

# Short Note: On estimating heritability according to practical applications

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## Summary

Attention is drawn to the association between practical application and appropriate formulae for estimating heritability. Individual heritability is traditionally calculated with variance due to environmental effects such as experimental blocks and sites excluded from the denominator. This exclusion of variance components requires the assumption that selection will be based on phenotypic measurements corrected for the appropriate effects. However, selection in forestry is often based on raw uncorrected measurements. Also discussed are the implications of estimating heritability following analyses of covariance with say height at planting as a covariate. Examples are given of bias in gain calculations due to ignoring assumptions of heritability estimation.

*Key words:* Heritability, block effects, site effects, covariates.

## Zusammenfassung

Es wird auf den Zusammenhang zwischen praktischer Anwendung und geeigneten Formeln für die Schätzung der Heritabilität hingewiesen. Individuelle Heritabilität wird herkömmlicherweise so geschätzt, daß die Varianz, die auf Umwelteffekte zurückgeführt wird, wie experimentelle Blöcke (Wiederholungen) und Standorte, im Nenner weggelassen wird. Dies macht es aber erforderlich, daß eine Selektion auf der Basis der für die entsprechenden Effekte korrigierten phänotypischen Merkmale stattfindet. In der Forstwirtschaft basiert eine Selektion oft aber auf den nicht korrigierten Rohdaten. Diskutiert werden auch die Implikationen einer Heritabilitätsschätzung nach Kovarianzanalyse mit beispielsweise der Höhe bei der Auspflanzung als Kovariablen. Es werden Beispiele für fehlerhafte Schätzungen des Züchtungsfortschrittes als Folge der Nichtbeachtung von Voraussetzungen für die Heritabilitätsschätzung angeführt.

## Introduction

The formulae originally recommended by NAMKOONG *et al.* (1966), and others, for estimating heritability in progeny trials in forestry have been widely employed. However, these traditional formulae require certain assumptions about the practical application of heritability estimates. These assumptions are often overlooked by tree breeders.

This short article attempts to highlight the association between practical application and the appropriate formulae for estimating heritability. Particular emphasis is placed on the omission of variance due to experimental block and site effects.

## Theory and Examples

### Variance due to Blocks

Individual heritability (denoted  $h^2_i$ ) is estimated as the ratio of variance between families ( $\sigma^2_f$ ) to the variance between families plus the variance within families ( $\sigma^2_w$ ) — (1)

$$h^2_i = \sigma^2_f / (\sigma^2_f + \sigma^2_w) r \quad (1)$$

where  $r$  is the coefficient of relationship among offspring in the progeny trial ( $r = 1/4$  for half-sib offspring and  $1/2$  for full-sibs). In the case of a progeny trial established at one site only the overall variance within families is the sum of the variance between block replications ( $\sigma^2_b$ ), family  $\times$  block interactions ( $\sigma^2_{fb}$ ), and residual error ( $\sigma^2_e$ ) due to differences among trees in a plot — (2)

$$\sigma^2_w = \sigma^2_b + \sigma^2_{fb} + \sigma^2_e \quad (2)$$

However, the between-block component of variance  $\sigma^2_b$ , is, in practice, invariably excluded from estimates of  $\sigma^2_w$  used in heritability estimation (e.g. COTTERILL and ZED, 1980; MATHESON and RAYMOND, 1984; DEAN *et al.*, 1986). The within-family variance commonly employed for calculating individual heritability for progeny trials at one site is — (3)

$$\sigma^2_w = \sigma^2_{fb} + \sigma^2_e \quad (3)$$

Although the exclusion of between-block variance from estimates of individual heritability has become almost a tradition in forestry, the justification for ignoring  $\sigma^2_b$ , and the implications for practical application of heritability are often overlooked. The consequences can be inefficient selection and biased calculations of expected genetic gain.

The omission of  $\sigma^2_b$  from the denominator of individual heritability is based on the fundamental assumption that corrections will be made for the effects of blocks prior to using phenotypic measurements to select superior advanced-generation trees (via index selection, independent culling, or some other method of selection). Likewise, expected genetic gains calculated using heritabilities with  $\sigma^2_b$  omitted are relevant only to predicting the outcome of selection based on block-corrected measurements. However, many breeding operations in Australia, and other countries, continue to base selection of superior trees on raw (uncorrected) measurements or even visual appraisal. There is clearly an important contradiction in forestry between the estimation and application of individual heritability. In circumstances where no correction is made for the effects of blocks prior to selection, heritabilities should be calculated with the component  $\sigma^2_b$  included in the denominator (i.e. using Equation 2 substituted in Equation 1).

