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SIMULTANEOUS JOINT SCALING TEST FOR SEVERAL CORRELATED TRAITS*

M. SINGH

Statistics Unit, International Crops Research Institute for the Semi Arid Tropics, Patancheru, Andhra Pradesh 502 324, India

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SUMMARY

For generation mean analysis a simultaneous joint scaling test with several correlated traits is proposed. Scaling test for individual traits were compared with this test and in general were not independent and are relatively less efficient for the correlated traits situation. The two and three traits cases have been illustrated with real data.

1. INTRODUCTION

Generation mean analysis is often used to estimate components of mean (additive and dominance effects and interaction and heterosis) of individual traits. A joint scaling test proposed by Cavalli (1952) and described in Mather and Jinks (1971) is generally used for testing the appropriateness of the mathematical model before estimating or testing the significance of the components of means. A number of papers (e.g., Pathak and Singh (1970), Law *et al.* (1978)) present generation mean analyses for several traits considered individually. However, the traits may be significantly correlated, perhaps due to linkage, so that inferences from scaling tests applied to individual traits are dependent. A simultaneous scaling test is proposed which tests genetic models for several traits and estimates various components while allowing for correlations among them. Estimators of the mean components from the simultaneous scaling test will be more efficient than those from scaling tests applied on individual traits. However, as far as is known, the improvement in efficiency is relatively small.

A simultaneous scaling test for any number of correlated traits is presented in section 2. The two traits case and some statistical consideration of the two tests are given in section 3 and illustrated in section 4 using the referee's analysis for two and three traits data of his colleagues.

2. Simultaneous joint scaling test

Consider the situation where a plant breeder is interested in generation mean analysis for p correlated traits using information from a set of m generations. Further assume that the generations permit the estimation of the components of means required. For instance, a set of four or more generations (e.g., P₁, P₂, F₁, F₂, B₁, B₂) may be raised to estimate the often needed components m, [d], [h] for a trait.

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If Y_{kij} is the measurement on the kth trait of the *j*th individual in *i*th generation the associated genetic model is

$$Y_{kij} = \mathbf{x}'_i \mathbf{\beta}_k + e_{kij} \qquad (k = 1, 2, \dots, p; j = 1, 2, n_i; i = 1, 2, \dots, m).$$
(1)

where n_i is the number of individuals in *i*th generation; x'_i is a row vector of known constants and β_k is a vector of q_k unknown parameters (components of means). For instance, if the generation observed is B_1 then for the three component model, $\beta_k = (m, [d], [h])$; $q_k = 3$ and x' = (1, 0.5, 0.5). e_{kij} is assumed to be normally distributed with zero mean and σ_{ik}^2 variance. Covariance between e_{kij} and $e_{k'i'j'}$ is $\sigma_{ikk'}$ for i = i', j = j' and zero otherwise $(k \neq k')$.

Model (1) can be rewritten in terms of observed generation means:

$$\bar{Y}_{ki} = \mathbf{x}_i' \mathbf{\beta}_k + \bar{e}_{ki}$$

or more compactly by

$$\vec{Y}_k = X_k \,\beta_k + \vec{e}_k \tag{2}$$

where $\bar{\mathbf{Y}}_k = (\bar{Y}_{k1}, \bar{Y}_{k2}, \dots, \bar{Y}_{km})'; \ \bar{e}_k = (\bar{e}_{k1}, \bar{e}_{k2}, \dots, \bar{e}_{km})';$



The variance of the generation means for a trait k can be written as

$$E(\bar{\boldsymbol{e}}_{ki}^2) = \sigma_{ki}^2 / n_i$$

and for the traits k and k' the covariance between means of the same *i*th generation as

$$\operatorname{cov}\left(\bar{e}_{ki},\,\bar{e}_{k'i}\right) = \sigma'_{ikk'}/n_i;$$

and

$$\operatorname{cov}\left(\bar{e}_{ki}, \bar{e}_{k'i'}\right) = 0 \quad \text{for } i \neq i'.$$
(3)

