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Parametric relationships between genotype × environment interaction and genetic correlation when two environments are involved

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Summary. Parametric relationships between the genotype × environment interaction and the genetic correlation of the same attribute measured in two different environments are derived. It is shown that the criticism by Fernando et al. (1984) of Yamada's method (1962) in the case of unbalanced data is irrelevant.

Key words: G × E interaction – Genetic correlation – Parametric relationships

Introduction

Falconer (1952) first proposed that for the purpose of quantitative genetic analysis, one trait measured in two environments may be considered two different traits; thus, the genotype × environment interaction can be incorporated into a prediction equation as the correlated genetic response in the other environment. Robertson (1959) derived the relationship between these parameters theoretically, with the condition of the same heritability in the two environments. Dickerson (1962) presented refinements in estimation formulae for the case in which the heritabilities differed among environments, and Yamada (1962) presented theory and formulae for dealing with traits with a greater variety of statistical properties than earlier works. The method has been widely used in animal breeding research (Hohenboken and Brinks 1971; Towelde 1981; Eisen and Saxton 1983; Tess et al. 1984; Mathur 1985). However, Fernando et al. (1984) have criticised Yamada's method, stating "this method gives biased estimates of genetic covariances unless the traits have identical genetic and residual variances", and proposed an alternative procedure to obtain an unbiased estimator of the covariance, when data are unbalanced.

The objectives of this paper are to re-examine in a more critical manner the genotype × environment interaction when two environments are involved, to present relationships among the genetic parameters involved and also to clarify the point of issue raised by Fernando et al. (1984). Nevertheless, the argument primarily concerns the concept of the parametric relationship between the interaction and genetic correlation rather than the estimation procedures of unbiased genetic variances and covariances.

Theory

In the earlier paper, Yamada (1962) attempted to make equivalence of the second moments of the variables being analysed under the two-way analysis of variance model with those under the one-way analyses of variance and covariance model, by expressing expected mean squares in the two-way ANOVA in terms of variance and covariance components in the one-way ANOVA and ANOCOVA. All derivations were made for balanced data.

Fernando et al. (1984) claimed that the direct application of Yamada's method would give biased estimates of the genetic covariance if the data were unbalanced. The point in dispute between these papers has been misunderstood by some readers because the notations used were so different. Therefore, in this paper we shall follow the same notations adopted by Fernando et al. (1984) to clarify the point at issue.

Model A (one-way analysis of variance model) for trait *i:*

$$y_{ijk}=\mu_i+u_{ij}+e_{ijk}\,, \qquad (1)$$
$$i=1 \text{ or } 2\,; \quad j=1,\dots,s\,; \quad k=1,\dots,n_{ij}\,.$$

Using matrix notation, this model can be rewritten as:

$$\mathbf{y}=\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{1}\mu_1\\ \mathbf{1}\mu_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_1 & 0\\ 0 & \mathbf{Z}_2\end{bmatrix}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix}+\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix} \qquad (1')$$

where $\mathbf{y}_i$ is an $n_i \times 1$ vector of data for trait i, $i=1$ or 2, and n_i is the number of observations for the trait i; μ_i is the expected value of trait i and $\mathbf{1}_i$ is an $n_i \times 1$ vector of all ones; $\mathbf{u}_i$ is a vector of genetic group effects for trait i; the order of $\mathbf{u}_1$ equals the order of $\mathbf{u}_2$; $\mathbf{Z}_i$ is a known matrix relating $\mathbf{u}_i$ to $\mathbf{y}_i$, and $\mathbf{e}_i$ is an $n_i \times 1$ vector of residuals for trait i. Equation (1′) is the structural model for the variance-component model.

Assumptions for Model A are:

$$\mathrm{E}(\mathbf{y}_i)=\mathbf{1}_i\mu_i,\quad \mathrm{E}(\mathbf{u}_i)=\mathbf{0},\quad \mathrm{E}(\mathbf{e}_i)=\mathbf{0},$$

$$\mathrm{Var}\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix}=\begin{bmatrix}\mathbf{I}\sigma_1^2 & \mathbf{I}\sigma_{12}\\ \mathbf{I}\sigma_{12} & \mathbf{I}\sigma_2^2\end{bmatrix},\quad \mathrm{Var}\begin{bmatrix}\mathbf{e}_1\\ \mathbf{e}_2\end{bmatrix}=\begin{bmatrix}\mathbf{I}_1\sigma_{e_1}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\sigma_{e_2}^2\end{bmatrix},$$

$$\mathrm{Cov}(\mathbf{u}_i,\mathbf{e}_j)=\mathbf{0}$$

where $\mathbf{I}$, $\mathbf{I}_1$ and $\mathbf{I}_2$ are identity matrices of appropriate order. Consequently, we obtain

