HERITABILITY CONSTRUCTION FOR PROVENANCE AND FAMILY SELECTION

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ABSTRACT.--Concepts and procedures for heritability estimations through the variance components and the unified F-statistics approach are described. The variance components approach is illustrated by five possible family selection schemes within a diallel mating test, while the unified F-statistics approach is demonstrated by a geographic variation study. In a balance design, the use of the heritability formula $h^2 = 1-(1/F)$ is recommended. The F value is the same computed F value used in the analysis of variance for testing quality of genetic units.

Heritability is defined as "degree to which a character is influenced by heredity as compared to environment" (Snyder 1972). Although the concept holds in a general sense, heritability estimates vary with the way they are calculated. Heritability can be calculated in four ways: (1) parent-offspring correlation estimates degree of resemblance between parents and offspring; (2) regression estimates the selection differential in offspring as dependent on the selection differential in the parent; (3) intraclass correlation estimates the degree of resemblance among individuals within a genetic classification, and (4) genetic gain divided by selection differential estimates the efficacy of selection. These four methods are interrelated and may be used interchangably, but in certain cases adjustments should be made (Franklin 1974, Squillace 1974).

Heritability and gain estimates apply only to the experiments from which they were obtained. Furthermore, the selection differentials and heritabilities must apply to the same things, which may be individual trees, or family means (Wright 1976). Although single

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tree heritability and family heritability are formulated in most textbooks (Lerner 1958, Falconer 1960, and Becker 1964), heritability for other genetic units such as stand, ecotype, family within stand, full-sib family within female parent, or family and site combination, are seldom available.

In this paper we show how to break down phenotypic variation and construct heritabilities according to the experimental design, mating system, and selection scheme that are being used. The purpose is to help persons to make heritability estimates clearer and more consistent. In addition, we propose a unified formula for heritability, $h^2 = 1-(1/F)$, where F is the computed value for testing the null hypothesis that all genetic units are equal. This heritability is useful for predicting genetic gain of the genetic units being tested and selected.

Variance Component Approach

The basic concept of heritability is the genetic variance among units divided by the phenotypic variance among units. Therefore, the procedure for constructing heritability from analysis of variance can be described as follows:

1. Compute phenotypic variance among units
2. Identify variance components
3. Assemble genetic variance
4. Divide genetic variance by phenotypic variance

h^2 in the Clonal Test

In the simplest case, a clonal test, each ramet is assumed to have received total and identical genetic information from the ortet. The phenotypic expression of a seedling is affected by the genetic effect of the ortet and the environmental effect, with the following model:

$$Y_{ij} = \mu + G_i + E_{ij}$$

where Y_{ij} = phenotypic expression of the jth ramet from the ith ortet

μ = population mean in the test

G_i = genetic effect due to the ith ortet (i = 1 to n)

E_{ij} = random independent and normally distributed environmental effect (i = 1 to n, and j = 1 to r)

The ANOVA table is shown in table 1, where Ve and Vg are variance components for environment and genetics, respectively.

Table 1.--Analysis-of-variance table for a completely randomized clonal test

Source	df	MS	EMS
Clone	n-1	$\frac{r}{n-1}\sum_{i=1}^{n}(Y_{i.}-Y_{..})^2$	Ve + rVg
Within	n(r-1)	$\frac{1}{n(r-1)}\sum_{i+1}^{n}\sum_{j=1}^{r}(Y_{ij}-Y_{i.})^2$	Ve
Total indiv.	nr-1	$\frac{1}{nr-1}\sum_{i=1}^{n}\sum_{j=1}^{r}(Y_{ij}-Y_{..})^2$	$Ve + \frac{(n-1)r}{nr-1} Vg$

To construct heritability for clonal selection, we proceed as follows:

1. Compute phenotypic variance among clones and record as the value for Clone Mean Square.

2. Identify variance components: obtain Ve + Vg from Expected Mean Square (EMS).

3. Assemble genetic variance; solve two simultaneous equations for Ve and Vg and compute the value for rVg.

4. Divide the value for rVg by the Clone Mean Square.

Clonal heritability obtained is the form of $rVg/(Ve_2 + rVg)$, which is equivalent to the commonly accepted formula: $h^2 = Vg/(V\bar{g} + Ve/r)$ (Burton and Devane 1953).

h^2 in a Diallel Mating Test

Following the same procedure, we can construct heritability formulas suitable for various selection schemes after a diallel mating test.

