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M. Singh · S. Ceccarelli

Estimation of heritability using variety trials data from incomplete blocks

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Abstract An assessment of the heritability of a trait is useful in formulating a breeding strategy for crop improvement. We have considered the estimation of broad-sense heritability from a single-location trial and from multi-locational trials conducted in incomplete blocks. Using residual maximum likelihood estimates of variance components, we estimated the heritability and obtained expressions for the estimate of its bias and its standard error. The estimation procedure is illustrated for 25 barley genotypes evaluated at four locations in West Asia and North Africa during 1992.

Key words Heritability · Incomplete block design · Standard error · Bias · Genotype by environment interaction

Introduction

The heritability of a trait has significant implications in breeding for crop improvement (Nyquist 1991). Besides predicting response to selection, heritability estimates are used to identify optimum environments for selection (Allen et al. 1978; Blum 1985; Ceccarelli 1989). Estimations of heritability and its confidence interval or standard error are available for parent-offspring data (Graybill et al. 1956; Bogyo and Becker 1963; Broemeling 1969). Confidence intervals for variance ratio or heritability are provided by Harville and Fenech (1985) for a mixed linear model. Exact confidence intervals of heritability on a progeny mean basis in the case of multi-environment trials were given by Knapp et al. (1985). In the case of data from incomplete blocks, the unequal coefficients of genotype – environment variance appearing in the expectations of mean squares for genotype-environment and genotype sources of variation may not necessarily facilitate an evaluation of the exact confidence intervals. When the data are from variety trials conducted in randomized complete block designs, Singh et al. (1993) gave an expression for the standard error of heritability estimate and used a simulation technique to show that the distribution of the estimate was reasonably close to a normal distribution. However, most variety trials are conducted in incomplete blocks (e.g., square lattices, rectangular lattices, α-lattices, etc.) at preliminary as well as at advanced stages of variety testing. Estimation of heritability using data from incomplete blocks has received little attention and its standard errors are not reported in the literature. Standard errors provide a measure of precision associated with the estimates and are required to make a comparative assessment of heritabilities.

In this paper we present a procedure for estimating heritability and its standard error using incomplete block designs at a single environment in Cyprus and several environments in Northern Syria. We illustrate the procedure using yield data from barley trials conducted by the Germplasm Program of ICARDA.

Materials and methods

Single trials

Let h^2 denote the heritability of trait Y from responses of a set of V inbred lines chosen randomly from a population of lines. Let these genotypes (lines) be evaluated in an incomplete block design (square lattices, rectangular lattices, α-lattices, etc.) in a single environment. The response Y_{ijk} from the i-th genotype grown in the k-th block of the j-th replicate is modelled as

$$Y_{ijk} = \mu + g_i + \rho_j + \beta_{jk} + \varepsilon_{ijk} \tag{1}$$

where μ is the general mean, g_i is the effect of the i-th genotype assumed to be independently and normally distributed with a zero mean and a variance of σ_g^2, ρ_j is the effect of the j-th replicate and is assumed to be fixed, β_{jk} is the effect of the k-th block in the j-th

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M. Singh · S Ceccarelli
International Center for Agricultural Research in the Dry Areas (ICARDA), P.O. Box 5466, Aleppo, Syria

replicate which is assumed to be independent and normally distributed with zero mean and variance σ_β^2, and ε_{ijk} values are experimental errors assumed to be independently and normally distributed with zero mean and variance $\sigma_\varepsilon^2 (i = 1,2,\ldots, V; j = 1,2,\ldots, r; k = 1,\ldots, b)$.