The importance of block effects in heritability estimation and gain prediction can be illustrated by examining results of a progeny trial of *Pinus caribaea* in northern Australia (progeny trial 467CRB reported by DEAN *et al.*, 1986) The trial involves about 1100 open-pollinated offspring of 25 families planted in single-tree plots across 48 randomised blocks. Trees were measured at 4½ years after planting for height and stem straightness assessed as a five-point subjective score with 5 = straight stems).

Variation between blocks ( $\sigma^2_b$ ) was found to account for 26% of the total variation in height of individual trees and the exclusion, or otherwise, of  $\sigma^2_b$  had a substantial influence on individual heritability. For instance, individual heritability for height estimated with  $\sigma^2_b$  omitted from the

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Table 1. — Variation due to families ( $\sigma_f^2$ ), blocks ( $\sigma_b^2$ ) and family  $\times$  block interactions ( $\sigma_{fb}^2$ ) in an open-pollinated progeny trial of *P. caribaea*. Figures in brackets give the percentage contribution of each component to total variation among trees. Individual heritabilities ( $h_I^2$ ) are estimated without and with  $\sigma_b^2$  included in the denominator, and corresponding expected gains ( $\Delta G$ ) are calculated for mass selection at an intensity of one tree in every 100 (standardised selection differential  $i = 2.67$ ).

	Height	Stem straightness
$\sigma_f^2$	0.0929 (5Z)	0.0315 (7Z)
$\sigma_b^2$	0.5215 (26Z)	0.0182 (4Z)
$\sigma_{fb}^2$	1.3595 (69Z)	0.3822 (89Z)
$h_I^2$ (without $\sigma_b^2$ ) <sup>A</sup>	0.26	0.30
$\hat{h}_I^2$ (with $\sigma_b^2$ ) <sup>B</sup>	0.19	0.29
$\Delta G^A$	0.84 m	0.52 point
$\Delta G^B$	0.71 m	0.51 point

<sup>A</sup> Estimated as:  $h_I^2 = 4\sigma_f^2 / (\sigma_f^2 + \sigma_{fb}^2)$ .

$$\Delta G = i h_I^2 \sigma_p \text{ where } \sigma_p = \sqrt{(\sigma_f^2 + \sigma_{fb}^2)}.$$

<sup>B</sup> Estimated as:  $\hat{h}_I^2 = 4\sigma_f^2 / (\sigma_f^2 + \sigma_b^2 + \sigma_{fb}^2)$ .

$$\Delta \hat{G} = i \hat{h}_I^2 \hat{\sigma}_p \text{ where } \hat{\sigma}_p = \sqrt{(\sigma_f^2 + \sigma_b^2 + \sigma_{fb}^2)}.$$

denominator was  $h_I^2 = 0.26$  (Table 1), while the corresponding estimate with  $\sigma_b^2$  included in the denominator was a considerably lower  $\hat{h}_I^2 = 0.19$ . Genetic gains in height which may be expected from individual selection of the tallest tree in every 100 in the progeny trial were 0.84 m for selection on block-corrected measurements, and 0.71 m for selection on raw measurements. The influence on expected gains of the higher heritability with  $\sigma_b^2$  omitted was partly offset by the fact that the phenotypic standard deviation  $\sigma_p$  (also important in determining expected gain) was reduced by the correction of data for blocks (see calculations of  $\sigma_p$ ; Table 1).

Nevertheless the correction of growth data for block effects can clearly have a substantial influence on the magnitude of both estimates of individual heritability and gains expected from selection. In comparing alternative progeny test designs SCHUTZ and COCKERHAM (1966) also found that adjustment for blocks may lead to significant increases in expected gain.

Variation between blocks was much lower in the case of stem straightness of *P. caribaea* with  $\sigma_b^2$  accounting for only 4% of the total variation in this trait (Table 1). The exclusion, or otherwise, of  $\sigma_b^2$  had little effect on estimates of individual heritability and expected gains for straightness. It is common for form traits to show much less variation across blocks compared with growth traits. For instance, in open-pollinated progeny trials of *P. radiata* in South Australia, variation across blocks commonly accounted for over 20% of the total variation in height but less than 5% of the total variation in straightness (COTTERILL and ZED, 1980). Nevertheless, both growth and form measurements should be routinely corrected prior to selection.

