Note on bias in estimates of the regression coefficient in the analysis of genotype–environmental interaction

HANS-PETER PIEPHO

Institut für Pflanzenbau and Pflanzenzüchtung, Christian-Albrechts-Universität, Olshausenstrasse 40, W-2300 Kiel, Germany

In this paper, bias of two estimates of the regression coefficient of genotypic response to the environmental index is investigated. It is concluded that both estimates are biased, but that the experimental design can be chosen so as to minimize bias.

Keywords: attenuation effect, environmental index, first-order approximation, Taylor series expansion.

Introduction

Wright (1976) has identified two sources of bias in the estimation of regression coefficients according to the method of Perkins & Jinks (1968), in which the independent variable is an environmental index computed as the mean of all genotypes. The first is the well-known attenuation effect (Sprent, 1969), which arises because the independent variable is unknown but estimated with error. Hardwick & Wood (1972) concluded that there is a tendency to underestimate the absolute value of the regression coefficient. The second bias arises because of a correlation between the response variable, i.e. the genotypic value, and the environmental index, onto which the genotypic value is regressed. Wright (1976) suggests a modified estimate of the regression coefficient which, supposedly, removes both of these biases. The following shows that Wright's estimate is biased. Bias in the estimate by Perkins & Jinks (1968) is also discussed.

Results and discussion

The model is

$$y_{ijk} = \mu + g_i + \varepsilon_j + b_k + f_{ij} + e_{ijk},$$

where y_{ijk} is the value of the ij th combination of the k th block, μ is the general mean, g_i the effect of the i th genotype, ε_j that of the j th environment, f_{ij} their interaction, b_k the k th block effect, and e_{ijk} the error associated with the plot (Wright, 1976). We assume random genotypic and environmental effects. The

results do not change, if genotypic effects are fixed provided that we do not impose the constraint $\sum_i f_{ij} = 0$, which is common but not necessary (Searle, 1971; McLean *et al.*, 1991). For the means over all r blocks we have

$$y_{ij} = \mu + g_i + \varepsilon_j + f_{ij} + b. + e_{ij}, \quad (1)$$

where

$$e_{ij} = \sum_k e_{ijk}/r \text{ and } b. = \sum_k b_k/r.$$

We are now interested in the regression of f_{ij} on ε_j , which leads to the regression coefficient β_i proposed by Perkins & Jinks (1968). Their estimate is biased as pointed out above. Wright's modified estimate is

$$\beta'_i = \frac{(m-1)}{(m-2)} (W'_i/\bar{W} - 1)$$

where m is the number of genotypes,

$$W'_i = (m/(m-1))(W_i - V_i/m), \text{ and } \bar{W} = \sum_i W'_i/m.$$

W_i is the observed covariance of values of the i th genotype with the corresponding y_j (the mean of all genotypes in the j th environment), and V_i is the observed variance of values y_{ij} of the i th genotype.

Wright's estimate of β_i is biased, which is a result of errors in the derivation of the expected value of W'_i . This error arises because Wright (1976) does not consider the fact that f_{ij} and $f_{i'j}$ ($i \neq i'$) as well as f_{ij} and ε_j are no longer uncorrelated, if a correlation between interaction and environmental effects is assumed. The derivation of expected values is simplified by writing

down the regression model explicitly instead of relying on the model without regression coefficients (equation 2), (Wright, 1976).

We now rewrite the model in equation (1) to account for the regression coefficient β_i . With $f_{ij} = \beta_i \varepsilon_j + a_{ij}$ and $d_{ij} = a_{ij} + e_{ij}$, one obtains

$$y_{ij} = \mu + b. + g_i + \varepsilon_j + \beta_i \varepsilon_j + d_{ij}. \quad (2)$$

Then, we place the usual constraint $\sum_i \beta_i = 0$ on the model, and find

$$y_{.j} = \mu + b. + g. + \varepsilon_j + d_{.j}, \quad (3)$$

where $d_{.j} = \sum_i d_{ij}/m$ and $g. = \sum_i g_i/m$.