$$\mathrm{Var}\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1'\sigma_1^2 & \mathbf{Z}_1\mathbf{Z}_2'\sigma_{12}\\ \mathbf{Z}_2\mathbf{Z}_1'\sigma_{12} & \mathbf{Z}_2\mathbf{Z}_2'\sigma_2^2\end{bmatrix}+\begin{bmatrix}\mathbf{I}_1\sigma_{e_1}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_1\sigma_{e_2}^2\end{bmatrix} \qquad (2)$$

which is identical to equation (7) of Fernando et al. (1984). The variances and covariance of $\mathbf{y}_i$'s are thus

$$\mathrm{Var}(\mathbf{y}_1)\quad=\mathbf{Z}_1\mathbf{Z}_1'\sigma_1^2+\mathbf{I}_1\sigma_{e_1}^2, \qquad (2a)$$

$$\mathrm{Var}(\mathbf{y}_2)\quad=\mathbf{Z}_2\mathbf{Z}_2'\sigma_2^2+\mathbf{I}_2\sigma_{e_2}^2, \qquad (2b)$$

$$\mathrm{Cov}(\mathbf{y}_1,\mathbf{y}_2)=\mathbf{Z}_1\mathbf{Z}_2'\sigma_{12}. \qquad (2c)$$

The parameter set of Model A is therefore $[\sigma_1^2, \sigma_{12}, \sigma_2^2, \sigma_{e_1}^2, \sigma_{e_2}^2]$.

Next, describe the data with the two-way analysis of variance model (Model B) in which the same attribute is measured in two *fixed* environments.

$$y_{ijk}=\mu_i+u_{G_j}+u_{I_{ij}}+e_{ijk}, \qquad (3)$$

$$i=1 \text{ and } 2;\quad j=1,\dots,s;\quad k=1,\dots,n_{ij}.$$

Using matrix notation, this model can be rewritten as:

$$\mathbf{y}=\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{1}\mu_1\\ \mathbf{1}\mu_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_1\\ \mathbf{Z}_2\end{bmatrix}\mathbf{u}_G+\begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\mathbf{u}_I+\mathbf{e} \qquad (3')$$

where $\mathbf{y}_i$, μ_i, $\mathbf{I}_i$ and $\mathbf{Z}_i$ are as defined earlier; $\mathbf{u}_G$ is a vector of genetic-group effects averaged over environments; $\mathbf{u}_I$ is a vector of genotype × environment interaction effects, and $\mathbf{e}$ is a vector of residual effects. Expectations and covariance matrices of random variables in Model B are:

$$\mathrm{E}(\mathbf{y}_i)=\mathbf{1}_i\mu_i,\quad \mathrm{E}(\mathbf{u}_G)=\mathbf{0},\quad \mathrm{E}(\mathbf{u}_I)=\mathbf{0},\quad \mathrm{E}(\mathbf{e})=\mathbf{0},$$

$$\mathrm{Var}(\mathbf{u}_G)=\mathbf{I}\sigma_G^2,\quad \mathrm{Var}(\mathbf{u}_I)=\mathbf{I}\sigma_I^2,\quad \mathrm{Cov}(\mathbf{u}_G,\mathbf{u}_I)=0,$$

$$\mathrm{Var}(\mathbf{e})=\mathbf{I}\sigma_e^2.$$

The parameter set in Model B is therefore $[\sigma_G^2, \sigma_I^2, \sigma_e^2]$. Equation (3′) is the same as Eq. (8) of Fernando et al. (1984).

Since we are dealing with two traits differing both in genetic and environmental variances in principle, equation (3′) is not appropriate to find the relationships of variance and covariance components between the Models A and B. The adequate model (designated as Model B′) should be:

$$\mathbf{y}=\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{1}\mu_1\\ \mathbf{1}\mu_2\end{bmatrix}+\begin{bmatrix}\mathbf{Z}_1\\ \mathbf{Z}_2\end{bmatrix}\mathbf{u}_G+\begin{bmatrix}\mathbf{Z}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\end{bmatrix}\mathbf{u}_I+\begin{bmatrix}\boldsymbol{\varepsilon}_1\\ \boldsymbol{\varepsilon}_2\end{bmatrix}. \qquad (4)$$