Under the diallel mating scheme, every male mates with every female parent. For monoecious species, diallel mating includes a cross and reciprocal cross with every other tree. The statistical model is a two-way analysis of variance:

$$Y_{ijk} = \mu + M_i + F_j + MF_{ij} + W_{ijk}$$

where Y_{ijk} = the phenotypic value of seedling K produced from the ith male parent and the jth female parent (k = 1 to K).

μ = population mean

M_i = genetic effect from the ith male parent (i = 1 to I)

F_j = genetic effect from the jth female parent (j = 1 to J)

MF_{ij} = interaction between the ith male and jth female parents

W_{ijk} = experimental error (k = 1 to K)

In the conventional diallel analysis, where components are estimated from the ANOVA, heritabilities are estimated for male parents, female parents, and interaction (full-sibs). However, there are other selection schemes possible and each has its own heritability. Computation is possible by considering the sum of squares for the components in the diallel mating scheme.

The partitioning of variance can be facilitated by working with the individual expectation of sum of squares as listed in table 2.

Table 2.--Expectations of sum of square in a completely randomized diallel mating test

Line no.	Item	Interpretation	Coefficient for μ	σ^2_m	σ^2_f	σ^2_{mf}	σ^2_w
1	$\Sigma\Sigma\Sigma X_{ijk}^2$	Individual	IJK	IJK	IJK	IJK	IJK
2	$\Sigma\Sigma X_{ij.}^2/K$	Full-sib	IJK	IJK	IJK	IJK	IJ
3	$\Sigma X_{i..}^2/JK$	Half-sib in male	IJK	IJK	I K	I K	I
4	$\Sigma X_{.j.}^2/IK$	Half-sib in female	IJK	JK	IJK	JK	J
5	$X^2_{...}/IJK$	Correction term	IJK	JK	I K	K	I

Once we obtain the expected variance components for the sum of squares, we can proceed to the intermediate steps in formulating heritability:

A. The sum of squares for a "m" genetic unit within a "n" unit, SSQ m in n, is $SSQ_m - SSQ_n$. For example:

SSQ individual in plantation = SSQ individual - SSQ correction term

SSQ individuals within full-sib = SSQ individual - SSQ full-sib

SSQ full-sib within male parent = SSQ full-sib - SSQ half-sib in male

B. Heritability for differences among "m" units with "n" units is:

$$\frac{\text{Genetic Variance Component in SSQ m in n}}{\text{SSQ m in n}}$$

If we divide both the numerator and the denominator of the above formula by the degrees of freedom associated with the "m in n" unit, the numerator becomes genetic variance (Vg) and the denominator becomes phenotypic variance (Vp), and the result is the commonly accepted formula, $h^2 = Vg/Vp$. It is easier to work with SSQ than MSQ and ignore the degrees of freedom.

If we want to construct heritability for differences among full-sib families within male parent, we first determine the variance components within the SSQ full-sib in male. From lines 2 and 3 of table 2 we have:

$$\text{SSQ full-sib in male} = \text{SSQ full-sib} - \text{SSQ male}$$
$$= IK(J-1)\sigma_f^2 + IK(J-1)\sigma_{mf}^2 + I(J-1)\sigma_w^2$$

If we consider the first two terms as genetic contribution, the numerator in the heritability formula is:

$$IK(J-1)\sigma_f^2 + IK(J-1)\sigma_{mg}^2$$

and the denominator is simply SSQ full-sib in male, or all of its associate variance components.

If we further consider the genetic parameters in terms of additive genetic variance (Va) and dominance variance (Vd), we have $\sigma_f^2 = 1/4\ (Va)$, $\sigma_{mxf}^2 = 1/4\ (Vd)$ and $\sigma_w^2 = 2/4\ (Va) + 3/4\ (Vd) + \sigma_e^2$, and the numerator becomes:

$$IK\ (J-1)1/4(Va) + IK(J-1)1/4(Vd) + I(J-1)\ \{2/4(Va) + 3/4\ (Vd)\ \}$$

and the denominator becomes:

$$IK(J-1)1/4(Va) + IK(J-1)1/4(Vd) + I(J-1)\ \{2/4(Va) + 3/4(Vd) + Ve\}.$$

While the second consideration is more complete and academic, the first consideration is practical and useful in gain prediction. Heritabilities for family selection are therefore constructed on the basis of the first consideration (table 3).