The simplest method of correction is to convert raw measurements to deviations ( $d_{jk}$ ) from the block means —

$$d_{jk} = Y_{jk} - \bar{Y}_{.k} \quad (4)$$

where  $Y_{jk}$  is the phenotypic measurement for say height at five years of the  $j$ th tree in the  $k$ th block, and  $\bar{Y}_{.k}$  the

block mean. In circumstances where multiple-trait selection indices are employed it is sometimes more convenient to compute index coefficients to combine absolute measurements of traits, rather than deviations. In this case the deviations  $d_{jk}$  for each trait can, of course, be converted to corrected absolute values by simply adding the overall mean  $\bar{Y}_{..}$  of the progeny trial.

More elaborate approaches such as least-squares, regressed least-squares or even best linear unbiased prediction (BLUP) may be used to correct data. However, in comparing alternative adjustment procedures COTTERILL *et al.*, (1983) found simple corrections (such as Equation 4) were reasonably reliable.

Discussion so far has been on individual heritabilities, but heritability may also be calculated on the basis of within-family deviations or family means. Much the same principles apply to the application of within-family heritability as for individual heritability. That is, variation between blocks should only be excluded from the denominator of within-family heritability where selection is to be based on within-family deviations which are corrected for the effects of blocks. Variation between blocks is always excluded from the denominator of family heritability because block effects should be eliminated (assuming a reasonably balanced experimental design) in the averaging of family performance across blocks.

Note that interactions between families and blocks (or families and sites; discussed later) are not considered in the strictly linear corrections for blocks (or sites) mentioned here. However, the components of variance due to these interactions are invariably included in the denominator of individual, within-family and family heritabilities (e.g.  $\sigma_{fb}^2$  in Equations 2 and 3) on the assumption that the effects are not removed from the data prior to selection. Of course, the selection of particular genotypes for particular sites would justify the omission of family  $\times$  site interaction variance from the denominators of heritabilities.

#### Variance due to Sites

Where progeny trials are replicated across multiple-sites, individual heritability is usually estimated with the variance due to sites ( $\sigma_s^2$ ) omitted from the denominator. In other words, using the following estimate of variance within-families —

$$\sigma_w^2 = \sigma_{fs}^2 + \sigma_{fb}^2 + \sigma_e^2 \quad (5)$$

where  $\sigma_{fs}^2$  is the variance due to family  $\times$  site interactions. The justification for excluding  $\sigma_s^2$  from the denominator of the individual heritability can only be that data is corrected for the effects of sites prior to selecting superior trees across multiple progeny trials. (This is assuming that trees are not being selected strictly for breeding for each particular site).

Corrections for the effects of site are most easily achieved by expressing phenotypic measurements as deviations from the site means. Of course, corrections would also be required for blocks within-site as well as site *per se*. In circumstances where site effects are large a preliminary log transformation is desirable to minimise scale effects and achieve greater homogeneity of variance. Another method of dealing with site effects is to employ selection indices which treat the expression of a single trait (say height) at different sites as different traits (BURDON, 1979).

In the case of within-family heritability the exclusion of variance due to site effects from the denominator obviously requires the assumption that within-family selection would

be on site-corrected data. In the case of family heritability variance due to sites is not included in the denominator because differences among families should be free of  $\sigma_s^2$  (assuming a balanced design and negligible scale effects). If, however, there is nonorthogonality in the representation of families across progeny trials a correction for site should be made to the family means before selecting best families (see methods given in COTTERILL *et al.*, 1983).

#### Variance due to Covariates

Heritability is sometimes calculated following analysis of covariance instead of analysis of variance. For instance, COTTERILL and ZED (1980) found individual heritabilities for stem diameter and volume of *P. radiata* at around five to eight years were increased by analysis of covariance using height measured at five months after planting as a linear covariate to remove maternal and nursery effects. However, the use of this sort of covariance analysis in estimating heritability implies that selection will be on phenotypic data corrected by regression techniques for differences in height at planting (i.e. corrected to a constant height at planting).