Expectations and covariance matrices of random variables in Model B′ are:

$$\mathrm{E}(\mathbf{y}_i)=\mathbf{1}_i\mu_i,\quad \mathrm{E}(\mathbf{u}_G)=\mathbf{0},\quad \mathrm{E}(\mathbf{u}_I)=\mathbf{0},\quad \mathrm{E}(\boldsymbol{\varepsilon}_i)=\mathbf{0}$$

$$\mathrm{Var}(\mathbf{u}_G)=\mathbf{I}\sigma_G^2,\quad \mathrm{Var}(\mathbf{u}_I)=\mathbf{I}\sigma_I^2,$$

$$\mathrm{Var}\begin{bmatrix}\boldsymbol{\varepsilon}_1\\ \boldsymbol{\varepsilon}_2\end{bmatrix}=\begin{bmatrix}\mathbf{I}_1\sigma_{\varepsilon_1}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\sigma_{\varepsilon_2}^2\end{bmatrix},$$

$$\mathrm{Cov}(\mathbf{u}_G,\boldsymbol{\varepsilon}_i)=\mathbf{0},\quad \mathrm{Cov}(\mathbf{u}_I,\boldsymbol{\varepsilon}_i)=\mathbf{0},$$

$$\mathrm{Cov}(\mathbf{u}_G,\mathbf{u}_I)=[\mathbf{I}\quad -\mathbf{I}]\,\sigma_{GI}.$$

The existence of this covariance between $\mathbf{u}_G$ and $\mathbf{u}_I$ is obvious if we consider the variance within a specific environment ($i=1$ *or* 2). Then, we obtain

$$\mathrm{Var}\begin{bmatrix}\mathbf{y}_1\\ \mathbf{y}_2\end{bmatrix}=\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1' & \mathbf{Z}_1\mathbf{Z}_2'\\ \mathbf{Z}_2\mathbf{Z}_1' & \mathbf{Z}_2\mathbf{Z}_2'\end{bmatrix}\sigma_G^2+\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1' & \mathbf{0}\\ \mathbf{0} & \mathbf{Z}_2\mathbf{Z}_2'\end{bmatrix}\sigma_I^2$$
$$+2\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1' & \mathbf{0}\\ \mathbf{0} & -\mathbf{Z}_2\mathbf{Z}_2'\end{bmatrix}\sigma_{GI}+\begin{bmatrix}\mathbf{I}_1\sigma_{\varepsilon_1}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\sigma_{\varepsilon_2}^2\end{bmatrix}. \qquad (5)$$

The variances and covariance of $\mathbf{y}_i$'s are thus

$$\mathrm{Var}(\mathbf{y}_1)=\mathbf{Z}_1\mathbf{Z}_1'(\sigma_G^2+\sigma_I^2+2\sigma_{GI})+\mathbf{I}_1\sigma_{\varepsilon_1}^2, \qquad (5a)$$

$$\mathrm{Var}(\mathbf{y}_2)=\mathbf{Z}_2\mathbf{Z}_2'(\sigma_G^2+\sigma_I^2-2\sigma_{GI})+\mathbf{I}_2\sigma_{\varepsilon_2}^2, \qquad (5b)$$

$$\mathrm{Cov}(\mathbf{y}_1,\mathbf{y}_2)=\mathbf{Z}_1\mathbf{Z}_2'\sigma_G^2. \qquad (5c)$$

The parameter set of Model B′ is $[\sigma_G^2, \sigma_I^2, \sigma_{GI}, \sigma_{\varepsilon_1}^2, \sigma_{\varepsilon_2}^2]$.

Next we find the relationships between the parameter sets of the two models, A and B′, instead of A and B, which was made by Fernando et al. (1984).

Since Model A and B′ are equivalent, Eqs. (2) and (5), or (2a)–(2c) and (5a)–(5c), should always be identical irrespective of the choice of $\mathbf{Z}_1$ or $\mathbf{Z}_2$. Thus, we have

$$\sigma_1^2\ =\sigma_G^2+\sigma_I^2+2\sigma_{GI}, \qquad (6a)$$

$$\sigma_2^2\ =\sigma_G^2+\sigma_I^2-2\sigma_{GI}, \qquad (6b)$$

$$\sigma_{12}=\sigma_G^2, \qquad (6c)$$

$$\sigma_{e_1}^2\ =\sigma_{\varepsilon_1}^2, \qquad (6d)$$

$$\sigma_{e_2}^2\ =\sigma_{\varepsilon_2}^2. \qquad (6e)$$

The variables given above are all parameters, so that those values should not be affected with balanced or unbalanced data.

Adding (6a) and (6b) gives

$$\sigma_1^2+\sigma_2^2=2(\sigma_G^2+\sigma_I^2)\,. \tag{7}$$

Substituting (6c) into (7) gives

$$\begin{aligned}\sigma_I^2&=\tfrac{1}{2}(\sigma_1^2+\sigma_2^2)-\sigma_{12}\\&=\tfrac{1}{2}(\sigma_1-\sigma_2)^2+\sigma_1\,\sigma_2(1-r_G)\,.\end{aligned} \tag{8}$$

Equation (8) is essentially the relationship of genetic parameters in Models A and B′. The same relationship was given by Robertson (1959) and Yamada (1962) from different approaches.