Table 3.--Heritability computation for family selections

h^2 for differences among "m" (m)	within "n" (n)	Denominator obtained from lines	Variance Components in the Denominator: Genetic (also used in the numerator) Coefficient for σ^2_m	σ^2_f	σ^2_{mf}	Error Coefficient for σ^2_w
Full-sib	Plantation	2-5	JK(I-1)	IK(J-1)	K(IJ-1)	IJ-1
	Male	2-3	--	IK(J-1)	IK(J-1)	I(J-1)
	Female	2-4	JK(I-1)	--	JK(I-1)	J(I-1)
Half-sib						
Male	Plantation	3-5	JK(I-1)	--	K(I-1)	(I-1)
Female	Plantation	4-5	--	IK(J-1)	K(J-1)	(J-1)

In short, the generalized procedure for constructing heritability from analysis of variance is modified as follows:

1. Compute sum of square among genetic units as the denominator.
2. Identify variance components which will have contributed to the genetic gain.
3. Assemble these contributing variance components with their coefficients as the numerator.

The $h^2 = 1-(1/F)$ Approach

The basic concept of this unified formula is that all sources of variance within a genetic classification are considered as error as far as predicting gain from selection among such classification is concerned. For example, in a half-sib progeny test, 3/4 of the additive genetic variance and all of the dominance genetic variance present within family are useless for mother tree selection and are consequently included in the error term.

The F value for testing equality of means is a variance ratio: among-group variance divided by within-group variance. Therefore, the formula $h^2 = 1/(1/F)$ is:

$$h^2 = 1-1/(\text{MS group}/\text{MS error})$$

$$= \frac{\text{MS group} - \text{MS error}}{\text{MS group}}$$

$$= \frac{\text{Phenotypic Variance} - \text{Error Variance}}{\text{Phenotypic Variance Among Groups}}$$

$$= \frac{\text{Genetic Variance Among Groups}}{\text{Phenotypic Variance Among Groups}}$$

The steps in constructing this heritability are simply:

1. Calculate the F value suitable for testing the quality among groups.

2. Insert the computed F value and solve for $h^2 = 1-(1/F)$.

Most geographic variation studies fit the nested model and are useful here as an example. Stands (S_{ij}) are nested in different regions (R_i). Within-stand variation is considered to be environmental random error (E_{ijk}). We can express the model as:

$$Y_{ijk} = \mu + R_i + S_{ij} + E_{ijk}$$

The analysis of variance table is as follows:

Table 4.--Analysis of variance table for a nested design

Source	: df	: MS	: F	: EMS
Region	r-1	MS_r	MS_r/MS_s	$\sigma_e^2 + n\sigma_s^2 + sn\sigma_r^2$
Stand/Region	s-r	MS_s	MS_s/MS_e	$\sigma_e^2 + n\sigma_s^2$
Error	rsn-s	MS_e		σ_e^2
Total	rsn-1			

To compute heritability for regional difference, the F value to be used in the formula is obtained from MS_r/MS_s. By the same token, to compute heritability for stand difference within region, the F value is MS_s/MS_e.

Fixed and Random Models and Corresponding Heritability

Analysis of variance models may be classified as fixed, random, or mixed effect models. An effect is considered to be fixed if the researcher is interested only in the various levels of treatment used in his experiment. On the contrary, an effect is considered to be random if the researcher is interested in the population from which the treatments were drawn. The mixed effect model includes some treatments in fixed effects and some in random effects. An example using a multiplantation multiyear half-sib progeny test under various assumptions will help to interpret the heritability formula (table 5). For fixed effects the variance component represents variance among treatments in the experiment. For

random effects the various components represent variance of the population from which the sample of treatments were drawn.

I. Fixed Effect: Mother Tree. Random Effect: Site and Year.

In this case we would be interested in selecting mother trees that would perform well on an average site through the years. The F test for mother tree is M/(MS + MY - MSY) (Kempthorne 1967). Substituting the expected mean square into the heritability formula, we have:

$$h^2 = 1-1/F$$

$$= (M - MS - MY + MSY)/M$$

$$= \frac{Vm}{\frac{Ve}{nsy} + \frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s} + Vm}$$

The interpretation of this formula is that all effects other than the mother tree are useless errors in selection.