A measure of broad-sense heritability of trait Y is the ratio of genetic variance (σ_g^2) to phenotypic variance ($\sigma_g^2 + \sigma_\varepsilon^2$):

$$h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_\varepsilon^2)$$

Model (1) has random effects with three unknown variances σ_β^2, σ_g^2, and σ_ε^2 that require estimation. A method for estimating variance components is the residual (or restricted) maximum likelihood (REML) procedure (Patterson and Thompson 1971). We have employed VCOMP and REML commands of GENSTAT 5 Release 2.2 (GENSTAT 5 Committee 1990) which produces estimates of the variance components as well as the estimated variance-covariance matrix of the estimates. Since σ_β^2 does not enter in the estimation of h^2, its variance or covariance with other estimates is not required. Let $\hat{\sigma}_g^2$ and $\hat{\sigma}_\varepsilon^2$ be REML estimates of σ_g^2 and σ_ε^2 respectively and let their estimated variances [$\widehat{\mathrm{var}}()$] and covariances [$\widehat{\mathrm{cov}}(\,,)$] be denoted by

$$\widehat{\mathrm{var}}(\hat{\sigma}_g^2) = v_{gg}, \widehat{\mathrm{var}}(\hat{\sigma}_\varepsilon^2) = v_{ee} \text{ and } \widehat{\mathrm{cov}}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2) = v_{ge}.$$

Estimate $\widehat{h^2}$ of h^2 is

$$\widehat{h^2} = \hat{\sigma}_g^2/(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2).$$

The quantity $\widehat{h^2}$is not an unbiased estimate of h^2. Estimates of its asymptotic bias (B) and standard error (SE) (derived in brief in the Appendix) are

$$B(\widehat{h^2}) = (1 - \widehat{h^2})^2[(1 - \widehat{h^2})v_{gg} - \widehat{h^2}\, v_{ge}]/(\widehat{h^2}\hat{\sigma}_\varepsilon^4)$$

$$\mathrm{SE}(\widehat{h^2}) = (1 - \widehat{h^2})[(1 - \widehat{h^2})^2 v_{gg} - 2\widehat{h^2}(1 - \widehat{h^2})v_{ge} + \widehat{h^4}\, v_{ee}]^{1/2}/\hat{\sigma}_\varepsilon^2. \quad (3)$$

Multi-environment trials

Let a series of trials with a common set of genotypes be conducted in L environments using the same incomplete block design. The response Y_{ijkl} on trait Y from the i-th line, the j-th replicate, the k-th block in the j-th replicate and the l-th environment can be modelled as

$$Y_{ijkl} = \mu + \rho_{jl} + \beta_{kjl} + g_i + \psi_l + \delta_{il} + \varepsilon_{ijkl} \quad (4)$$

where μ is the general mean, ρ_{jl} is the effect of the j-th replicate in the l-th environment, ψ_l is the effect of the l-th environment, β_{kjl} is the effect of the k-th incomplete block in the j-th replicate of the l-th environment, g_i, is the effect of the i-th genotype, δ_{il} is the interaction between the i-th genotype and the l-th environment and ε_{ijkl} are random errors ($i = 1,2,\ldots V$; $j = 1,2,\ldots, r$; $k = 1,2,\ldots, b$; $l = 1,2\ldots, L$). The quantities μ, ρ_{jl} and ψ_l are assumed to be fixed effects while β_{kjl}, g_i, δ_{il} and ε_{ijkl} are random effects with zero means and variances σ_β^2, σ_g^2, σ_δ^2, and σ_ε^2 respectively. The heritability measure in the case of several environments is defined as

$$h^2 = \sigma_g^2/(\sigma_g^2 + \sigma_\delta^2 + \sigma_\varepsilon^2). \quad (5)$$

We now apply REML to estimate the variance components of model (4) and denote the estimates of σ_g^2, σ_δ^2 and σ_ε^2 by $\hat{\sigma}_g^2$, $\hat{\sigma}_\delta^2$ and $\hat{\sigma}_\varepsilon^2$ respectively, with estimated variances and covariances given by $\widehat{\mathrm{var}}(\hat{\sigma}_g^2) = v_{gg}$, $\widehat{\mathrm{var}}(\hat{\sigma}_\delta^2) = v_{\delta\delta}$, $\widehat{\mathrm{var}}(\hat{\sigma}_\varepsilon^2) = v_{ee}$, $\widehat{\mathrm{cov}}(\hat{\sigma}_g^2, \hat{\sigma}_\delta^2) = v_{g\delta}$, $\widehat{\mathrm{cov}}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2) = v_{ge}$, $\widehat{\mathrm{cov}}(\hat{\sigma}_\delta^2, \hat{\sigma}_\varepsilon^2) = v_{\delta e}$.