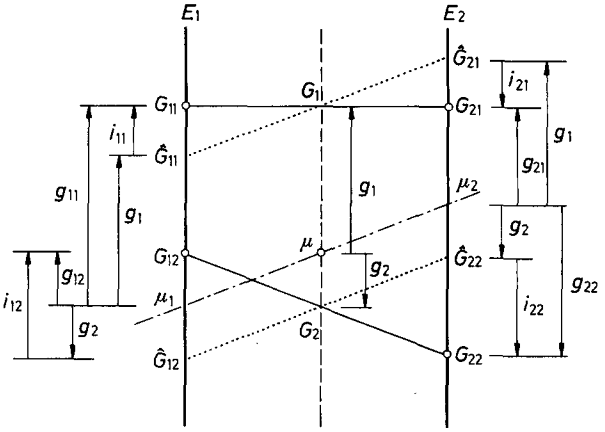

Fig. 1. Relationships between randomly sampled two genetic group effects and the interaction effects in two environments; μ = overall population mean, E_i = the environmental scale and u_i = the average in the i-th environment, G_j = the j-th genetic group and g_j = its effect, G_{ij} = the j-th genetic group in the i-th environment and g_{ij} = its effect, $\hat{G}_{ij}$ = the expected value of the j-th genetic-group in the i-th environment, $G_{ij}-\hat{G}_{ij}$ = the interaction associated with the j-th group in the i-th environment, i_{ij} = its effect. The sign of a vector (effect) is indicated by the direction of the *arrow*, being positive for up, while negative for down. Thus, $\mathrm{Cov}(G_j, I_{ij})=(g_1\times i_{11})+(g_2\times i_{12})+(g_1\times i_{21})+(g_2\times i_{22})=0$, because $i_{ij}=-i_{2j}$. On the other hand, taking the covariance within one environment, $\mathrm{Cov}(G_j, I_{1j})=(g_1\times i_{11})+(g_2\times i_{12})\neq 0$ and $\mathrm{Cov}(G_j, I_{2j})=(g_1\times i_{21})+(g_2\times i_{22})\neq 0$

Discussion

Fernando et al. (1984) stated that Yamada's method for estimating genetic correlation would lead to an unbiased estimate only if $\sigma_1^2=\sigma_2^2$ and $\sigma_{e_1}^2=\sigma_{e_2}^2$ and they presented alternative estimators. However, in deriving the relationship of the parameters between the two models, they may have been unaware of the existence of the covariance between the genetic-group effect and the interaction effect, and this would explain their erroneous claims for equal genetic and residual variances. The covariance term, σ_{GI}, certainly exists as is illustrated in Fig. 1. This was shown previously by Eisen et al. (1963). It does not exist in an ordinary analysis of variance in the two-way model (Model B). However, when one considers the variance structure of the attribute in a particular environment ($i=1$ or 2, instead of 1 and 2) within a framework of the two-way layout, this covariance becomes abvious. Inspection of (6a) and (6b) gives $\sigma_{GI}=\frac{1}{4}(\sigma_1^2-\sigma_2^2)$. In other words, the covariance between and I emerges as a result of unequal genetic variances in the two environments. In addition to the above, Fernando et al. (1984) set

$$\begin{bmatrix}\mathbf{I}_1 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\end{bmatrix}\sigma_e^2=\begin{bmatrix}\mathbf{I}_1\,\sigma_{e_1}^2 & \mathbf{0}\\ \mathbf{0} & \mathbf{I}_2\,\sigma_{e_2}^2\end{bmatrix}$$

which automatically leads to $\sigma_{e_1}^2=\sigma_{e_2}^2=\sigma_e^2$. In our derivation, these two points mentioned above were taken into consideration. As mentioned in the original paper (Yamada 1962, p 504), the assumption of homogeneous error variances in two environments was disregarded as a matter of convenience, although it is essential to use Model B.

As to the formula for estimating the genetic correlation between the two traits suggested by Yamada (1962), Fernando et al. (1984) claimed that the σ_G^2 would be a biased estimator of σ_{12} unless $\sigma_1^2=\sigma_2^2$ and $\sigma_{e_1}^2=\sigma_{e_2}^2$, and the "adjusted" denominator yielded a biased estimator of $\sigma_1\,\sigma_2$. Thus they concluded that Yamada's method should not be used with unbalanced data. Nevertheless, the above statements are not relevant, because $\sigma_{12}=\sigma_G$ in Eq. (6c) is the relationship between parameters rather than the relationship between estimators. Thus, they should not be influenced by sampling or unequal subclass numbers.