With equations (2) and (3), derivation of expected values is straightforward. We obtain

$$E(V_i) = (1 + \beta_i)^2 \sigma_\varepsilon^2 + \sigma_{di}^2 \quad (4)$$

where σ_{di}^2 is the variance of d_{ij} of the i th genotype, and

$$E(W_i) = \text{COV}(y_{ij}, y_{.j}) = (1 + \beta_i) \sigma_\varepsilon^2 + \sigma_{di}^2/m. \quad (5)$$

Hence,

$$\begin{aligned} E(W'_i) &= [m/(m-1)][E(W_i) - E(V_i)/m] \\ &= [m/(m-1)][(1 + \beta_i) \sigma_\varepsilon^2 + \sigma_{di}^2/m - (1 + \beta_i)^2 \sigma_\varepsilon^2/m \\ &\quad - \sigma_{di}^2/m] \\ &= [m/(m-1)][(1 + \beta_i) - (1 + \beta_i)^2/m] \sigma_\varepsilon^2 \end{aligned} \quad (6)$$

and

$$\begin{aligned} E(\bar{W}) &= [m/(m-1)][(1 - (1 + \sum_i \beta_i^2/m)/m) \sigma_\varepsilon^2] \\ &= [1 - \sum_i \beta_i^2/m(m-1)] \sigma_\varepsilon^2. \end{aligned} \quad (7)$$

Equations (5)–(7) are in disagreement with the equivalent formulas in Wright (1976), which is a result of the errors mentioned above. So Wright's estimate of β_i is not unbiased.

In the derivation of an unbiased estimate of β_i , Wright (1976) implicitly makes the assumption that

$$E(W'_i/\bar{W}) = E(W'_i)/E(\bar{W}).$$

This assumption is only approximately correct. It is in fact an approximation of the Taylor series expansion of $E(W'_i/\bar{W})$ about $E(W'_i)/E(\bar{W})$, in which terms of order higher than 1 are neglected, which adds to the bias in Wright's estimate. It should be scrutinized whether terms of order two and higher are really negligible. On including, for example, terms of order 2 (see Johnson & Kotz, 1971; Hühn, 1990), one obtains:

$$\begin{aligned} E(W'_i/\bar{W}) &\approx [E(W'_i)/E(\bar{W})] \\ &\quad \times \{1 - \text{COV}(W'_i, \bar{W})/E(\bar{W})E(W'_i) \\ &\quad + \text{VAR}(\bar{W})/[E(\bar{W})]^2\}. \end{aligned}$$

It appears to be a complicated task to evaluate $\text{COV}(W'_i, \bar{W})$ and $\text{VAR}(\bar{W})$, so we have not pursued this problem further. The use of the Taylor series expansion is in itself a potential source of bias.

An error is also present in Wright's (1976) formula for the expected value of V_x , the observed variance of the environmental index $y_{.j}$. We find

$$\begin{aligned} E(V_x) &= \text{VAR}(y_{.j}) = \sigma_\varepsilon^2 + \text{VAR}(m^{-1} \sum_i d_{ij}) \\ &= \sigma_\varepsilon^2 + m^{-2} \sum_i \sigma_{di}^2 = \sigma_\varepsilon^2 + m^{-1} \sigma_d^2 \end{aligned}$$

where $\sigma_d^2 = \sum_i \sigma_{di}^2/m$. With Wright, we use the approximation

$$E(W_i/V_x - 1) \approx E(W_i)/E(V_x) - 1.$$

Again, this is only a first-order approximation by Taylor series expansion of $E(W_i/V_x)$ about $E(W_i)/E(V_x)$, and it should be specified as such. More accurate results could be obtained by including terms of higher order. With the first-order approximation, we find