From the measurements made on the characters k and k', the variance σ_{ik}^2 and covariance $\sigma_{ikk'}$ within *i*th generation can be estimated by

$$\hat{\sigma}_{ik}^{2} = \sum_{j=1}^{n_{i}} (Y_{kij} - \bar{Y}_{ki})^{2} / (n_{i} - 1)$$
$$\hat{\sigma}_{ikk'} = \sum_{j=1}^{n_{i}} (Y_{kij} - \bar{Y}_{ki}) (Y_{k'ij} - \bar{Y}_{k'i}) / (n_{i} - 1).$$

The model (2) for $k = 1, 2, \ldots, p$ becomes

$$Y = Z\beta + e \tag{4}$$

where

$$\boldsymbol{Y} = (\bar{\boldsymbol{Y}}_1', \dots, \bar{\boldsymbol{Y}}_p')'mp \times 1$$
$$\boldsymbol{Z} = \begin{bmatrix} \boldsymbol{X}_1 & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X}_2 & \boldsymbol{0} \\ \boldsymbol{0} & \cdots & \boldsymbol{X}_p \end{bmatrix}_{mp \times qp} \qquad \boldsymbol{\beta} = \begin{bmatrix} \boldsymbol{\beta}_1 \\ \vdots \\ \boldsymbol{\beta}_p \end{bmatrix}_{qp \times 1}$$

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When the same types of components of means are considered in all traits, then

and

$$\boldsymbol{X}_1 = \boldsymbol{X}_2 = \cdots = \boldsymbol{X}_p = \boldsymbol{X}$$

 $Z = I_p \Theta X$

where I_p is an identity matrix of order p and Θ represents Kronecker product of the two matrices involved.

$$\boldsymbol{e}' = (\boldsymbol{\bar{e}}'_1, \ldots, \boldsymbol{\bar{e}}'_p)$$

is an mp-component row vector of normal variables with

and

$$D(e) = W.$$

E(e) = 0

Where $E(\cdot)$ and $D(\cdot)$ represent the expectation vector and dispersion matrix of the random vector inside the operand. For W, we can write

$$\boldsymbol{W} = \begin{bmatrix} \boldsymbol{W}_{11} & \boldsymbol{W}_{12} & \boldsymbol{W}_{1p} \\ \vdots & & \\ \boldsymbol{W}_{1p} & \cdots & \boldsymbol{W}_{pp} \end{bmatrix}_{mp \times mp}$$

where the $m \times m$ diagonal submatrices

 $W_{kk} = \operatorname{diag}\left(\sigma_{1k}^2/n_1, \ldots, \sigma_{mk}^2/n_m\right)$

represent variance covariances of generation means for kth trait and

$$W_{kk'} = \operatorname{diag}\left(\sigma_{1\,kk'}/n_1,\ldots,\sigma_{mkk'}/n_m\right)$$

covariances between generation means of different k and k'th traits. Under the above model we shall consider the following.

(i) Individual trait analysis

For the kth trait (k = 1, 2, ..., p) we have below the statistic Q_k for testing the appropriateness of model (2) and the weighted least squares estimates $\hat{\beta}_k$ of β_k .

$$Q_k = (\bar{Y}_k - X_k \hat{\beta}_k)' W_{kk}^{-1} (\bar{Y}_k - X_k \hat{\beta}_k)$$
$$\hat{\beta}_k = (X' W_{kk}^{-1} X_k)^{-1} X'_k W_{kk}^{-1} \bar{Y}_k.$$

The distribution of Q_k is approximately χ^2 with $m - q_k$ degrees of freedom. It is approximate since W_{kk} contains estimated variances (Mather and Jinks 1971; Gale *et al.*, 1977). The variance-covariance matrix of the estimated components of $\hat{\beta}$ is given by

$$D(\hat{\boldsymbol{\beta}}_k) = (\boldsymbol{X}_k' \boldsymbol{W}_{kk}^{-1} \boldsymbol{X}_k)^{-1}.$$