Let us look at Yamada's method from another angle. His method assumed only balanced data and the covariance between G and I was not assumed either. In this paper, we have obtained the relationships between the parameters by a direct comparison of variances between two models, while Yamada (1962) obtained those from the comparison of expected mean squares in the two models. Furthermore, the notations used were so different that the derivations made by him look inconsistent with the present one. However, as far as balanced data are concerned, the two methods are identical to each other (see Appendix).

It is worthwhile to note that the intra-class correlation, $r'_G=\sigma_G^2/(\sigma_G^2+\sigma_I^2)$, gives sufficient information as to the association of the ranking of genetic-group means between two or more environments, because r'_G is the lower limit of the genetic correlation, r_G, as shown below:

$$r_G=\frac{\sigma_{12}}{\sigma_1\sigma_2}=\frac{\sigma_G^2}{\sqrt{\sigma_G^2+\sigma_I^2+2\sigma_{GI}}\sqrt{\sigma_G^2+\sigma_I^2-2\sigma_{GI}}}$$
$$=\frac{\sigma_G^2}{\sqrt{(\sigma_G^2+\sigma_I^2)^2-4\sigma_{GI}^2}}$$
$$\geqq\frac{\sigma_G^2}{\sigma_G^2+\sigma_I^2}=r'_G$$

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Appendix

Using the same model and notations, we re-evaluated Yamada's method (1962). We adopted similar presentations to those of Fernando et al. (1984), so that their criticism could be easily understood.

First, rewrite Model B′ as:

$$\mathbf{y}=\mathbf{X}_1\boldsymbol{\beta}+\mathbf{X}_2\mathbf{u}_G+\mathbf{X}_3\mathbf{u}_I+\boldsymbol{\varepsilon}$$

where

$$\mathbf{X}_1=\begin{bmatrix}\mathbf{1}&\mathbf{0}\\\mathbf{0}&\mathbf{1}\end{bmatrix},\quad \mathbf{X}_2=\begin{bmatrix}\mathbf{Z}_1\\\mathbf{Z}_2\end{bmatrix},\quad \mathbf{X}_3=\begin{bmatrix}\mathbf{Z}_1&\mathbf{0}\\\mathbf{0}&\mathbf{Z}_2\end{bmatrix},$$

$$\boldsymbol{\beta}=\begin{bmatrix}\mu_1\\\mu_2\end{bmatrix},\quad \boldsymbol{\varepsilon}=\begin{bmatrix}\boldsymbol{\varepsilon}_1\\\boldsymbol{\varepsilon}_2\end{bmatrix}.$$

Let $\mathbf{W}_1=\mathbf{X}_1$, $\mathbf{W}_2=[\mathbf{X}_1\ \ \mathbf{X}_2]$, $\mathbf{W}_3=[\mathbf{X}_1\ \ \mathbf{X}_2\ \ \mathbf{X}_3]$. Thus the reductions in the sum of squares can be written as:

$$\mathrm{R}(\boldsymbol{\beta})=\mathbf{y}'\mathbf{W}_1(\mathbf{W}_1'\mathbf{W}_1)^-\mathbf{W}_1'\mathbf{y},$$

$$\mathrm{R}(\boldsymbol{\beta},\mathbf{u}_G)=\mathbf{y}'\mathbf{W}_2(\mathbf{W}_2'\mathbf{W}_2)^-\mathbf{W}_2'\mathbf{y},$$

$$\mathrm{R}(\boldsymbol{\beta},\mathbf{u}_G,\mathbf{u}_I)=\mathbf{y}'\mathbf{W}_3(\mathbf{W}_3'\mathbf{W}_3)^-\mathbf{W}_3'\mathbf{y}.$$

The expected values of the quadratic forms shown above are

$$\mathrm{E}(\mathbf{y}'\mathbf{Q}_i\mathbf{y})=\mathrm{tr}[\mathbf{Q}_i\,\mathrm{Var}(\mathbf{y})]+\mathrm{E}(\mathbf{y}')\mathbf{Q}_i\mathrm{E}(\mathbf{y})\qquad\text{(A1)}$$

in which $\mathbf{Q}_i=\mathbf{W}_i(\mathbf{W}_i'\mathbf{W}_i)^-\mathbf{W}_i'(i=1,2,3)$.

