DETERMINING TEST AND BLOCK NUMBERS IN CONSIDERATION OF PROGENY TESTING QUALITY AND COST: AN EXAMPLE OF HALF-SIB FAMILIES WITH RCB DESIGN AND SINGLE-TREE PLOTS

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ABSTRACT

Cost-effective test and block numbers for tree progeny testing using randomized complete block designs (RCB) with single-tree plots were investigated through a generalization of the relationships between progeny testing quality criteria and test design parameters. Optimal test and block numbers were defined as those that achieve an adequate level of testing quality using the minimum resources. Results indicated that the desirable test and block numbers were functions of the target quality criteria, genetic architecture of a character and costs associated with each additional test site. A trait with low heritability and strong G × E interaction generally required a larger number of test sites than one with high heritability and weak G × E interaction to reach the same level of testing quality. Higher cost for each additional site favored using fewer test sites and more blocks per site. A testing quality standard higher than 90 % in the reliability of breeding value prediction consumed substantially more resources than one of 75–85 %. Desirable test and block numbers were provided to satisfy different progeny testing quality requirements under various scenarios of genetic architecture of a trait and the cost associated with each additional site.

Key words: progeny test, field design, test numbers, family heritability, sampling variance.

INTRODUCTION

Progeny testing is an essential component of a tree improvement program. Major goals of progeny tests are to estimate genetic parameters and rank genotypes (parents and offspring) for selection (LIBBY 1973; WHITE 1987; WHITE & HODGE 1989; HUBER *et al.* 1992; WHITE *et al.* 1993; WHITE 1996). Progeny tests are, however, costly to establish, maintain and measure, which often constitute a prominent proportion of a tree improvement budget (WHITE *et al.* 1993, 1999). Optimal field test designs are required to allocate reasonable resources to achieve adequate progeny testing quality while avoiding excessive investment.

A number of studies have been carried out to determine the optimal numbers of test sites and/or offspring per genetic entry per site. ROBERTSON (1957) studied the optimum family size in a single test based on a complete random (CR) design with the constraint of fixed total test units. COTTERILL and JAMES (1984) investigated the optimal number of offspring needed to detect certain levels of difference among family means at a single site. Because a tree improvement program is usually implemented in a relatively large breeding zone, in which varying environmental conditions are expected, multi-site tests are therefore necessary to provide information on genotype × environment (G × E) interactions (JOHNSON & BURDON 1990; CARSON 1991; HUBER *et al.* 1992; DIETERS *et al.* 1995; WHITE 1996; JOHNSON 1997; POWARAYI *et al.* 1997).

For multi-site solutions, DICKERSON (1962) and WRIGHT (1976) investigated the effects of test numbers on the efficiency of selection response under a constraint of fixed number of test units. HUBER *et al.* (1992) studied the efficiency of test numbers on the estimation of G × E interactions. LINDGREN (1985) further attempted to search for the cost-efficient numbers of progeny tests for ranking genetic entries by integrating economic constraints, such as extra costs associated with an additional test site. Although results from these studies may be optimal from the perspectives of statistical or economic efficiencies under the imposed constraints, they did not give sufficient consideration of progeny testing quality. Results are sometimes difficult to apply to tree improvement operations because some of the "optimal solutions" become less

biologically or practically meaningful. For instance, with DICKERSON (1962) and WRIGHT (1976)'s approach, the highest efficiency of selection response would be achieved by using the fewest replications per test (LINDGREN 1985) or a single site because selection efficiency monotonically decreases as the number of test unit increases. Under certain levels of economic constraints and variance structures, LINDGREN's (1985) cost-efficient optimum solution also resulted in a single test site, which would not allow for the partitioning of additive genetic variance from that of G × E interaction. From an operational perspective, WHITE and HODGE (1992) searched for the necessary test numbers by examining the effects of a range of test sites on the precision of breeding value prediction (*i.e.*, $Corr(g,\hat{g})$) using empirical tree improvement data with a RCB design, 4 blocks and 5-tree plots. Their study emphasized the minimum resources required to maintain an adequate progeny testing quality.

Recent studies in experimental designs have suggested that a RCB design using single-tree plots is more statistically efficient in tree progeny test (LOO-DINKINS & TAUER 1987; LOO-DINKINS *et al.* 1990; WHITE 1996). Moreover, different traits and/or species may have different genetic architectures and G × E interactions to be considered in progeny testing designs, especially at the early stages of tree improvement. In this study, we extended the concept of WHITE and HODGE (1992) with a generalized approach that incorporated many possible progeny test scenarios in determining desirable test and block numbers. We attempted to search for the minimum progeny test and block numbers to ensure an adequate progeny testing quality using a RCB design with single-tree plots.

METHODS

Main assumptions

In contrast to an assumption of fixed number of test units in some of the previous studies, it was assumed that resources were not limited to achieve a certain level of progeny testing quality. Therefore, necessary progeny testing quality was not sacrificed for unnecessarily lower cost or higher statistical efficiency, because higher statistical or economic efficiencies did not necessarily assure an acceptable progeny testing quality. For many operational tree improvement programs, such an assumption would be reasonable because acceptable quality often takes priority to a lower cost. A constraint on fixed test units was imposed in previous studies to search for a relative maximum (or minimum) with a monotonically increasing (or decreasing) asymptotic function, which would, otherwise, exist only at the boundaries of their domains. Optimal solutions from such approaches were, therefore, likely to be functions of the test units assumed.

In the current study, it was attempted to search for the test and block numbers that accomplish a predetermined testing quality using the fewest resources possible. Different scenarios of genetic architectures (*i.e.*, h^2, r_B) of a trait and cost penalties for each additional site were taken into consideration. While the experimental design was based on RCB with single-tree plots, the results were easily extendable to complete random (CR) or RCB design using plots as experimental units, such as in plant breeding.

Progeny testing quality criteria

1) Precision in breeding value prediction

An essential goal of progeny testing is to rank genotypes based on predicted breeding values (BVs) (WHITE & HODGE 1989; WHITE *et al.* 1993). Prediction error variance is larger for predicted BVs when genotypes are poorly tested (WHITE & HODGE 1989; HUBER 1993; MRODE 1996; HODGE 1997), which means that a relatively genetically inferior genotype could be ranked higher, resulting in potential wrong decisions in selection. Thus, a certain level of breeding value prediction precision is necessary to reduce uncertainties in genotype ranking and selection (WHITE *et al.* 1993; WHITE 1996).

For genetically unrelated parents, it can be shown that the precision of breeding value prediction (*i.e.*, $Corr(g,\hat{g})$) is equivalent to the square-root of the parental heritability (*e.g.*, family heritability for half-sibs) (WHITE & HODGE 1989; MRODE 1996). Therefore, a multi-site family heritability for half-sib families and its sampling variances are appropriate criteria to evaluate the quality of breeding value prediction.