The asymptotic bias $B(\widehat{h^2})$ and standard error $\mathrm{SE}(\widehat{h^2})$ are estimated by

$$\hat{B}(\widehat{h^2}) = \widehat{h^2}[v_{gg} - \widehat{h^2}(v_{gg} + v_{ge} + v_{g\delta})]/\hat{\sigma}_g^4$$

$$\mathrm{SE}(\widehat{h^2}) = \widehat{h^2}[v_{gg} + \widehat{h^4} A - 2h^2(v_{gg} + v_{g\delta} + v_{ge})]^{1/2}/\hat{\sigma}_g^2.$$

where $A = v_{gg} + v_{\delta\delta} + v_{ee} + 2(v_{g\delta} + v_{ge} + v_{\delta e})$.

Experimental data

Grain-yield data were collected on yield trials of advanced breeding lines. For illustration, we use yield data (in t/ha) on 25 barley breeding lines (F_6 and F_7) evaluated in 5 × 5 simple lattices conducted in 1992 at one location in Cyprus (Athalassa) and three locations in northern Syria (Tel Hadya, Breda and Bouider). Plot size was 6.0 m^2 (eight rows at 20 cm inter-row spacing, 5 m long). Plots were planted by plot drill and the six central rows were harvested.

Results and discussion

Grain yields were 4.8, 3.7, 1.3 and 1.0 t/ha at Athalassa, Tel Hadya, Breda and Bouider, respectively. Yield differences primarily reflected differences in rainfall. Using the analysis of the simple lattice design, coefficients of variation were 11.2, 17.7, 12.0 and 11.6% in the four locations, respectively, and 11.4, 19.2, 12.7 and 11.6% with the randomized complete block design analysis. For the yield data, the estimates of variance components σ_g^2, σ_δ^2 and σ_ε^2 and their estimated variance-covariance matrix for each environment individually, as well as combined under genotype × environment interaction, are presented in Table 1. The estimates of heritabilities are in Table 2. We have also included in these tables estimates of variance components and heritability when block effects are ignored in order to assess the effectiveness of blocking. GENSTAT 5 Codes to facilitate the required computations can be obtained from the authors.

The high magnitude of biases, ranging from 0.035 to 0.134 indicates that in many cases correction would be worthwhile, although these estimates of bias are themselves large sample approximations. The corrected estimates would be obtained by subtracting the bias from the estimate. The estimates of heritability, when block effects are accounted for, are generally higher than when they are not. In these data sets the differences in the two estimates (i.e., under the incomplete block design and under the complete block design) range from 0.02 to 0.05 (over four locations). When genotype × environment interaction is included, the estimate of heritability and the effectiveness of incomplete blocks are reduced. A comparison of heritabilities based on independent estimates can be performed by computing a weighted sum of squares deviations of these estimates from their weighted mean and comparing it against a chi-square variable, where the weights are the inverse of the square of the standard errors of the estimates.

The relationship between yield level and magnitude of heritability will be examined in a subsequent paper using a much larger data set. However, the data used in this paper suggest that heritability can be largely independent of the yield level at which it is measured.