Substituting (5) into (A1), we can evaluate a reduction in the sum of squares in Model B′, i.e.,

$$\mathrm{E}(\mathbf{y}'\mathbf{Q}_i\mathbf{y})=\mathrm{tr}\,\mathbf{Q}_i\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1'&\mathbf{Z}_1\mathbf{Z}_2'\\\mathbf{Z}_2\mathbf{Z}_1'&\mathbf{Z}_2\mathbf{Z}_2'\end{bmatrix}\sigma_G^2+\mathrm{tr}\,\mathbf{Q}_i\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1'&\mathbf{0}\\\mathbf{0}&\mathbf{Z}_2\mathbf{Z}_2'\end{bmatrix}\sigma_I^2$$
$$+2\,\mathrm{tr}\,\mathbf{Q}_i\begin{bmatrix}\mathbf{Z}_1\mathbf{Z}_1'&\mathbf{0}\\\mathbf{0}&\mathbf{Z}_2\mathbf{Z}_2'\end{bmatrix}\sigma_{GI}+\mathrm{tr}\,\mathbf{Q}_i\begin{bmatrix}\mathbf{I}\sigma_{\varepsilon_2}^2&\mathbf{0}\\\mathbf{0}&\mathbf{I}\sigma_{\varepsilon_2}^2\end{bmatrix}$$
$$+\boldsymbol{\beta}'\mathbf{X}_1'\mathbf{X}_1\boldsymbol{\beta}.\qquad\text{(A2)}$$

Expressing

$$\mathbf{Q}_i=\begin{bmatrix}\mathbf{Q}_{i_{11}}&\mathbf{Q}_{i_{12}}\\\mathbf{Q}_{i_{12}}'&\mathbf{Q}_{i_{22}}\end{bmatrix},$$

Eq. (A2) can be expressed as:

$$\mathrm{E}(\mathbf{y}'\mathbf{Q}_i\mathbf{y})=[\mathrm{tr}(\mathbf{Q}_{i_{11}}\mathbf{Z}_1\mathbf{Z}_1')+2\,\mathrm{tr}(\mathbf{Q}_{i_{12}}\mathbf{Z}_2\mathbf{Z}_1')+\mathrm{tr}(\mathbf{Q}_{i_{22}}\mathbf{Z}_2\mathbf{Z}_2')]\sigma_G^2$$
$$+[tr(\mathbf{Q}_{i_{11}}\mathbf{Z}_1\mathbf{Z}_1')+\mathrm{tr}(\mathbf{Q}_{i_{22}}\mathbf{Z}_2\mathbf{Z}_2')]\sigma_I^2$$
$$+2[\mathrm{tr}(\mathbf{Q}_{i_{11}}\mathbf{Z}_1\mathbf{Z}_1')-\mathrm{tr}(\mathbf{Q}_{i_{22}}\mathbf{Z}_2\mathbf{Z}_2')]\sigma_{GI}$$
$$+\mathrm{tr}\,\mathbf{Q}_{i_{11}}\sigma_{\varepsilon_1}^2+\mathrm{tr}\,\mathbf{Q}_{i_{22}}\sigma_{\varepsilon_2}^2+\boldsymbol{\beta}'\mathbf{X}_1'\mathbf{X}_1\boldsymbol{\beta}.\qquad\text{(A3)}$$

For balanced data, $\mathbf{Z}_1=\mathbf{Z}_2$ and $\mathbf{Q}_{i_{11}}=\mathbf{Q}_{i_{22}}$, and thus Eq. (A3) is:

$$\mathrm{E}(\mathbf{y}'\mathbf{Q}_i\mathbf{y})=2\,\mathrm{tr}[\mathbf{Q}_{i_{11}}+\mathbf{Q}_{i_{12}})\mathbf{Z}_1\mathbf{Z}_1']\sigma_G^2+2\,\mathrm{tr}(\mathbf{Q}_{i_{11}}\mathbf{Z}_1\mathbf{Z}_1')\sigma_I^2$$
$$+\mathrm{tr}\,\mathbf{Q}_{i_{11}}(\sigma_{\varepsilon_1}^2+\sigma_{\varepsilon_2}^2)+\boldsymbol{\beta}'\mathbf{X}_1'\mathbf{X}_1\boldsymbol{\beta}.\qquad\text{(A3′)}$$