A simple linear method of correcting a measurement  $Y_j$  (say height of the  $j$ th tree at five years) for an independent variable  $X_j$  (say height at planting) is the regression — (6)

$$\hat{Y}_j = Y_j - b (X_j - \bar{X}_j) \quad (6)$$

where  $b$  is the regression coefficient of height at five years ( $Y_j$ ) on height at planting ( $X_j$ ), and  $\hat{Y}_j$  represents the corrected value for height at five years. HENDERSON *et al.* (1954) propose a similar approach for correcting the progeny performance of dairy sires for herd effects.

In the case of within-family heritabilities and family heritabilities estimated following analysis of covariance the

subsequent selection of trees or families should be on data corrected for the effect of the covariate.

#### Conclusions

Classical textbook formulae for estimating heritability can be at odds with the practical application of the parameter. In particular, variance due to environmental effects such as blocks and sites are invariably excluded from the denominator of estimates of individual (or within-family) heritability, regardless of whether the parameters are used to estimate gain from selection on corrected or uncorrected data. Gain calculations based on heritabilities with  $\sigma_b^2$  and/or  $\sigma_s^2$  omitted from the denominator may significantly overestimate the response which can be expected from selection on uncorrected data.

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## Buchbesprechungen

**Amélioration génétique des arbres forestiers.** Par L'E.N.-G.R.E.F. (Ed). *Revue Forestière Française*, Numéro spécial. Ministère de l'Agriculture, Nancy 1986. 288 pp.

After the description of the historical development of forest tree breeding in France and its research organization, well-known french forest tree breeders and esteemed international forest geneticists describe the actual stand of forest tree improvement and its future prospects from a french and international point of view. Aims, methods, strategies, current and anticipated results of breeding, programs in temperate and tropical zones and consequences for forestry practice are discussed. Achievements and economic evaluation of forest tree breeding conclude the comprehensive and well founded volume, and a short glossary describes the main technical terms.

The value of this volume would have been increased by the addition of summaries or abstracts in english language for each one of the articles, or at least a few chapters in english. Nevertheless it is hoped that this issue finds a world wide distribution, as it merits.

G. H. MELCHIOR (Großhansdorf)

**Lehrbuch der Genetik.** Von ELISABETH GÜNTHER. Grundbegriffe der modernen Biologie, Bd. 4, 5. Auflage. Gustav Fischer Verlag, Stuttgart, New York, 1986. 485 Seiten. DM 49,50.

Nachdem die 4. Auflage dieses Werkes schon kurz nach dem Erscheinen 1984 vergriffen war, ist nun eine unveränderte 5. Auflage erhältlich. Die in Greifswald, DDR, lesende Genetik-Professorin hat ein Lehrbuch verfaßt, das zur Aufgabe hat, Studierenden der Biologie, Medizin, Landwirtschaft u. a. genetisches Grundwissen zu vermitteln. Am Anfang des Buches steht ein Kapitel über die chemische Struktur der Erbanlagen, erweitert um moderne Methoden der Nucleinsäureforschung in der Genetik. Es folgt ein Kapitel über die Zytologie der Nucleinsäure enthaltenden Strukturen, wobei eine einführende Übersicht über die verschiedenen genetischen Systeme gegeben und Virus-, Bakterien-, und Eukaryotengenome, transponierbare Elemente, Plasmide, Mitochondrien- und Plastiden-DNA behandelt werden. Es schließen sich für das Verständnis genetischer Prozesse grundlegende Kapitel über Replikation, Verteilung, Merkmalsausbildung, Regulation und Modifikation an. Viele der folgenden Kapitel, die fast die Hälfte des Buches ausmachen, befassen sich mit Mutation und Rekombination, dabei wird auch die Rekombination durch parasexuelle Prozesse behandelt, die für die Biotechnologie von Bedeutung sind. Am Schluß stehen Kapitel, die kurze Einführung in umfassende Kenntnisse voraussetzende Bereiche der Genetik geben, wie Immunogenetik, rekombinante DNA, Populationsgenetik und nichtchromosomale Vererbung. Für diejenigen, die auf dem Gebiet der Genetik arbeiten, ist ein Lehrbuch natürlich nicht ausreichend, aber es bietet auf fast 500 Seiten mit zahlreichen Abbildungen, Beispielen und umfassendem Literatur- sowie Sachregister einen guten, aktualisierten Überblick über das Gesamtgebiet der Genetik.

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