$$\begin{aligned} E(W_i/V_x - 1) &\approx \frac{(1 + \beta_i) \sigma_\varepsilon^2 + \sigma_{di}^2/m}{\sigma_\varepsilon^2 + m^{-1} \sigma_d^2} - 1 \\ &= \frac{(1 + \beta_i) \sigma_\varepsilon^2 + \sigma_{di}^2/m - (\sigma_\varepsilon^2 + m^{-1} \sigma_d^2)}{\sigma_\varepsilon^2 + m^{-1} \sigma_d^2} \\ &= \frac{\beta_i \sigma_\varepsilon^2 + m^{-1} (\sigma_{di}^2 - \sigma_d^2)}{\sigma_\varepsilon^2 + m^{-1} \sigma_d^2} \\ &= \beta_i k_1 + k_2 \end{aligned}$$

$$k_1 = \frac{\sigma_\varepsilon^2}{\sigma_\varepsilon^2 + m^{-1} \sigma_d^2} = 1 - \frac{\sigma_d^2}{m \sigma_\varepsilon^2 + \sigma_d^2}$$

$$k_2 = \frac{m^{-1} (\sigma_{di}^2 - \sigma_d^2)}{\sigma_\varepsilon^2 + m^{-1} \sigma_d^2} = \frac{\sigma_{di}^2 - \sigma_d^2}{m \sigma_\varepsilon^2 + \sigma_d^2}.$$

Then the bias is

$$E(\hat{\beta}_i) - \beta_i = \beta_i k_1 + k_2 - \beta_i = \beta_i (k_1 - 1) + k_2.$$

We see from this equation that there is a bias unless $\beta_i = k_2/(1 - k_1) = (\sigma_{di}^2/\sigma_d^2) - 1$. Whether this bias is upward or downward depends on the magnitude of k_1 and k_2 , and therefore on the values of σ_ε^2 , σ_d^2 , σ_{di}^2 , and m . Generally, the bias will be small when m and σ_ε^2 are large. Theoretically, the bias vanishes as either of these parameters tends to infinity.

If $\sigma_{di}^2 = \sigma_d^2$ for all i , as assumed by Hardwick & Wood (1972), then $k_2 = 0$, and

$$E(\hat{\beta}_i) = \frac{\beta_i \sigma_\varepsilon^2}{\sigma_\varepsilon^2 + m^{-1} \sigma_d^2} = \beta_i \left[1 - \frac{\sigma_d^2}{m \sigma_\varepsilon^2 + \sigma_d^2} \right]. \quad (8)$$

And if $m \sigma_\varepsilon^2 \gg \sigma_d^2$, then

$$E(\hat{\beta}_i) = \beta_i \left[1 - \frac{\sigma_d^2}{m\sigma_e^2} \right]. \quad (9)$$

This is equivalent to the approximation by Hardwick & Wood (1972), when environmental effects are random. From equations (8) and (9) there follows a tendency to underestimate β_i (Hardwick & Wood, 1972). The underlying assumption of homogeneous σ_{di}^2 , however, is rather restrictive; and in many situations it is more realistic to allow for heterogeneous variances σ_{di}^2 . In fact, in the analysis of genotype-environmental interaction, σ_{di}^2 is often considered a parameter of phenotypic stability of the i th genotype (Perkins & Jinks, 1968; Shukla, 1972), which implies a potential heterogeneity of σ_{di}^2 . In this case the bias of β_i may be either up or down as discussed above. All these statements are subject to the qualifications that we have used only a first-order approximation of $E(W_i/V_x)$.

Conclusion

It has been shown that Wright's estimate of β_i does not remove bias as expected (Wright, 1976). It therefore seems impossible to derive an unbiased estimate of β_i with Wright's approach. This discussion, however, has

demonstrated that the potential bias in the estimate by Perkins & Jinks (1968) can be reduced by increasing the number of genotypes and by selecting a sufficiently diverse set of testing environments.

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