2 may even have a somewhat larger bias than D_1 . A number of studies (Weber, 1982; Kearsley, 1985) conclude that the influence of linkage is unimportant, when we are regarding D as the F_∞ -variance and not as the "true" additive variance (Pooni and Jinks, 1986). The latter can be interpreted as the theoretical F_∞ -variance that would be obtained if linked loci were segregating independently. Because from the breeder's point of view the F_∞ -variance rather than the true additive variance is relevant, the present paper focuses on D as the F_∞ -variance. Therefore, linkage is not likely to invalidate the main results. The influence of epistasis depends on the relative magnitude of its parameters. Pooni and Jinks (1979) describe methods to obtain estimates of these parameters. However, and this applies also to the paper of Jinks and Pooni (1982), in which methods are introduced that try to correct for linkage, (1) these methods are always too elaborate to include in a practical breeding programme (cf. Van der Veen, 1959), and (2) the more parameters have to be estimated, the less accurate the estimates usually become.

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