It is worth noting, and to our surprise also, that the expected value of the reduction in the sum of squares for balanced data does not include the term σ_{GI}. From Eq. (A3′), the expected sums of squares for $\mathbf{u}_G$, $\mathbf{u}_I$ and $\boldsymbol{\varepsilon}$ are expressed as:

$$\begin{bmatrix}\mathrm{E}[\mathrm{R}(\boldsymbol{\beta},\mathbf{u}_G)-\mathrm{R}(\boldsymbol{\beta})]\\\mathrm{E}[\mathrm{R}(\boldsymbol{\beta},\mathbf{u}_G,\mathbf{u}_I)-\mathrm{R}(\boldsymbol{\beta},\mathbf{u}_G)]\\\mathrm{E}[\mathbf{y}'\mathbf{y}-\mathrm{R}(\boldsymbol{\beta},\mathbf{u}_G,\mathbf{u}_I)]\end{bmatrix}=\begin{bmatrix}2\,\mathrm{tr}[(\mathbf{Q}_{2_{11}}+\mathbf{Q}_{2_{12}}-\mathbf{Q}_{1_{11}}-\mathbf{Q}_{1_{12}})\mathbf{Z}_1\mathbf{Z}_1']&2\,\mathrm{tr}[(\mathbf{Q}_{2_{11}}-\mathbf{Q}_{1_{11}})\mathbf{Z}_1\mathbf{Z}_1']&2\,\mathrm{tr}(\mathbf{Q}_{2_{11}}-\mathbf{Q}_{1_{11}})\\2\,\mathrm{tr}[(\mathbf{Q}_{3_{11}}+\mathbf{Q}_{3_{12}}-\mathbf{Q}_{2_{11}}-\mathbf{Q}_{2_{12}})\mathbf{Z}_1\mathbf{Z}_1']&2\,\mathrm{tr}[(\mathbf{Q}_{3_{11}}-\mathbf{Q}_{2_{11}})\mathbf{Z}_1\mathbf{Z}_1']&2\,\mathrm{tr}(\mathbf{Q}_{3_{11}}-\mathbf{Q}_{2_{11}})\\2\,\mathrm{tr}[(\mathbf{I}-\mathbf{Q}_{3_{11}}-\mathbf{Q}_{3_{12}})\mathbf{Z}_1\mathbf{Z}_1']&2\,\mathrm{tr}[(\mathbf{I}-\mathbf{Q}_{3_{11}})\mathbf{Z}_1\mathbf{Z}_1']&2\,\mathrm{tr}(\mathbf{I}-\mathbf{Q}_{3_{11}})\end{bmatrix}\begin{bmatrix}\sigma_G^2\\\sigma_I^2\\\frac{1}{2}(\sigma_{\varepsilon_1}^2+\sigma_{\varepsilon_1}^2)\end{bmatrix}.$$

Let us assume two environments, *s* genetic-groups and *n* individuals per group in each environment, then the right hand side of the above equation reduces to the following:

$$=\begin{bmatrix}2n(s-1)&n(s-1)&s-1\\0&n(s-1)&s-1\\0&0&2s(n-1)\end{bmatrix}\begin{bmatrix}\sigma_G^2\\\sigma_I^2\\\frac{1}{2}(\sigma_{\varepsilon_1}^2+\sigma_{\varepsilon_2}^2)\end{bmatrix}.\qquad\text{(A4)}$$

The expected values of the reductions in the sum of squares in Model A can be obtained by substituting Eq. (2) into (A1). Namely,

$$\mathrm{E}(\mathbf{y}'\mathbf{Q}_i\mathbf{y})=\mathrm{tr}(\mathbf{Q}_{i_{11}}\mathbf{Z}_1\mathbf{Z}_1')\sigma_1^2+2\,\mathrm{tr}(\mathbf{Q}_{i_{12}}\mathbf{Z}_2\mathbf{Z}_1')\sigma_{12}$$
$$+\mathrm{tr}(\mathbf{Q}_{i_{22}}\mathbf{Z}_2\mathbf{Z}_2')\sigma_2^2+\mathrm{tr}\,\mathbf{Q}_{i_{11}}\sigma_{e_1}^2+\mathrm{tr}\,\mathbf{Q}_{i_{22}}\sigma_{e_2}^2$$
$$+\boldsymbol{\beta}'\mathbf{X}_1'\mathbf{X}_1\boldsymbol{\beta}.$$

Again, we assume balanced data, and substitute $\mathbf{Z}_1=\mathbf{Z}_2$ and $\mathbf{Q}_{i_{11}}=\mathbf{Q}_{i_{22}}$, thus,

$$\mathrm{E}(\mathbf{y}'\mathbf{Q}_i\mathbf{y})=\mathrm{tr}(\mathbf{Q}_{i_{11}}\mathbf{Z}_1\mathbf{Z}_1')(\sigma_1^2+\sigma_I^2)+2\,\mathrm{tr}(\mathbf{Q}_{i_{12}}\mathbf{Z}_1\mathbf{Z}_2')\sigma_{12}$$
$$+\mathrm{tr}\,\mathbf{Q}_{i_{11}}(\sigma_{e_1}^2+\sigma_{e_2}^2)+\boldsymbol{\beta}'\mathbf{X}_1'\mathbf{X}_1\boldsymbol{\beta}.\qquad\text{(A5)}$$