The situation of estimating heritability on a progeny mean basis is quite frequent in plant breeding. In such cases, models (1) and (4) would require modifying genotypic effects in terms of family effects and progeny effects within families and, therefore, introduce family

Table 1 Estimates of variance components and estimates of their variances and covariances for grain yield (t/ha)

Individual locations

Location	Design	Comp[a]	Estimate	SE	Variance-covariance matrix (× 10⁶) σ_g^2	σ_ε^2
Cyprus	Lattice	σ_g^2	0.23660	0.11770	1 385	
		σ_ε^2	0.2642	0.08677	−3556	7 530
	RCB[b]	σ_g^2	0.2320	0.1189	14 149	
		σ_ε^2	0.3025	0.08734	−3 814	7 628
Tel Hadya	Lattice	σ_g^2	0.1902	0.1324	17 540	
		σ_ε^2	0.3694	0.1225	−3 830	15 010
	RCB	σ_g^2	0.1853	0.1471	21 640	
		σ_ε^2	0.5113	0.1476	−10 890	21 780
Breda	Lattice	σ_g^2	0.03096	0.01312	172.24	
		σ_ε^2	0.0236	0.007795	−27.4	60.76
	RCB	σ_g^2	0.02976	0.01298	168.35	
		σ_ε^2	0.02641	0.007624	−29.06	58.13
Bouider	Lattice	σ_g^2	0.02593	0.009604	92.23	
		σ_ε^2	0.01218	0.004097	−7.64	16.79
	RCB	σ_g^2	0.02644	0.009794	95.92	
		σ_ε^2	0.0136	0.003925	−7.7	15.41

All locations combined under G × E interaction

Design	Comp[a]	Estimate	SE	Variance-covariance matrix (× 10⁶) σ_g^2	σ_δ^2	ρ_ε^2
Lattice	σ_g^2	0.05296	0.02796	781.8		
	σ_δ^2	0.06865	0.03063	−183.8	937.9	
	σ_ε^2	0.1693	0.02784	−0.1	−388.8	774.9
RCB	σ_g^2	0.06001	0.03003	901.9		
	σ_δ^2	0.05831	0.03152	−189.1	993.8	
	σ_ε^2	0.2134	0.03081	< 0.01	−474.5	949

[a] Comp = Variance component

[b] RCB: randomized complete blocks

Table 2 Mean yields (t/ha) and estimates of heritability ($\hat{h}^2$) from individual locations and combined locations

Location	Yield	$\hat{h}^2$	Lattice design SE	Bias	$\hat{h}^2$	RCB[a] design SE	Bias
Athalassa	4.81	0.4724	0.1707	0.0758	0.4340	0.1657	0.0779
Tel Hadya	3.72	0.3399	0.2029	0.1338	0.2660	0.1897	0.1456
Breda	1.28	0.5675	0.1480	0.0533	0.5298	0.1468	0.0566
Bouider	1.01	0.6805	0.1188	0.0351	0.6604	0.1151	0.0356
All locations combined using G × E interaction		0.1820	0.0848	0.0437	0.1809	0.0794	0.0388

[a] RCB = Randomized complete blocks: Athalassa in Cyprus; Tel Hadya, Breda and Bouider in Syria

variance and progeny variance within families in a single trial, while variances of their interactions with environments would be two additional components of variance in the case of multi-locational trials. The estimates of the variance components along with their variance covariance matrix can be obtained using REML and then standard errors using the Taylor series approximation. This technique can be applied to estimate heritability when the trait of interest results from any general unbalanced classification.

Appendix

Asymptotic expression of bias and standard error of a ratio of two random variables

Let $\hat{h}^2$ be the ratio of two random variables N and D. Then, from Kendall and Stuart (1969),

$$\mathrm{Bias}(\hat{h}^2) = [\mathrm{E}(N)/\mathrm{E}(D)]\{\mathrm{var}(N)/[\mathrm{E}(N)]^2 - \mathrm{cov}\,(N,D)/[\mathrm{E}(N)\,\mathrm{E}(D)]\}.$$

$$\mathrm{var}(\widehat{h}^2) = [\mathrm{E}(N)/\mathrm{E}(D)]^2\{\mathrm{var}(N)/[\mathrm{E}(N)]^2 + \mathrm{var}(D)/[\mathrm{E}(D)]^2$$
$$- 2\,\mathrm{cov}(N,D)/[\mathrm{E}(N)\mathrm{E}(D)]\}.$$