2) Sampling variances of genetic parameter estimates

A unique purpose of multi-site progeny testing is to estimate G × E interaction. Partitioning G × E variance from additive genetic variance is critical for unbiased estimation of heritability (HUBER *et al.* 1992; WHITE 1996; LU *et al.* 1999), which, in turn, affects the estimation accuracy of responses from selections (FALCONER 1981; WHITE 1996). Thus, sampling variances of the estimates of G × E variance components and heritability are appropriate indicators.

Generalization of relationships for multi-site half-sib progeny tests

Assuming that (f) genetically unrelated half-sib families are tested over (t) site using a RCB design and single-

tree plots with (n) blocks per site, if approximate information is available about individual heritability (h_i^2) and type-B genetic correlation (r_B) (BURDON 1977) for the character of interest, it can be shown (see Appendix 1–3) that there exist the following relationships:

1) Multi-site family heritability:

$$h_f^2 = \frac{tn}{\frac{4}{h_i^2}+\left(\frac{1}{r_B}-1\right)(n-1)+tn-1} \quad [1]$$

2) Sampling variance of variance component for G × E interaction:

$$\mathrm{Var}(\sigma_{fe}^2) = \frac{2(\sigma_p^2)^2}{n^2}\left[\frac{\left[1+\frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B}-1\right)-1\right]\right]^2}{(t-1)(f-1)+2}+\frac{\left(1-\frac{h_i^2}{4r_B}\right)^2}{t(n-1)(f-1)+2}\right] \quad [2]$$

where, f is the number of half-sib families tested across t sites, σ_p^2 is the total phenotypic variance (see Appendix 2).

3) Approximate sampling variance of h_f^2:

$$\mathrm{Var}(h_f^2) \approx \frac{2}{f+1}+\frac{2\left[1+\frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B}-1\right)-1\right]\right]^2}{[(t-1)(f-1)+2]\left[1+\frac{h_i^2}{4}\left[\left(\frac{1}{r_B}-1\right)(n-1)+tn-1\right]\right]^2} \quad [3]$$

Eq. 3 implies that: $\lim_{\substack{t\to\infty \\ n\to\infty}}\left[var(h_f^2)\right] \approx \frac{2}{f+1}$ [4]

4) Approximate sampling variance for estimates of h_i^2:

$$Var(h_i^2) \approx \frac{32}{(tn)^2}\left[\frac{\left[1+\frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B}-1\right)+tn-1\right]\right]^2}{(f-1)+2}+\frac{\left[1+\frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B}-1\right)-1\right]\right]^2}{(t-1)(f-1)+2}\right] \quad [5]$$

and $\lim_{\substack{t\to\infty \\ n\to\infty}}\left[var(h_i^2)\right] \approx \frac{2(h_i^2)^2}{f+1}$ [6]

Eq. 1, 2, 3 & 5 are functions of test design parameters. Once h_i^2 and r_B are estimated, it is simple to estimate the sampling variances of heritability estimates. Eq. 4 & 6 further indicate that the lower limits for sampling errors of heritability estimates can only be further lowered through using more genetic entries in a progeny test.

Economic considerations

LINDGREN (1985) indicated the necessity of considering economic factors in determining the optimal number of test sites. The argument was that more costs would accrue for each additional test site. Thus, using more test sites and fewer blocks per site may not necessarily be economically efficient.

It is reasonable to assume that a part of progeny testing costs are linearly related to the total number of progeny per genetic entry, while the other part is a function of the number of test sites (LINDGREN 1985). If the cost for using each additional site is expressed as an undetermined proportion (P %) of the costs had one site been used, the total costs for testing each genetic entry over t sites can be expressed as:

$$Cost = tn + tn*p(t-1) = tn[1+p(t-1)] \quad [7]$$

and a relative efficiency for the increase in per cost unit can be expressed as:

$$E = \frac{h_f^2}{\cos t} = \frac{h_f^2}{tn[1+p(t-1)]} \quad [8]$$

where, t and n are, again, the numbers of test sites and blocks per site.

Because test designs with different block numbers at each site will need different numbers of sites to reach the same level of h_f^2, Eq. 8 can provide an assessment for their relative economic advantages under different P values.

Optimal numbers of tests and blocks

Optimal numbers of test sites and blocks per site were defined as the numbers that result in the minimum cost to achieve an adequate level of progeny testing quality. This excluded, however, scenarios that are purely statistically or economically optimal but unable to produce acceptable progeny testing quality. For example, test designs using a single-site were not considered optimal for reasons discussed above. Evidently from Eq. 1–5, h_f^2 is larger and $var(\sigma_{fe}^2)$, $var(h_f^2)$ and $var(h_i^2)$ are smaller as t and n increase. There is no straightforward mathematical approach to derive the optimal t and n from the above monotonically increasing or decreasing asymptotic functions because the relative maximum or minimum only occurs at the boundaries of the domains. One approach was to computationally compare a range of t and n combinations for their costs to achieve a given level of progeny test quality criteria (*i.e.*, h_f^2, $var(\sigma_{fe}^2)$, $var(h_f^2)$ and $var(h_i^2)$) under different scenarios of genetic architectures (h_i^2 and r_B) and economic penalties (P %). A second approach was to firstly find the most efficient block numbers (n) per site for a reasonable progeny test target quality (*i.e.*, h_f^2 $var(\sigma_{fe}^2)$, $var(h_f^2)$ and $var(h_i^2)$) based on economic analyses, and then reverse Eq. 1 to calculate the test site numbers as:

$$t = \frac{h_f^2\left[4 + h_i^2\left[\left(\frac{1}{r_B} - 1\right)(n-1) - 1\right]\right]}{nh_i^2(1-h_f^2)} \quad [9]$$

The former approach was used in this study to search for the desirable test and block numbers for a predetermined level of progeny testing quality in Table 1.

RESULTS

Effects of t and n on h_f^2

The effects of test and block numbers on the estimates of h_f^2 are shown in Fig. 1 based on Eq. 1. To reach a certain level of h_f^2, different numbers of test site were needed for designs using different block numbers per site. The more blocks per site, the fewer tests needed, and vice versa. The increase of h_f^2, however, became flat for all block numbers when the test numbers were large. Although using more blocks per site could reduce the number of test sites required, the efficiency was substantially lowered, especially when block numbers exceeded 20. For instance, h_f^2 increased more from 5 to 10 blocks per site than from 10 to 20 blocks per site, and using 30 blocks per site showed very limited increase in h_f^2 over 20 blocks per site given the same number of test sites (Fig. 1).