(ii) Several traits simultaneous analysis

We apply Aitken's (1935) generalised least squares analysis to obtain the statistic

$$Q = (\boldsymbol{Y} - \boldsymbol{Z}\hat{\boldsymbol{\beta}})' \boldsymbol{W}^{-1} (\boldsymbol{Y} - \boldsymbol{Z}\hat{\boldsymbol{\beta}})$$

and test the appropriateness of the model (4) and $\hat{\hat{\beta}}$ as the estimator of β where

$$\hat{\hat{\boldsymbol{\beta}}} = (\boldsymbol{Z}' \boldsymbol{W}^{-1} \boldsymbol{Z})^{-1} \boldsymbol{Z}' \boldsymbol{W}^{-1} \boldsymbol{Y}.$$

Writing W^{-1} as

$$\boldsymbol{W}^{-1} = \begin{bmatrix} \boldsymbol{W}^{11} & \cdots & \boldsymbol{W}^{1p} \\ \vdots \\ \boldsymbol{W}^{p1} & \cdots & \boldsymbol{W}^{pp} \end{bmatrix}$$

we have

$$\boldsymbol{Z}'\boldsymbol{W}^{-1}\boldsymbol{Z} = \begin{bmatrix} \boldsymbol{X}_1'\boldsymbol{W}^{11}\boldsymbol{X}_1 & \cdots & \boldsymbol{X}_1'\boldsymbol{W}^{1p}\boldsymbol{X}_p \\ \vdots & & \\ \boldsymbol{X}_p'\boldsymbol{W}^{p1}\boldsymbol{X}_1 & \cdots & \boldsymbol{X}_p'\boldsymbol{W}^{pp}\boldsymbol{X}_p \end{bmatrix}$$

and

$$\mathbf{Z}' \mathbf{W}^{-1} \mathbf{Y} = \begin{bmatrix} \mathbf{X}_1' \mathbf{W}^{11} \, \bar{\mathbf{Y}}_1 \\ \vdots \\ \mathbf{X}_p' \mathbf{W}^{1p} \, \bar{\mathbf{Y}}_p \end{bmatrix}$$

The estimator $\hat{\boldsymbol{\beta}}_k$ of $\boldsymbol{\beta}_k$ for the k-th trait is

$$\hat{\hat{\boldsymbol{\beta}}}_{k} = \sum_{l=1}^{p} \boldsymbol{P}^{lk} \boldsymbol{X}_{1}' \boldsymbol{W}^{lk} \boldsymbol{Y}_{k}$$

where p^{lk} are $q_l \times q_k$ submatrices in the inverse of $Z' W^{-1} Z$ represented below

$$(\mathbf{Z}'\mathbf{W}^{-1}\mathbf{Z})^{-1} = \begin{bmatrix} \mathbf{P}^{11} & \cdots & \mathbf{p}^{1p} \\ \vdots & & \\ \mathbf{P}^{p1} & \cdots & \mathbf{P}^{pp} \end{bmatrix}$$

The expression for Q reduces to

$$Q = \sum_{k} \sum_{k'} \mathbf{r}'_{k} \mathbf{W}^{kk'} \mathbf{r}_{k'}$$

where residuals $\mathbf{r}_k = \mathbf{\bar{Y}}_k - \mathbf{X}_k \hat{\mathbf{\beta}}_k$. The distribution of Q is approximately χ^2 with $mp = \sum_k q_k$ degrees of freedom. Q simultaneously tests the appropriateness of model (4) for p traits. The variances-covariances of estimates of various parameters are given by $D(\hat{\beta}) = (Z'W^{-1}Z)^{-1}$. Thus the variance-covariance matrices of the estimates of parameters of the same and different traits are

$$D(\hat{\hat{\boldsymbol{\beta}}}_k) = \boldsymbol{P}^{kk}$$

cov $(\hat{\hat{\boldsymbol{\beta}}}_k, \hat{\hat{\boldsymbol{\beta}}}_{k'}) = \boldsymbol{P}^{kk'}$ $k \neq k' = 1, 2, ..., p.$

We can easily establish that the efficiency in sense of minimum variance of the two estimators $\hat{\beta}_{k}$, using individual trait analysis, is less than or equal to that of $\hat{\beta}_{k}$, using simultaneous analysis by the method of Rao (1973, p. 223, ii).