(1) In a single trial: $N = \hat{\sigma}_g^2$ and $D = \hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2$. E($x$) can be estimated by x itself ($x = N, D$) while $\mathrm{var}(D) = \mathrm{var}(\hat{\sigma}_g^2) + \mathrm{var}(\hat{\sigma}_\varepsilon^2) + 2\,\mathrm{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2)$, $\mathrm{cov}(N,D) = \mathrm{var}(\hat{\sigma}_g^2) + \mathrm{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2)$ and are available from REML as follows:

$$\hat{\mathrm{var}}(N) = v_{gg}, \hat{\mathrm{var}}(D) = v_{gg} + v_{ee} + 2v_{ge}, \hat{\mathrm{cov}}(D,N) = v_{gg} + v_{ge}.$$

Replacing various parameters in expression of bias [Bias($\widehat{h}^2$)] and variance [var($\widehat{h}^2$)], one gets their estimates. Thus the estimate $B(\widehat{h}^2)$ of the bias is

$$B(\widehat{h}^2) = (N/D)\{\hat{\mathrm{var}}(N)/(\hat{\sigma}_g^2)^2 - \hat{\mathrm{cov}}(N,D)/[(\hat{\sigma}_g^2)(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)]\}$$
$$= \widehat{h}^2\{v_{gg}/\hat{\sigma}_g^4 - (v_{gg} + v_{ge})/[\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)]\}.$$

Now using $\widehat{h}^2 = \hat{\sigma}_g^2/(\hat{\sigma}_g^2 + \hat{\sigma}_e^2)$, we can express $\hat{\sigma}_g^2$ in terms of $\widehat{h}^2$ and $\hat{\sigma}_\varepsilon^2$:

$\hat{\sigma}_g^2 = \widehat{h}^2(1 - \widehat{h}^2)^{-1}\hat{\sigma}_\varepsilon^2$ and $\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2 = (1 - \widehat{h}^2)^{-1}\hat{\sigma}_\varepsilon^2$ and simplify the expression for bias.

$$B(\widehat{h}^2) = \widehat{h}^2[v_{gg}\widehat{h}^{-4}(1 - \widehat{h}^2)^2\hat{\sigma}_\varepsilon^{-4}$$
$$- (v_{gg} + v_{ge})\widehat{h}^{-2}(1 - \widehat{h}^2)\hat{\sigma}_\varepsilon^{-2}(1 - \widehat{h}^2)\hat{\sigma}_\varepsilon^{-2}]$$
$$= (1 - \widehat{h}^2)^2[v_{gg}\widehat{h}^{-2} - (v_{gg} + v_{ge})]\hat{\sigma}_\varepsilon^4$$
$$= (1 - \widehat{h}^2)^2[v_{gg}(1 - \widehat{h}^2) - \widehat{h}^2 v_{ge}]/(\widehat{h}^2\hat{\sigma}_\varepsilon^4).$$

Similarly

$$\hat{\mathrm{var}}(\widehat{h}^2) = [N/D]^2\{\hat{\mathrm{var}}(N)/\hat{\sigma}_g^4 + \hat{\mathrm{var}}(D)/(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)^2$$
$$- 2\,\hat{\mathrm{cov}}(N,D)/[\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)]\}$$
$$= \widehat{h}^4\{v_{gg}/\hat{\sigma}_g^4 + (v_{gg} + v_{ee} + 2v_{ge})/(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)^2$$
$$- 2(v_{gg} + v_{ge})/[\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\varepsilon^2)]\}.$$

Using the above expression for $\hat{\sigma}_g^2$ in terms of $\widehat{h}^2$ and $\hat{\sigma}_\varepsilon^2$ we get

$$\hat{\mathrm{var}}(\widehat{h}^2) = \widehat{h}^4[v_{gg}\widehat{h}^{-4}(1 - \widehat{h}^2)^2\hat{\sigma}_\varepsilon^{-4} + (v_{gg} + v_{ee} + 2v_{ge})$$
$$\times (1 - \widehat{h}^2)^2\hat{\sigma}_\varepsilon^{-4} - 2(v_{gg} + v_{ge})\widehat{h}^{-2}(1 - \widehat{h}^2)^2\hat{\sigma}_\varepsilon^{-4}]$$
$$= (1 - \widehat{h}^2)^2[v_{gg} + (v_{gg} + v_{ee} + 2v_{ge})\widehat{h}^4 - 2(v_{gg} + v_{ge})\widehat{h}^2]/\hat{\sigma}_\varepsilon^4.$$