The number of sites needed to reach a certain value of h_f^2 was also strongly affected by the genetic architectures of the trait of interest. When heritability was low and G x E interaction was strong, more tests were needed to achieve an adequate precision in breeding value prediction. For example, for a constant 20 blocks per site, 11 tests would be necessary to achieve BV prediction precision of 0.90 (*i.e.*, $h_f^2 = 0.81$) if $h_i^2 = 0.1$ and $r_B = 0.6$. This number could, however, be reduced to 8 tests if when $h_i^2 = 0.1$ and $r_B = 0.9$, or 3 tests if $h_i^2 = 0.3$ and $r_B = 0.9$.

Effects of t and n on sampling variances of G x E variance

The relative importance of sampling errors of G x E variances (*i.e.*, $s.e.[\sigma_{fe}^2]$) was expressed as $s.e.[\sigma_{fe}^2]/\sigma_f^2$, assuming the total phenotypic variance being 1.0 after data standardization (Fig. 2). This expression was more

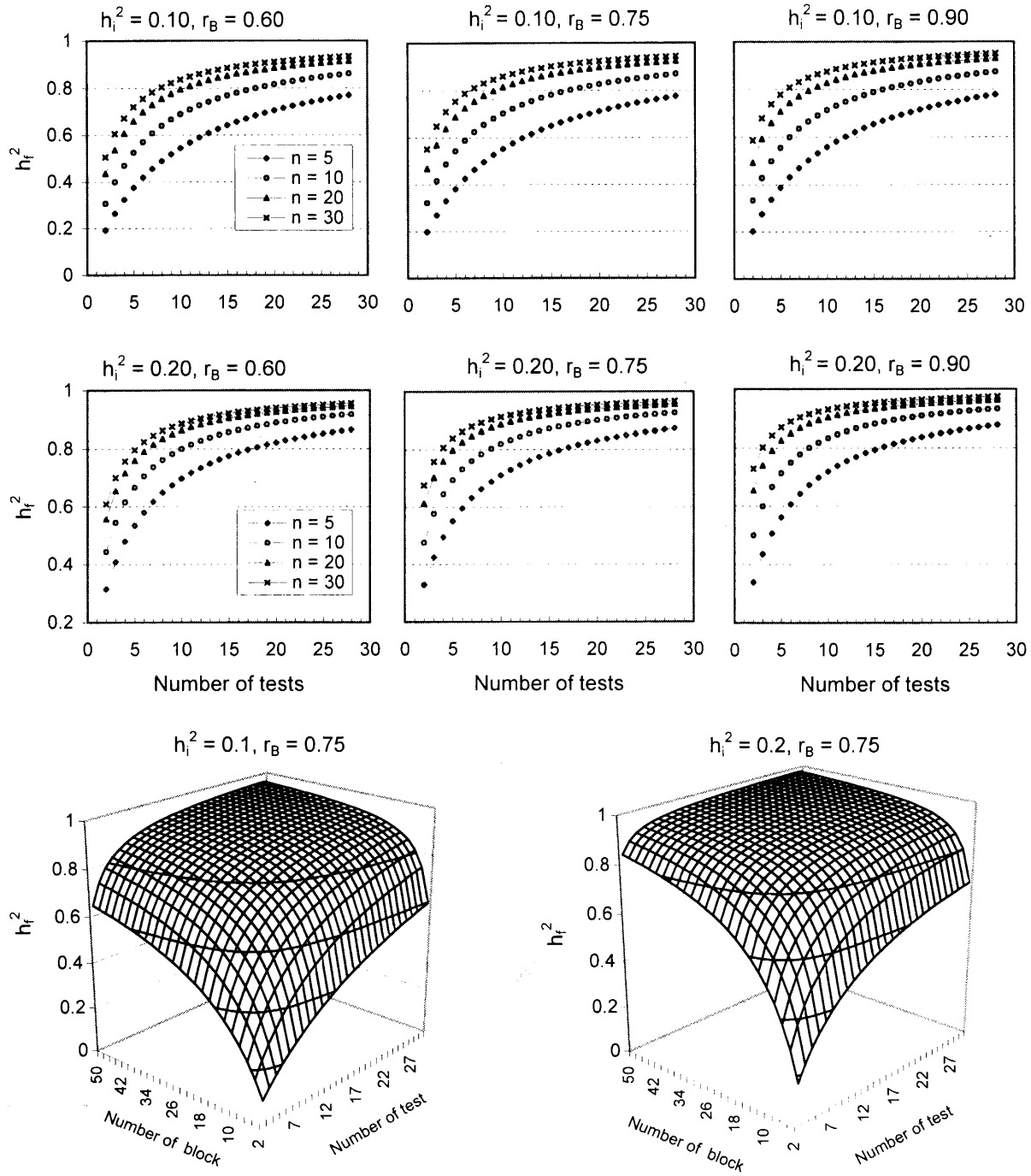

Figure 1. Effects of test and block numbers on the estimates of family heritability under varying genetic architectures (h_i^2 and r_B) and arbitrary metric trait. Note, $r_B=\sigma_f^2/(\sigma_f^2+\sigma_{fe}^2)$.

meaningful than $s.e.[\sigma_{fe}^2]$ itself because it eliminated the scale effects and could show the degrees that the sampling errors of σ_{fe}^2 might complicate the estimates of σ_f^2 and r_B, since the estimation of the latter depends on the precision of σ_{fe}^2 under the traditional ANOVA approach (SEARLE *et al.* 1992). Fig. 2 shows that the sampling error of σ_{fe}^2 could be reduced as the number of test increases. The reduction, however, became very limited after approximately 5 tests for test designs with different numbers of blocks per site. It was noted that the magnitudes and patterns of $s.e.[\sigma_{fe}^2]/\sigma_f^2$ were very similar between n = 20 and n = 30, suggesting, again, that more than 20 blocks per site would do little to

Table 1. Desirable test (t) and blocks/replication (n) numbers for a RCB design with single-tree plots to achieve a level of precision in breeding value prediction under different cost levels for each additional test site.