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3. The case of two traits

This section illustrates the application of the simultaneous scaling test to the two traits situation. We also exhibit the dependence of the two tests based on Q_1 and Q_2 by working out the correlation between Q_1 and Q_2 for correlated traits.

For two traits situation,

$$\boldsymbol{W} = \begin{bmatrix} \boldsymbol{W}_{11} & \boldsymbol{W}_{12} \\ \boldsymbol{W}_{12} & \boldsymbol{W}_{22} \end{bmatrix}.$$
(5)

To obtain the inverse of the matrices of type (5) we shall make use of *Lemma* 1 (Rao, 1973, p. 33).

Let A and D be two symmetric matrices such that inverses which occur in the expressions exist, then

$$\begin{bmatrix} \boldsymbol{A} & \boldsymbol{B} \\ \boldsymbol{B}' & \boldsymbol{D} \end{bmatrix}^{-1} = \begin{bmatrix} \boldsymbol{A}^{-1} + \boldsymbol{F}\boldsymbol{E}^{-1}\boldsymbol{F}' & -\boldsymbol{F}\boldsymbol{E}^{-1} \\ -\boldsymbol{E}^{-1}\boldsymbol{F}' & \boldsymbol{E}^{-1} \end{bmatrix}$$

where

$$\boldsymbol{E} = \boldsymbol{D} - \boldsymbol{B}' \boldsymbol{A}^{-1} \boldsymbol{B}$$
 and $\boldsymbol{F} = \boldsymbol{A}^{-1} \boldsymbol{B}$.

Thus, in

$$W^{-1} = \begin{bmatrix} W^{11} & W^{12} \\ W^{12} & W^{22} \end{bmatrix}$$
$$W^{11} = \text{diag}(W_{111}, \dots, W_{11m})$$
$$W^{12} = \text{diag}(W_{121}, \dots, W_{12m})$$
$$W^{22} = \text{diag}(W_{221}, \dots, W_{22m})$$

where

$$W_{11i} = \sigma_{i2}^2 / \omega$$
$$W_{12i} = -\sigma_{i12} / \omega$$
$$W_{22i} = \sigma_{i1}^2 / \omega$$
$$\omega = \sigma_{i1}^2 \sigma_{i2}^2 - \sigma_{i12}^2.$$

Using Lemma 1, we can evaluate matrices P's in

$$(\boldsymbol{Z}'\boldsymbol{W}^{-1}\boldsymbol{Z})^{-1} = \begin{bmatrix} \boldsymbol{P}^{11} & \boldsymbol{P}^{12} \\ \boldsymbol{P}^{21} & \boldsymbol{P}^{22} \end{bmatrix}$$

by

$$P^{22} = (X'_2(W^{22} - W^{12}X_1(X'_1W^{11}X_1)^{-1}X'_1W^{12})X_2)^{-1}$$

$$P^{12} = P^{21'} = -(X'_1W^{11}X_1)^{-1}X'_1W^{12}X_2P^{22}$$

$$P^{11} = (X'_1W^{11}X_1)^{-1}(I_{q1} + X'_1W^{12}X_2P^{22}X'_2W^{12}X_1(X'_1W^{11}X_1)^{-1}).$$

Furthermore

$$\boldsymbol{Z}'\boldsymbol{W}^{-1}\boldsymbol{\bar{Y}} = \begin{bmatrix} \boldsymbol{U}_1\\ \boldsymbol{U}_2 \end{bmatrix},$$

where

$$U_1 = X'_1 W^{11} \bar{Y}_1 + X'_1 W^{12} \bar{Y}_2, \qquad U_2 = X'_2 W^{12} \bar{Y}_1 + X'_2 W^{22} \bar{Y}_2.$$

Therefore

$$\hat{\hat{\beta}}_1 = P^{11}U_1 + P^{12}U_2, \qquad \hat{\hat{\beta}}_2 = P^{21}U_1 + P^{22}U_2.$$