Table 5.--Multiplantation and multiyear model for heritability computation (only the relevant EMS are listed)

Source	: df :	MSQ	: EMS
Site	s-1	S	
Year	y-1	Y	
SxY	(s-1)(y-1)	SxY	
Mother tree	(m-1)	M	Ve+nVsym+nsVym+nyVsm+nsyVm
MxS	(m-1)(s-1)	MS	Ve+nVsym +nyvSm
MxY	(m-1)(y-1)	MY	Ve+nVsym+nsVym
MxSxY	(m-1)(s-1)(y-1)	MSY	Ve+nVsym
Replication	sy(n-1)	R	
Error	sy(n-1)(m-1)	E	Ve

II. Fixed Effect: Mother Tree and Site. Random Effect: Year

In this case we would be interested in selecting mother trees that would perform well on a specific site. The F test is M/MY. So we have:

$$h^2 = 1 - 1/F$$

$$= (M-MY)/M$$

$$= \frac{\frac{Vsm}{s} + Vm}{\frac{Ve}{nsy} + \frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s} + Vm}$$

Under this model both mother tree and mother tree x site interaction are genetic and useful, while error, mother tree x year x site and mother tree x year, are considered as non-genetic and useless.

III. Fixed Effect: Mother Tree, Site and Year

If the year effect is found to be related to some controllable factors (for example, amount of rainfall and pattern of rainfall can be simulated by irrigation), then we might be interested in selecting mother trees under a specific site and repeatable conditions. The F test in this model is M/E. So we have:

$$h^2 = 1 - 1/F$$

$$= (M - E)/M$$

$$= \frac{\frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s} + Vm}{\frac{Ve}{nsy} + \frac{Vsym}{sy} + \frac{Vym}{y} + \frac{Vsm}{s}}$$

The interpretation would be that of all the mother tree effect and its interaction with site and year are genetic and useful for selection.

Discussion and Conclusions

For a given model, both approaches yield an identical estimate of heritability. When the experimental design is balanced, the $h^2 = 1-(1/F)$ approach is recommended. The procedure is simple and useful for predicting genetic gain for the units being tested. The F-value is readily available from the analysis-of-variance table used for testing the quality of genetic unit means. There is no need to compute variance components and their coefficients, no worry about negative components, and no doubt about what goes into the heritability formula. However, the model that is being used and its implications must be thoroughly defined, and the F-value should be significant at a certain level. For example, it would be in error in a one-parent progeny test to consider families as fixed effects and then apply heritability and genetic gain values to the parent population. The concept of model effects and the appropriate F-value are more common than the expected variance components in most introductory statistics books (Li 1964, Ostle 1964, Bliss, 1967, and Daniel

1974). It appears to be easier for tree improvement workers to find the appropriate F-ratio than to determine which genotypic x environmental interactions should be included in the error term of the heritability formula.

If the experimental design is not balanced, the task of formulating a valid F-value may be as difficult as solving variance components. In an unbalanced design, the F-ratio and consequently the heritabiility is only an approximate value. Most provenance tests can be handled as nested analysis of variance with unequal sample sizes. Sokal and Rohlf (1969) gave two good examples in computing variance components and the approximate test of significance based on a reconstituted mean square.

The $h^2 = 1-(1/F)$ concept regards any repeatable effect present among genetic units as inheritable. For example, when testing wind pollinated progenies, the mother-tree effect includes not only the additive genetic contribution of the mother tree, but also the contribution of the wind-borne pollen as well as the extra chromosomal inheritance. On the other hand, this formula disregards any genetic variance within units. The variance components approach, by defining genetic and non-genetic variances, can demonstrate explicitly the definition of heritability (that portion of phenotypic variance due to genetic effects). However, the $h^2 = 1-(1/F)$ approach is functional for predicting gain in family, stand, and ecotype units.

The $h^2 = 1-(1/F)$ approach is restricted to the units being tested and selected, whereas the variance components approach is more flexible in estimating other related heritabilities. For example, in a progeny test, heritability of individual differences, useful in predicting gain in mass selection, can be constructed only by the variance components method.

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