Genetic architecture		Target	Cost factor (P)							
			$P = 0.05$		$P = 0.15$		$P = 0.25$		$P = 0.35$	
h_i^2	r_B	h_f^2	t	n	t	n	t	n	t	n
0.10	0.60	0.80	11	18	8	29	7	35	6	46
	0.70	0.80	8	24	5	46	4	67	4	67
	0.80	0.80	7	25	4	50	3	75	3	75
0.20	0.60	0.80	10	10	7	17	6	22	5	30
	0.70	0.80	7	14	5	23	4	33	4	33
	0.80	0.80	6	15	4	25	3	38	2	72
0.30	0.60	0.80	8	9	7	11	6	14	5	19
	0.70	0.80	7	9	6	11	5	14	4	20
	0.80	0.80	5	12	4	16	3	24	2	46
0.10	0.60	0.75	7	23	6	29	5	38	4	57
	0.70	0.75	6	25	5	31	4	43	3	68
	0.80	0.75	4	36	3	51	2	93	2	93
0.20	0.60	0.75	7	11	6	14	5	19	5	19
	0.70	0.75	6	12	5	15	4	21	3	33
	0.80	0.75	6	11	3	25	3	25	2	45
0.30	0.60	0.75	9	5	7	7	5	12	4	18
	0.70	0.75	6	8	5	10	3	21	3	21
	0.80	0.75	6	7	4	11	3	16	2	29
0.10	0.60	0.70	6	20	5	26	4	36	4	36
	0.70	0.70	6	18	4	30	3	45	3	45
	0.80	0.70	4	26	3	37	2	64	2	64
0.20	0.60	0.70	7	8	5	13	4	18	3	29
	0.70	0.70	5	11	4	14	3	22	3	22
	0.80	0.70	4	13	3	18	2	31	2	31
0.30	0.60	0.70	7	5	5	8	4	11	4	11
	0.70	0.70	4	9	4	9	3	14	3	14
	0.80	0.70	3	12	2	20	2	20	2	20
0.10	0.60	0.65	6	15	5	19	4	26	3	40
	0.70	0.65	5	17	3	32	3	32	2	59
	0.80	0.65	4	20	3	28	2	47	2	47
0.20	0.60	0.65	5	9	4	12	3	19	3	19
	0.70	0.65	4	11	3	16	2	28	2	28
	0.80	0.65	4	10	2	23	2	23	2	23
0.30	0.60	0.65	5	6	4	8	3	12	3	12
	0.70	0.65	4	7	3	10	3	10	2	18
	0.80	0.65	3	9	2	15	2	15	2	15

Note, BURDON's type-B genetic correlation is expressed as: $r_B = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2}$.

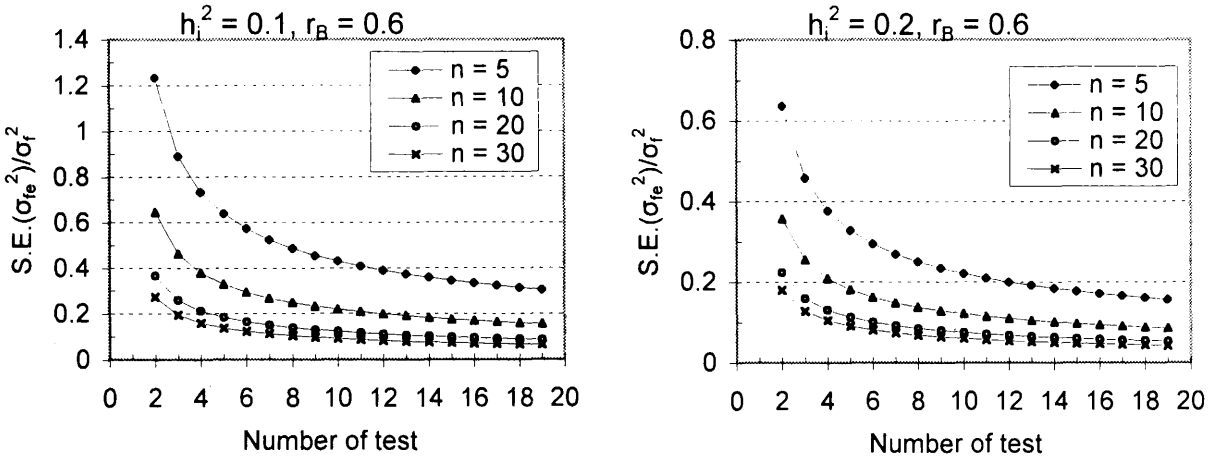

Figure 2. Effects of test and block numbers on the sampling variances of G × E interaction expressed as: $s.e.(\sigma_{fe}^2)/\sigma_f^2$. Note, $r_B=\sigma_f^2/(\sigma_f^2+\sigma_{fe}^2)$.

improve the precision of variance component estimation.

Similar to the estimates of h_f^2, genetic architectures of traits under consideration affected the number tests needed to reduce the ratio of $s.e.[\sigma_{fe}^2]/\sigma_f^2$ at a certain degree. Only 3 tests were required to control the ratio under 0.1 when h_i^2 = 0.3 and r_B = 0.8, as compared with 11 tests when h_i^2 = 0.1 and r_B = 0.6 (Fig. 2).

Effects of *t* and *n* on sampling variances of h_f^2 and h_i^2

Fig.3 shows the effects of test and block numbers on the sampling errors of family and individual heritability estimates based on Eq. 3 & 5, expressed as the proportion of standard error relative to the h_f^2 or h_f^2 estimates (*i.e.*, S.E.[h_f^2]/h_f^2*100%). The genetic entries used in the calculation were 100 half-sib families, which was a fairly common number in tree progeny trials using single-tree plots (WHITE 1996). Evidently, the precision of heritability estimation was a concern because s.e.[h_f^2] and s.e.[h_i^2] could account for quite large a proportion of the estimates when test numbers were too few. For example, when h_i^2 = 0.1 and r_B = 0.60, s.e.[h_f^2] and s.e.[h_i^2] could account for 30 % to 100 % of their respective estimates when 2 sites were used, depending on the number of blocks per site, which varied between 5 and 30 in this calculation. To control S.E.[h_f^2] and S.E.[h_f^2] under 20 % relative to their estimates, at least 5 sites were required for traits with low heritability or strong G × E interaction (Fig. 3). Interestingly, it was shown (Appendix 4) that s.e.[h_f^2]/h_f^2 = s.e.[h_i^2]/h_i^2 = $s.e.[\sigma_f^2]/\sigma_f^2$, which indicated that the relative precision of heritability estimation was almost entirely determined by the precision of additive genetic variance estimation.

Relative economic efficiency

To reach a given level of family heritability, different numbers of total test units were required for designs using different numbers of blocks per site (Fig. 1). For example, to achieve h_f^2 = 0.80, approximately 90, 110, 150 and 195 test units were required for *n* = 5, 10, 20 and 30, respectively, which involved approximately 19, 11, 8 and 7 test sites. If no extra cost were to incur for an additional test site (*P* = 0 %), the test design with the fewest blocks per site would win. The pattern was, however, changed considerably when 10% or more of the total costs were added for each additional test site being included (Fig. 4 I–III). Economic efficiency for 30 blocks per site was, however, close to that of 20 blocks for P values ranging from 10 % to 30 %. Economic efficiencies for using fewer blocks per site were compromised by the extra cost associated with an additional site. Economic efficiencies were also lower for using more blocks per site because the improvement in progeny test quality became minor when block number were too large. The relative efficiency steadily decreased as the total number of test units increased, either through more test sites or blocks per site (Fig. 4 IV).