For the statistic Q, we have

$$Q = (\bar{Y} - Z\hat{\beta})'W^{-1}(\bar{Y} - Z\hat{\beta})$$

= $\bar{Y}_1'W^{11}\bar{Y}_1 + 2\bar{Y}_1'W^{12}\bar{Y}_2 + Y_2'W^{22}\bar{Y}_2 - \hat{\beta}_1'U_1 - \hat{\beta}_2'U_2$
= $r_1'W^{11}r_1 + 2r_1'W^{12}r_2 + r_2'W^{22}r_2$

Here r_1 and r_2 are residual vectors obtained by fitting model (4).

Now, consider the analysis done on the individual traits and we have

$$Q_k = (\bar{\mathbf{Y}}_k - \mathbf{X}_k \hat{\mathbf{\beta}}_k)' \mathbf{W}_{kk}^{-1} (\bar{\mathbf{Y}}_k - \mathbf{X}_k \hat{\mathbf{\beta}}_k)$$
$$\hat{\mathbf{\beta}}_k = (\mathbf{X}_k' \mathbf{W}_{kk}^{-1} \mathbf{X}_k)^{-1} \mathbf{X}_k' \mathbf{W}_{kk}^{-1} \bar{\mathbf{Y}}_k.$$

with

In order to evaluate the covariance between
$$Q_1$$
 and Q_2 we shall need *Lemma* 2 (Anderson, 1971, pp. 67, 73).

Let $\sum_{ij} a_{ij}U_iU_j = U'AU$, where A is symmetric and $E(U_i) = 0$, $E(U_iU_j) = 0$, $i \neq j$, $E(U_i^4) = k_4 + 3\sigma^4$, $E(U_i^2U_j^2) = \sigma^4$, $i \neq j$, and $E(U_iU_jU_kU_l) = 0$ unless subscripts are equal in pairs. Then the mean and variance of the quadratic form U'AU are

$$E(U'AU) = \sigma^2 \operatorname{tr} A$$

Var(U'AU) = $k_4 \sum a_{ii}^2 + 2\sigma^4 \operatorname{tr} A^2$.

The covariance between two quadratic forms $\sum_{ij} a_{ij}U_iU_j = U'AU$ and $\sum_{ii} b_{ij}U_iU_j = U'BU$ is

$$\operatorname{cov}(U'AU, U'BU) = k_4 \sum a_{ii}b_{ii} + 2\sigma^4 \operatorname{tr}(AB)$$

where tr stands for the trace of the matrix.

With a little algebra on the matrices we can write

$$Q_1 = U'B_1U$$

$$Q_2 = U'B_2U$$
(6)

where

$$U = \Omega^{-1}\varepsilon, \qquad \varepsilon = (e'_1, e'_2)'$$
$$B_k = \Omega H_k \Omega$$
$$\Omega = W^{1/2}$$
$$H_1 = \begin{bmatrix} A_1 & 0 \\ 0 & 0 \end{bmatrix}, \qquad H_2 = \begin{bmatrix} 0 & 0 \\ 0 & A_2 \end{bmatrix}$$
$$A_k = (I_m - W_{kk}^{-1} X_k (X'_k W_{kk}^{-1} X_k)^{-1} X_k) W_{kk}^{-1}$$

Also note that $A_k X_k = 0$,

$$\operatorname{tr}\left(\boldsymbol{A}_{k}\boldsymbol{W}_{kk}\right)=\boldsymbol{m}-\boldsymbol{q}_{k}, \qquad k=1,\,2.$$

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By writing

$$\mathbf{\Omega} = \begin{bmatrix} \mathbf{\Omega}_{11} & \mathbf{\Omega}_{12} \\ \mathbf{\Omega}_{21} & \mathbf{\Omega}_{22} \end{bmatrix}$$

we can further show that (6) satisfies the assumptions of Lemma 2 with

$$\boldsymbol{B}_{1} = \begin{bmatrix} \boldsymbol{\Omega}_{11}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{11} & \boldsymbol{\Omega}_{11}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{12} \\ \boldsymbol{\Omega}_{21}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{11} & \boldsymbol{\Omega}_{12}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{12} \end{bmatrix}$$
$$\boldsymbol{B}_{2} = \begin{bmatrix} \boldsymbol{\Omega}_{12}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{21} & \boldsymbol{\Omega}_{12}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{22} \\ \boldsymbol{\Omega}_{21}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{21} & \boldsymbol{\Omega}_{22}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{22} \end{bmatrix}.$$