Consequently, the expected sums of squares in Model A are

$$\begin{bmatrix} \mathrm{E}[\mathrm{R}(\boldsymbol{\beta}, \mathbf{u}_G) - \mathrm{R}(\boldsymbol{\beta})] \\ \mathrm{E}[\mathrm{R}(\boldsymbol{\beta}, \mathbf{u}_G, \mathbf{u}_I) - \mathrm{R}(\beta, \mathbf{u}_G)] \\ \mathrm{E}[\mathbf{y}'\mathbf{y} - \mathrm{R}(\boldsymbol{\beta}, \mathbf{u}_G, \mathbf{u}_I)] \end{bmatrix} = \begin{bmatrix} 2\,\mathrm{tr}[(\mathbf{Q}_{2_{11}} - \mathbf{Q}_{1_{11}})\mathbf{Z}_1\mathbf{Z}_1'] & 2\,\mathrm{tr}[(\mathbf{Q}_{2_{12}} - \mathbf{Q}_{1_{12}})\mathbf{Z}_1\mathbf{Z}_1'] & 2\,\mathrm{tr}(\mathbf{Q}_{2_{12}} - \mathbf{Q}_{1_{11}}) \\ 2\,\mathrm{tr}[(\mathbf{Q}_{3_{11}} - \mathbf{Q}_{2_{11}})\mathbf{Z}_1\mathbf{Z}_1'] & 2\,\mathrm{tr}[(\mathbf{Q}_{3_{12}} - \mathbf{Q}_{2_{12}})\mathbf{Z}_1\mathbf{Z}_1'] & 2\,\mathrm{tr}(\mathbf{Q}_{3_{11}} - \mathbf{Q}_{2_{11}}) \\ 2\,\mathrm{tr}[(\mathbf{I} - \mathbf{Q}_{3_{11}})\mathbf{Z}_1\mathbf{Z}_1'] & 2\,\mathrm{tr}(-\mathbf{Q}_{3_{12}}\mathbf{Z}_1\mathbf{Z}_1') & 2\,\mathrm{tr}(\mathbf{I} - \mathbf{Q}_{3_{11}}) \end{bmatrix} \begin{bmatrix} \frac{1}{2}(\sigma_1^2 + \sigma_2^2) \\ \sigma_{12} \\ \frac{1}{2}(\sigma_{e_1}^2 + \sigma_{e_1}^2) \end{bmatrix}$$

For balanced data substituting *s* and *n* as before, we obtain:

$$= \begin{bmatrix} n(s-1) & n(s-1) & s-1 \\ n(s-1) & -n(s-1) & s-1 \\ 0 & 0 & 2s(n-1) \end{bmatrix} \begin{bmatrix} \frac{1}{2}(\sigma_1^2 + \sigma_2^2) \\ \sigma_{12} \\ \frac{1}{2}(\sigma_{e_1}^2 + \sigma_{e_2}^2) \end{bmatrix}. \qquad \text{(A6)}$$

Since (A4) and (A6) are equivalent expected sums of squares, we have (A4) = (A6). Dividing each row by the corresponding degrees of freedom, we obtain the following equations of the expected mean squares:

$$\begin{bmatrix} 2n & n & 1 \\ 0 & n & 1 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \sigma_G^2 \\ \sigma_I^2 \\ \frac{1}{2}(\sigma_{\varepsilon_1}^2 + \sigma_{\varepsilon_2}^2) \end{bmatrix} = \begin{bmatrix} n & n & 1 \\ n & -n & 1 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \frac{1}{2}(\sigma_1^2 + \sigma_2^2) \\ \sigma_{12} \\ \frac{1}{2}(\sigma_{e_1}^2 + \sigma_{e_2}^2) \end{bmatrix}.$$

Using

$$\begin{bmatrix} 2n & n & 1 \\ 0 & n & 1 \\ 0 & 0 & 1 \end{bmatrix}^{-1} = \begin{bmatrix} 1/2n & -1/2n & 0 \\ 0 & 1/n & -1/n \\ 0 & 0 & 1 \end{bmatrix},$$

we obtain

$$\begin{bmatrix} \sigma_G^2 \\ \sigma_I^2 \\ \frac{1}{2}(\sigma_{\varepsilon_1}^2 + \sigma_{\varepsilon_2}^2) \end{bmatrix} = \begin{bmatrix} 0 & 1 & 0 \\ 1 & -1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} \frac{1}{2}(\sigma_1^2 + \sigma_2^2) \\ \sigma_{12} \\ \frac{1}{2}(\sigma_{e_1}^2 + \sigma_{e_2}^2) \end{bmatrix}$$

which agrees with Eqs. (6a)–(6e) in this paper.

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