Desirable test and block numbers

Table 1 provides some desirable test and block numbers that have higher economic efficiencies under different scenarios of biological and economic considerations and quality requirements. These numbers were obtained through the comparisons on the relative efficiencies (*i.e.*, Eq. 8) for a range of possible combinations of test and block numbers under different genetic architectures of a trait and the economic penal-

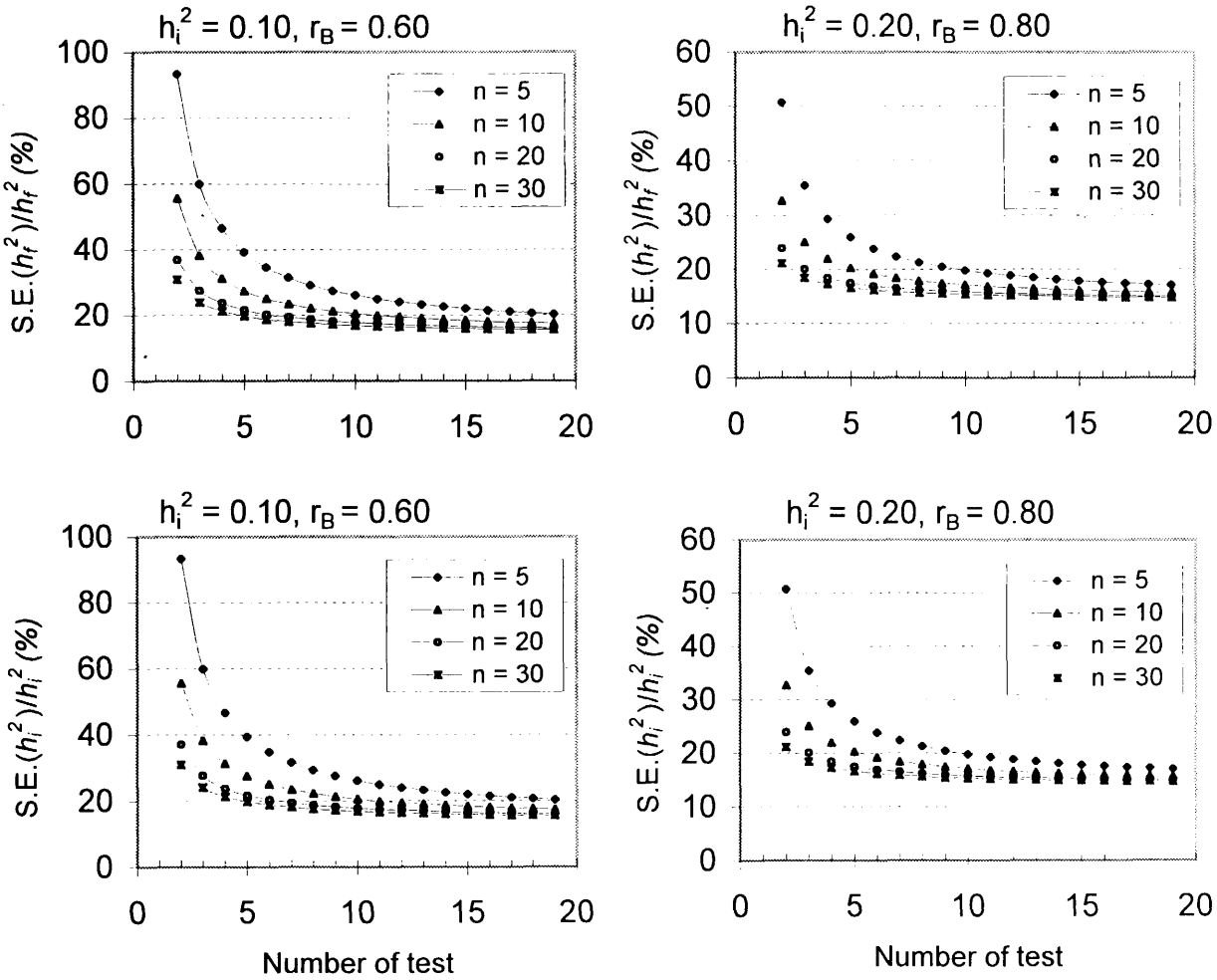

Figure 3. Effects of test and block numbers of progeny test design on the precision of heritability estimates as expressed in the form : $s.e.(h_x^2)/h_x^2 * 100\%$. Note, $r_B = \sigma_f^2/(\sigma_f^2 + \sigma_{fe}^2)$.

ties for using an additional test site. Although these selected numbers might not have the globally highest statistical or economical efficiency, they ensured a certain level of progeny testing quality with the possibly lowest costs.

DISCUSSION

The established relationships between progeny test design parameters (*i.e.*, test site and block numbers) and progeny testing quality criteria have provided a convenient display of the changes of progeny testing quality over a range of test design scenarios. Tree improvement practitioners can use these equations to produce the graphic curves to predict the anticipated progeny testing quality for a chosen test design. The by-products from this study were the approximate sampling variances for some key genetic parameter estimates which can be easily calculated when estimates of individual heritability and type-B genetic correlation (BURDON 1977) become available.

The monotonically increasing asymptotic curves of progeny testing quality criteria as functions of test and block numbers (Fig. 1) indicated that the most statistically or economically efficient solutions may not be biologically optimal. Because the highest statistical or economic efficiencies were achieved through using the fewest test sites or/and blocks per test (LINDGREN 1985; HUBER *et al.* 1992) and selection efficiency monotonically decreased as the number of test unit increased (Fig. 4), they were unlikely to yield acceptable precision in breeding value prediction and genetic parameter estimation (Fig. 1–3). Therefore, it only became meaningful to seek higher statistical efficiency after ensuring an adequate progeny testing quality. Optimal test and block numbers could, therefore, be more appropriately defined as the minimum resources necessary to achieve a target progeny testing quality. Genetic architectures of a trait of interest considerably