Under the assumption that random vector ε has multivariate normal distribution ($k_4 = 0$, in Lemma 2) the variances of and covariance between the quadratic forms Q_1 and Q_2 are below (when W is assumed to have true population values of variances and covariances).

- . . .

$$E(Q_k) = \operatorname{tr} \boldsymbol{B}_k$$

= $m - q_k$
var $(Q_k) = 2 \operatorname{tr} \boldsymbol{B}_k^2$
= $2(m - q_k)$

and

$$\operatorname{cov}(Q_1, Q_2) = 2 \operatorname{tr} \boldsymbol{B}_1 \boldsymbol{B}_2.$$

We further note that

$$tr \ \boldsymbol{B}_{1}\boldsymbol{B}_{2} = tr \left(\boldsymbol{\Omega}_{11}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{11}\boldsymbol{\Omega}_{12}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{21} + \boldsymbol{\Omega}_{11}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{12}\boldsymbol{\Omega}_{22}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{21} + \boldsymbol{\Omega}_{21}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{11}\boldsymbol{\Omega}_{12}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{22} + \boldsymbol{\Omega}_{21}\boldsymbol{A}_{1}\boldsymbol{\Omega}_{12}\boldsymbol{\Omega}_{22}\boldsymbol{A}_{2}\boldsymbol{\Omega}_{22}\right)$$
$$= tr \left(\boldsymbol{A}_{1}\boldsymbol{W}_{12}\boldsymbol{A}_{2}\boldsymbol{W}_{21}\right)$$

using the relations

$$\boldsymbol{\Omega}_{11}\boldsymbol{\Omega}_{12} + \boldsymbol{\Omega}_{12}\boldsymbol{\Omega}_{22} = \boldsymbol{W}_{12}.$$

Further in terms of W's and X's we have

tr
$$\boldsymbol{B}_{1}\boldsymbol{B}_{2} =$$
tr $(\boldsymbol{W}_{11}^{-1}\boldsymbol{W}_{12}\boldsymbol{W}_{22}^{-1}\boldsymbol{W}_{21} - (\boldsymbol{X}_{1}'\boldsymbol{W}_{11}^{-1}\boldsymbol{X}_{1})^{-1}\boldsymbol{X}_{1}'\boldsymbol{W}_{11}^{-1}\boldsymbol{W}_{12}\boldsymbol{W}_{22}^{-1}\boldsymbol{W}_{21}\boldsymbol{W}_{11}^{-1}\boldsymbol{X}_{1}$
 $-(\boldsymbol{X}_{2}'\boldsymbol{W}_{22}^{-1}\boldsymbol{X}_{2})^{-1}\boldsymbol{X}_{2}'\boldsymbol{W}_{22}^{-1}\boldsymbol{W}_{21}\boldsymbol{W}_{11}^{-1}\boldsymbol{W}_{12}\boldsymbol{W}_{22}^{-1}\boldsymbol{X}_{2}$
 $+(\boldsymbol{X}_{1}'\boldsymbol{W}_{11}^{-1}\boldsymbol{X}_{1})^{-1}\boldsymbol{X}_{1}'\boldsymbol{W}_{11}^{-1}\boldsymbol{W}_{12}\boldsymbol{W}_{22}^{-1}\boldsymbol{X}_{2}$
 $\times(\boldsymbol{X}_{2}'\boldsymbol{W}_{22}^{-1}\boldsymbol{X}_{2})^{-1}\boldsymbol{X}_{2}'\boldsymbol{W}_{22}^{-1}\boldsymbol{W}_{22}\boldsymbol{W}_{11}^{-1}\boldsymbol{X}_{1}).$ (7)

The expression (7) of covariance between Q_1 and Q_2 reduces to zero when the two traits are uncorrelated *i.e.*, $W_{12} = 0$. Thus the tests based on Q_1 and Q_2 are dependent in general for testing the genetic model for two correlated traits.