Collecting the terms of v_{gg}, v_{ge}, and v_{ee}, we get

$$\hat{\mathrm{var}}(\widehat{h}^2) = (1 - \widehat{h}^2)^2[(1 - \widehat{h}^2)^2 v_{gg} - 2\widehat{h}^2(1 - \widehat{h}^2)v_{ge} + \widehat{h}^4 v_{ee}]/\hat{\sigma}_\varepsilon^4.$$

(2) In a multi-environment trial: $N = \hat{\sigma}_g^2, D = \hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2$

$$\mathrm{var}(D) = \mathrm{var}(\hat{\sigma}_g^2) + \mathrm{var}(\hat{\sigma}_\delta^2) + \mathrm{var}(\hat{\sigma}_\varepsilon^2) + 2\mathrm{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\delta^2)$$
$$+ 2\mathrm{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2) + 2\mathrm{cov}(\hat{\sigma}_\delta^2, \hat{\sigma}_\varepsilon^2) \text{ and}$$

$$\mathrm{cov}(N,D) = \mathrm{var}(\hat{\sigma}_g^2) + \mathrm{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\delta^2) + \mathrm{cov}(\hat{\sigma}_g^2, \hat{\sigma}_\varepsilon^2).$$

These estimates of these variances and covariances are then available from REML:

$$\hat{\mathrm{var}}(N) = v_{gg}, \hat{\mathrm{var}}(D) = v_{gg} + v_{\delta\delta} + v_{ee} + 2(v_{g\delta} + v_{ge} + v_{\delta e}) = A, \text{ and}$$

$$\hat{\mathrm{cov}}(N,D) = v_{gg} + v_{g\delta} + v_{ge}.$$

The estimate $B(\widehat{h}^2)$ of the bias is

$$B(\widehat{h}^2) = (N/D)\{\hat{\mathrm{var}}(N)/(\hat{\sigma}_g^2)^2 - \hat{\mathrm{cov}}(N,D)/[(\hat{\sigma}_g^2)(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)]\}$$
$$= \widehat{h}^2\{v_{gg}/\hat{\sigma}_g^4 - (v_{gg} + v_{ge} + v_{ee})/[\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)]\}.$$

Using $\widehat{h}^2 = \hat{\sigma}_g^2/(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)$, we can write $\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2 = \hat{\sigma}_g^2/\widehat{h}^2$ and on substitution we get

$$B(\widehat{h}^2) = \widehat{h}^2[v_{gg} - \widehat{h}^2(v_{gg} + v_{ge} + v_{ee})]/\hat{\sigma}_g^4.$$

Further,

$$\hat{\mathrm{var}}(\widehat{h}^2) = [N/D]^2\{\hat{\mathrm{var}}(N)/\hat{\sigma}_g^4 + \hat{\mathrm{var}}(\mathrm{D})/(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)^2$$
$$- 2\,\hat{\mathrm{cov}}(N,D)/[\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)]\}$$
$$= \widehat{h}^4\{v_{gg}/\hat{\sigma}_g^4 + A/(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)^2$$
$$- 2(v_{gg} + v_{g\delta} + v_{ge})/[\hat{\sigma}_g^2(\hat{\sigma}_g^2 + \hat{\sigma}_\delta^2 + \hat{\sigma}_\varepsilon^2)]\}$$
$$= \widehat{h}^4[v_{gg} + A\,\widehat{h}^4 - 2\widehat{h}^2(v_{gg} + v_{g\delta} + v_{ge})]/\hat{\sigma}_g^4.$$

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