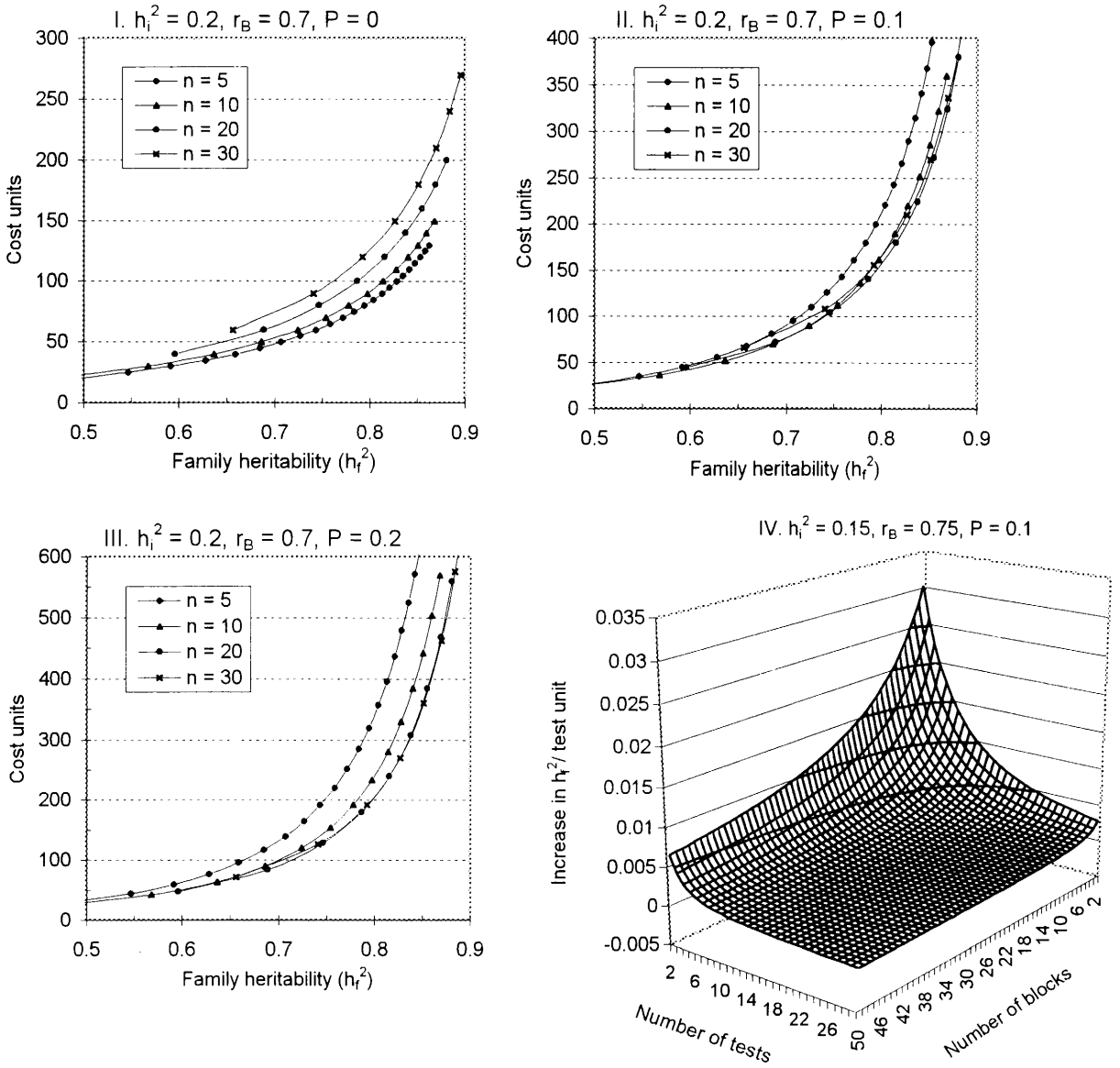

Figure 4. Relationship between cost unit and family heritability for different numbers of blocks per site under the assumption of varying extra cost for each additional site to be used (I–III) and the relative efficiency in increasing family heritability with increasing test units (IV). Note, $r_B=\sigma_f^2/(\sigma_f^2+\sigma_{fe}^2)$.

influenced the number of test needed to achieve the quality goals. Lower heritability and stronger G × E interaction generally required more test sites than higher heritability and weaker G × E interaction. But, relatively speaking, heritability was more influential than G × E interaction (Fig. 1–3). For example, for the same levels of G × E interaction (r_B = 0.75) and block number (n = 20), only 5 tests were required to reach a level of h_f^2 = 0.80 when h_i^2 = 0.2, in contrast to 9 tests if h_i^2 = 0.1 (Fig. 1). Implications to tree breeding were that it may be more beneficial to have fewer, but well-established and intensively maintained progeny tests to achieve higher heritability by creating more homogeneous environmental conditions than have more extensively managed progeny tests of low heritability due to environmental noises. For the same levels of heritability and target progeny testing quality, it seemed more desirable to use more tests and fewer blocks per test to achieve higher economic efficiency for a trait showing strong G × E interaction. Weak G × E interaction, on the other hand, favored using fewer tests and more blocks per test (Table 1).

Statistical efficiency was higher for test designs with smaller number of blocks per site and larger

number of test sites for a fixed number of test units. Extra costs incurring to each additional test, however, quickly reversed such trends when P % = 10 % or larger (Fig. 4). Larger P % values favored using more blocks per sites and fewer test sites. Large number of blocks per site could not, however, steadily increase progeny testing quality. The improvement in progeny testing quality was substantially reduced when block number exceeded 20 (Fig. 1–3), although 30–40 blocks per site could still be as economically efficient as 20 blocks per site if P % was large (Fig. 4). Also, a target progeny test quality should not be set too high, substantially more test units and costs were required to achieve h_f^2 higher than 0.8 for a trait with h_i^2 around 0.1 and 0.85 for h_i^2 = 0.2 (Table 1, Fig. 4), because the surfaces of h_f^2 became very flat thereafter. Therefore, 0.80 for the reliability of breeding value prediction (*i.e.*, $Cor(g,\hat{g}) \approx 0.90$) seemed to be an upper limit for most scenarios of tree progeny testing.

Desirable test and block numbers should simultaneously satisfy the precision in breeding value prediction and the estimation of genetic parameters. The probability was high that the recommended numbers in Table 1 could produce such desirable results with the lowest costs possible under different progeny test scenarios. Other combinations of test and block numbers were also possible with only slightly lower economic efficiencies. For example, appropriate test numbers could be calculated using Eq. 9 or from the h_f^2 surfaces in Fig. 1 when the target testing quality and blocks per site were chosen. But, more than 40 blocks per site seemed to be excessive.

In operational tree improvement practices of major commercial species, varying numbers of progeny test sites and blocks per site were used to evaluate genetic entries, ranging from as few as 2 test sites (JOYCE & NITSCHE 1993) to as many as 10 to 14 tests (CARSON 1991; WHITE *et al.* 1993, 1999; JOHNSON 1997). Empirical data also seemed to suggest different optimal test numbers. For example, CARSON (1991) suggested that 2, 3, or 4 best tests could achieve 95 % of possible gain from a total of 11 tests in a progeny testing of *Pinus radiata* in New Zealand, in which 120 half-sib progeny of a parent were tested per site. WHITE and HODGE (1992), however, indicated that, to achieve 95 % of maximum gain, at least 6 progeny tests are necessary for height growth which had low heritability and appreciable G × E interaction (r_B = 0.6–0.7) with 20 progeny per family per site. The discrepancies between these empirical studies were apparently attributable to the different settings of the specific tests, such as the number of progeny per family per site. Those empirically optimal test numbers were, however, predictable from Eq. 9 with the input of the specific test conditions.