4. Illustration

An application of the method discussed in this paper has been made by the referee and his colleague on their data (details of the data available

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on request from Dr H. S. Pooni) and is produced in the following with their consent. The data were obtained on four traits (H_1 , H_2 : juvenile height, measured on two occasions two weeks apart; H_F : height at flowering and L_S : leaf spread) in *Nicotiana rustica*. The total number of plants raised was 500.

Table 1 presents the correlation coefficients for the pairs of traits used in analysis.

TABLE 1

Generations	H_1, H_2	H_l, H_F	H_l, L_s	H _F , H _S
P	0.96	-0.17	0.44	0.66
P ₂	0.86	-0.48	-0.28	0.76
F_1	0.93	-0.35	-0.26	0.70
F,	0.94	-0.38	-0.37	0.52
B	0.93	-0.48	-0.42	0.66
B ₂	0.88	-0.60	-0.33	0.56

The estimates of the parameters m, [d], [h] for the two highly correlated traits H_1 and H_2 are given in table 2 using individual traits and simultaneous traits analyses. The variances of the estimates are given in parentheses.

TABLE 2

Estimates of parameters m, [d], [h] and their variances for traits H_1 and H_2 Traits and estimation method

	H ₁		H ₂	
Parameters	Individual	Simultaneous	Individual	Simultaneous
m	5-341 (0-027)	5.346 (0.027)	15.776 (0.255)	15.764 (0.254)
[d]	1.090 (0.025)	1.101 (0.025)	3.388 (0.235)	3.374 (0.235)
[h]	0.386 (0.095)	0·349 (0·094)	1.314 (0.890)	1.323 (0.888)

In table 2 simultaneous method means that H_1 and H_2 , but no other characters, were analysed simultaneously.

We now consider the estimation of parameters for three traits H_1 , H_F and L_S analysed individually and according to schemes

(a) H_1 , H_F simultaneously

(b) H_1 , L_s simultaneously

(c) H_1 , H_F and L_S simultaneously

From the comparison of the variances of the estimates of the various parameters resulting from individual and simultaneous traits analyses in table 2 and table 3, we notice that there is improvement in efficiency by inclusion of two or more traits in analyses. However, this improvement is relatively small. The improvement in efficiency will be determined by the degree of correlation between the traits over these generations. It is expected that improvement in efficiency will be greatest when correlations are intermediate. When all correlations are zero then simultaneous traits analysis

Traits	Parameter	Estimation method				
		Individual	Scheme (a)	Scheme (b)	Scheme (c)	
H	m	5.341 (0.027)	5.330 (0.026)	5.335 (0.027)	5.341 (0.026)	
	[d]	1.090 (0.027)	1.094 (0.024)	1.087 (0.025)	1.099 (0.023)	
	[d] [h]	0.386 (0.095)	0.462 (0.091)	0.417 (0.094)	0.421 (0.089)	
H _F	m	67.813 (0.682)	67.789 (0.681)		67.836 (0.678)	
•	[d]	-5.896 (0.666)	-5.869 (0.663)		-5.985 (0.654)	
	[h]	6.137 (0.457)	6.176 (0.447)		6.395 (0.429)	
Ls	m	42.762 (0.240)		42.747 (0.239)	42.749 (0.234)	
3	[d]	-0.383 (0.223)		-0.379 (0.222)	-0.418 (0.219)	
	[h]	6.585 (0.894)		6.608 (0.888)	6.628 (0.863)	

TABLE	3
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Estimates of parameters m, [d], [h] and their variances for traits H_1 , H_F and L_S

reduces to the individual trait analyses. This procedure breaks down if any of the correlations is unity. An empirical study can be made to examine the performance of the estimates obtained by the two methods by taking several values for correlation coefficients for generations in its admissible range. (Also see section 2(ii).)

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