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Appendix 1. Multi-site family heritability estimation with half-sib families and RCB design using single-tree plots

Analytical linear model: $y_{ijk} = \mu + s_i + b_{j(i)} + f_k + fe_{ik} + e_{ijk}$

where: y_{ijk} is the observation of the kth family in the jth block of the ith site;
μ is overall mean;
s_i is fixed effect of the ith site;
$b_{j(i)}$ is the fixed effect of the jth block within the ith site;
f_k is the random effect of the kth family, $f_k \sim \text{NID}(0,\sigma_f^2)$;
fe_{ik} is the random effect of interaction between the ith site and the kth family, $fe_{ik} \sim \text{NID}(0,\sigma_{fe}^2)$;
e_{ijk} is the residual effect; $e_{ijk} \sim \text{NID}(0,\sigma_e^2)$;

$$E(y_{ijk}) = \mu + s_i + b_{ij} \qquad Var(y_{ijk}) = \sigma_f^2 + \sigma_{fe}^2 + \sigma_e^2 \qquad E(\bar{y}_{..k}) = \mu, \qquad Var(\bar{y}_{..k}) = \sigma_f^2 + \frac{\sigma_{fe}^2}{t} + \frac{\sigma_e^2}{tn}$$

Thus, $$h_i^2 = \frac{4\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2 + \sigma_e^2} \qquad \text{[A1.1]}$$

$$h_f^2 = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2/t + \sigma_e^2/tn} \qquad \text{[A1.2]}$$

By BURDON (1977) the type B genetic correlation is:

$$r_B = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2} \qquad [A.1.3]$$

From A1.3, $\frac{1}{r_B} = 1 + \frac{\sigma_{fe}^2}{\sigma_f^2}$

From A1.1 $\frac{4}{h_i^2} = 1 + \frac{\sigma_{fe}^2}{\sigma_f^2} + \frac{\sigma_e^2}{\sigma_f^2}$

So $\frac{\sigma_e^2}{\sigma_f^2} = \frac{4}{h_i^2} - \frac{1}{r_B}$ (by substitution)

From A1.2 $\frac{t}{h_f^2} = t + \frac{\sigma_{fe}^2}{\sigma_f^2} + \frac{\sigma_e^2}{n\sigma_f^2} = t + \frac{1}{r_B} - 1 + \frac{1}{n}\left(\frac{4}{h_i^2} - \frac{1}{r_B}\right)$ (by substitution)

$$\frac{tnh_i^2}{h_f^2} = tnh_i^2 + n\frac{h_i^2}{r_B} - nh_i^2 + \frac{4h_i^2}{h_i^2} - \frac{h_i^2}{r_B} = tnh_i^2 + \frac{h_i^2}{r_B}(n-1) - nh_i^2 + 4$$

Thus, $$h_f^2 = \frac{tnh_i^2}{tnh_i^2 + \frac{h_i^2}{r_B}(n-1) - nh_i^2 + h_i^2 - h_i^2 + 4} = \frac{tn}{\frac{4}{h_i^2} + \left(\frac{1}{r_B} - 1\right)(n-1) + tn - 1} \qquad [A1.4]$$

For a single site, where $t = 1$ and $r_B = 1$, Eq. A1.4 reduces to

$$h_f^2 = \frac{\frac{1}{4}nh_i^2}{1 + \frac{1}{4}h_i^2(n-1)} \qquad [A1.5]$$

which is identical to that of ROBERTSON (1957). When only one block is used at each site, where $n = 1$, Eq. 1 reduces to

$$h_f^2 = \frac{\frac{1}{4}th_i^2}{1 + \frac{1}{4}h_i^2(t-1)} \qquad [A1.6]$$

Eq. A1.6 is in the same form as Eq. A1.5 if n replaces t, suggesting that multi-site progeny test over t sites with a single block per site is equivalent to a single-site test with t blocks. It is noted that a differing relationship from Eq. A1.5 between family heritability and individual heritability at a single site is given by FALCONER (1981, Chapter 13, Eq. 13.4) as:

$$h_f^2 = \frac{1 + (n-1)r}{1 + (n-1)t} h^2 \qquad [A1.7]$$

where, $t=\sigma_B^2/\sigma_T^2$, $r = 1/4$, and σ_B^2 and σ_T^2 are between family variance component and total phenotypic variance. The difference between Eq. A1.5 and Eq. A1.7 is that Eq. A1.5 is a traditional approach used in forest genetics data analysis with the assumption of large sample sizes, while Eq. A1.7 applies to both small and large sample sizes.

Appendix 2. Sampling variance of variance component for genotype x environment (G x E) interaction with half-sib families and RCB design of single-tree plots.

Let $\sigma_P^2 = \sigma_f^2 + \sigma_{fe}^2 + \sigma_e^2$ [A2.1]

Then $h_i^2 = \frac{4\sigma_f^2}{\sigma_p^2}$, and $\sigma_f^2 = \frac{h_i^2}{4}\sigma_p^2$ [A2.2]

Since $r_B = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2} = \frac{h_i^2\sigma_p^2}{h_i^2\sigma_p^2 + 4\sigma_{fe}^2}$

$$\sigma_{fe}^2 = \frac{h_i^2\sigma_p^2}{4}\left(\frac{1}{r_B} - 1\right) \quad [A2.3]$$

From expected mean squares (EMS), it is known that

$$MS_{fe} = \sigma_e^2 + n\sigma_{fe}^2 \text{ and } MS_e = \sigma_e^2 \quad [A2.4]$$

From A2.1 $\sigma_f^2 - n\sigma_{fe}^2 + \sigma_{fe}^2 + n\sigma_{fe}^2 + \sigma_e^2 = \sigma_f^2 - (n-1)\sigma_{fe}^2 + MS_{fe} = \sigma_p^2$

Thus, $MS_{fe} = \sigma_p^2 - \sigma_f^2 + (n-1)\sigma_{fe}^2 = \sigma_p^2\left[1 + \frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B} - 1\right) - 1\right]\right]$ [A2.5]

$$MS_e = \sigma_e^2 = \sigma_p^2 - \sigma_f^2 - \sigma_{fe}^2 = \sigma_p^2\left[1 - \frac{h_i^2}{4}\left[\left(\frac{1}{r_B} - 1\right) + 1\right]\right]$$

According to DIETERS *et al.* (1995b),

$$Var(\sigma_{fe}^2) = Var[(MS_{fe} - MS_e)/n] = \frac{2}{n^2}\left[\frac{MS_{fe}^2}{(t-1)(f-1)+2} + \frac{MS_e^2}{t(n-1)(f-1)+2}\right] \quad [A2.6]$$

$$= \frac{2(\sigma_p^2)^2}{n^2}\left[\frac{\left[1 + \frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B} - 1\right) - 1\right]\right]^2}{(t-1)(f-1)+2} + \frac{\left[1 - \frac{h_i^2}{4}\left(\frac{1}{r_B} - 1\right) + 1\right]^2}{t(n-1)(f-1)+2}\right]$$

Appendix 3. Sampling variance of family heritability with half-sib families and RCB design of single-tree plots.

From expected mean square (EMS), it is known that

$$MS_f = \sigma_e^2 + n\sigma_{fe}^2 + tn\sigma_f^2 \qquad \text{and} \qquad MS_{fe} = \sigma_e^2 + n\sigma_{fe}^2 \qquad \text{[A3.1]}$$

Since $\sigma_e^2 + n\sigma_{fe}^2 + tn\sigma_f^2 + \sigma_{fe}^2 - n\sigma_{fe} + \sigma_f^2 - tn\sigma_f^2 = \sigma_p^2$

$$MS_f + (1-n)\sigma_{fe}^2 + (1-tn)\sigma_f^2 = \sigma_P^2$$

$$MS_f = \sigma_P^2 - (1-n)\sigma_{fe}^2 - (1-tn)\sigma_f^2$$

$$= \sigma_p^2\left[1 + \frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B} - 1\right) + tn - 1\right]\right]$$

(by substituting of σ_{fe}^2 and σ_f^2 from Appendix 2) [A3.2]

According to DIETERS *et al.* (1995b),

$$Var(\sigma_f^2) = Var[(MS_f - MS_e)/tn] = \frac{2}{(tn)^2}\left[\frac{MS_f^2}{(f-1))+2} + \frac{MS_{fe}^2}{(t-1)(f-1)+2}\right]$$

$$= \frac{2(\sigma_p^2)^2}{(tn)^2}\left[\frac{\left[1 + \frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B} - 1\right) + tn - 1\right]\right]^2}{(f-1)+2} + \frac{\left[1 + \frac{h_i^2}{4}\left[(n-1)\left(\frac{1}{r_B} - 1\right) - 1\right]\right]^2}{(t-1)(f-1)+2}\right] \qquad \text{[A3.3]}$$

Because $h_f^2 = \dfrac{\sigma_f^2}{\sigma_f^2 + \sigma_{fe}^2/t + \sigma_e^2/tn}$, let

$$\sigma_{Pf}^2 = \sigma_f^2 + \sigma_{fe}^2/t + \sigma_e^2/tn = \frac{\sigma_P^2}{tn}\left[\frac{h_i^2}{4}\left[\left(\frac{1}{r_B} - 1\right)(n-1) + tn - 1\right] + 1\right] \qquad \text{[A3.4]}$$

(by substituting of σ_{fe}^2, σ_f^2 and σ_e^2 from Appendix 2).

According to DICKERSON (1969) and DIETERS *et al.* (1995b), an approximate estimate of variance of the ratio cx_1/x_2 is:

$$Var\left(\frac{cx_1}{x_2}\right) = \frac{c^2 Var(x_1)}{x_2^2}$$

Thus, $Var\left(h_f^2\right) = Var\left(\dfrac{\sigma_f^2}{\sigma_{Pf}^2}\right) \approx \dfrac{Var\left(\sigma_f^2\right)}{(\sigma_{Pf}^2)^2}$

$$= \frac{\dfrac{2(\sigma_P^2)^2}{(tn)^2}\left[\dfrac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)+tn-1\right]\right]^2}{(f-1)+2}+\dfrac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)-1\right]\right]^2}{(t-1)(f-1)+2}\right]}{\left[\dfrac{\sigma_P^2}{tn}\left[\dfrac{h_i^2}{4}\left[\left(\dfrac{1}{r_b}-1\right)(n-1)tn-1\right]+1\right]\right]^2} \qquad [A3.5]$$

$$= \frac{2}{f+1}+\frac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)\right]\right]^2}{[(t-1)(f-1)+2]\left[\dfrac{h_i^2}{4}\left[\left(\dfrac{1}{r_B}-1\right)(n-1)+tn-1\right]+1\right]^2}$$

$$Var(h_i^2) \approx Var\left(4\frac{\sigma_f^2}{\sigma_P^2}\right) = \frac{16\,Var\left(\sigma_f^2\right)}{(\sigma_P^2)^2}$$

$$= \frac{\dfrac{32\left(\sigma_P^2\right)^2}{(tn)^2}\left[\dfrac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)+tn-1\right]\right]^2}{(f-1)+2}+\dfrac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)-1\right]\right]^2}{(t-1)(f-1)+2}\right]}{(\sigma_P^2)^2} \qquad [A3.6]$$

$$= \frac{32}{(tn)^2}\left[\frac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)+tn-1\right]\right]^2}{(f-1)+2}+\frac{\left[1+\dfrac{h_i^2}{4}\left[(n-1)\left(\dfrac{1}{r_B}-1\right)-1\right]\right]^2}{(t-1)(f-1)+2}\right]$$

Appendix 4. The relationship between the relative sampling errors of heritability estimates.

From Appendix 3,

$$Var(h_f^2) = Var\left(\frac{\sigma_f^2}{\sigma_{Pf}^2}\right) = \frac{Var(\sigma_f^2)}{(\sigma_{Pf}^2)^2}, \qquad h_f^2 = \frac{\sigma_f^2}{\sigma_{Pf}^2}$$

$$\text{Thus, } \frac{s.e.[h_f^2]}{h_f^2} = \frac{\sqrt{(Var(\sigma_f^2)}}{\sigma_{Pf}^2} \Big/ \frac{\sigma_f^2}{\sigma_{Pf}^2} = \frac{\sqrt{(Var(\sigma_f^2))}}{\sigma_f^2} = \frac{s.e.(\sigma_f^2)}{\sigma_f^2} \qquad \text{[A4.1]}$$

$$\text{Similarly, } Var(h_i^2) = Var\left(4\frac{\sigma_f^2}{\sigma_P^2}\right) = \frac{16\,Var(\sigma_f^2)}{(\sigma_P^2)^2}, \qquad h_i^2 = \frac{4\sigma_f^2}{\sigma_P^2}$$

$$\text{Thus, } \frac{s.e.[h_i^2]}{h_i^2} = \frac{4\sqrt{(Var(\sigma_f^2)}}{\sigma_P^2} \Big/ \frac{4\sigma_f^2}{\sigma_P^2} = \frac{\sqrt{(Var(\sigma_f^2))}}{\sigma_f^2} = \frac{s.e.[\sigma_f^2]}{\sigma_f^2} = \frac{s.e.[h_f^2]}{h_f^2} \qquad \text{[A4.2]}$$