to investigate the relationship between greenhouse and field planted trees belonging to the same full-sib family. Like the field material, the data illustrated considerable additive as well as non-additive genetic variancas. Maternal effects were significant at two months but seemed to disappear in older trees, indicating a possible effect of seed size and endosperm viability. Reciprocal effects were generally negligible, and high correlations were obtained between most traits.

General combining ability of the parents showed much fluctuation from two to five months, and extrapolation of greenhouse results to field data generally showed poor correlations for growth characteristics. An exception was for branch features where a meaningful trend was found between the two groups of material. It was concluded that, for traits related to volume production, early appraisal of offspring is not recommended, but for branch and crown features such early assessments might have merit.

Key words: Eucalyptus grandis, greenhouse, full-diailel, progeny test, variance components, maternal effects, reciprocal effects, correlations.

## Zusammenfassung

Zur Prüfung der Nachkommenschaften aus einem vollen Kreuzungsdiallel unter kontrollierter Bestäubung wurden zugleich im Freiland und im Gewächshaus 13 Einzelbaumabsaaten von Eucalyptus grandis vorgenommen. Danach erfolgte an 4 Stichtagen im Monat die Untersuchung, die auf vier Ziele gerichtet war: 1. Abschätzung relativer Größen genetischer Varianzen, 2 mütterliche und wechselseitige Wirkungen, 3. phaenotypische und genetische Verhältnisse und 4. das Verhältnis zwischen im Treibhaus und frei ausgepflanzten Bäumen der gleichen Familie.

Sowohl an den Nachkommenschaften im Freiland als auch an denen im Gewächshaus war beträchtliche additive und nicht additive genetische Varianz zu erkennen. Mütterliche Einflüsse waren bis zum Alter von etwa 2 Monaten zu kmerken. An Hand der meisten Eigenschaften wurde ein hoher Grad an Wechselbeziehungen ermittelt. Die allgemeine Kombinationseignung der Elternbäume schwankte innerhalb von 5 Monaten beträchtlich. Die Wachstumsunterschiede waren insgesamt gesehen unerheblich im Gegensatz zur Ästigkeit, bei der sowohl bei den Nachkommenschaften im Freiland als auch im Gewächshaus gemeinsame Trends zu beobachten waren.

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# Estimation of Number of Embryonic Lethal Alleles in Conifers: I. Self-Pollinated Seed

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## Introduction

Controlling seed losses is a major concern in forestry, especially in tree breeding programs. One cause for seed losses is embryo abortion resulting from the matching of recessive embryonic lethal alleles after inbreeding.

Reduced seed yield following inbreeding has been reported for Pseudotsuga menziesii (MIRB.) Franco by Orr-Ewing (1957), *Pseudotsuga* menziesii var. menziesii by Sorensen (1967, 1969, 1971), Picea abies L. and Pinus sylvestris L. by Sarvas (1962, 1968), Pinus peuce Griseb. by Hagman and Mikkola (1963), Picea glauca (Moench) Voss. by Mergen et al. (1965), Pinus banksiana Lamb and Pinus resinosa Ait. by Fowler (1965), Picea abies L. and Pinus

sylvestris L. by Koski (1971), Pinus taeda L. by Franklin (1972), and Pinus virginiana Mill. by Bramlett and Pepper (1974).

Assuming that losses due to injury of ovules and fertilization failure are negligible and accounting for the polyembryonic reproduction system in conifers, Bramlett and Popham (1971) and Koski (1971) postulated a model for probability of unsound seed. With self fertilization in a tree having n loci heterozygous for embryonic recessive lethal alleles, they found the probability of unsound seed to be

$$p = P \text{ (Unsound seed)} = \sum_{r=0}^{n} \frac{1}{2^{r}} {n \choose r} (1 - 2^{-r})f.$$
 (1)

In this formula, the quantity  $\frac{1}{2^r}\binom{n}{r}$  represents the binomial probability that in a particular female gamete there are r loci containing recessive lethal alleles. The quantity f is the number of fertilizations in an ovule, assumed to be the same for all ovules.

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Examples of computations relating to this model as well as models involving outcrossing, in the cases when f=1 or f=2, may be found in Lindgren (1975).

The purpose of the present paper is to formalize a procedure for point estimation of number of lethals, to construct an interval estimator and evaluate its precision, and to examine the consequences of treating fertilization frequency as a random variable, rather than a known constant. A second paper will describe procedures for estimating the total number of embryonic lethals in a population.

### A Probability model for variable numbers of fertilizations

The equation (1) is derived on the assumption that the number of fertilizations is a constant f. However, the actual number of archegonia penetrated by pollen tubes is dependent on the number of archegonia per ovule and the number of pollen grains per pollen chamber. Experimental findings show that the number of fertilizations is a random variable F, with values typically ranging from zero to five (Sarvas, 1962; 1968). The above formula represents the conditional probability

P (Unsound seed 
$$| F = f$$
).

Thus a more accurate representation of the probability of unsound seed is

$$q = P \text{ (Unsound seed)} = \sum_{f=0}^{m} P (F = f) P \text{ (Unsound seed } | F = f)$$

$$= \sum_{f=0}^{m} P (F = f) \sum_{r=0}^{n} \frac{1}{r} {n \choose r} (1 - 2^{-r})^{f}. (2)$$

The number m is the largest observed number of fertilizations. Most often, m=5. The numbers  $P\left(F=f\right)$  are ordinarily estimated from observed frequencies.

# Estimation of the number of recessive alleles in the selfed parent

Number of Fertilizations per Ovule Assumed Constant

Suppose a sample of S seeds produces u seeds which are unsound. Then, the number n of heterozygous lethal loci may be estimated by choosing that number which makes the theoretical probability p in equation (1) closest to the observed frequency u/S. In almost all cases this number turns out to be the maximum likelihood estimate of n.

To establish this fact, let U denote the random number of unsound seeds in a sample of S seeds. Assuming that individual seeds are independent, U is a binomial random variable with distribution

$$T_u = P(U = u) = {s \choose u} p^u (1 - p)S^{-u}; u = 0, 1, ..., S.$$
 (3)

The likelihood  $T_{\rm u}$  is the probability that the sample produces u unsound seeds. A maximum likelihood estimate is obtained by choosing that value of n which maximizes  $T_{\rm u}$ .

It is well known that the value of p which maximizes  $T_u$  is the maximum likelihood estimate p=u/S. We show in Appendix I that, whatever the value of f, p is a strictly increasing function p(n) of n, varying from zero, when n=0, to values approaching 1 as n approaches infinity. As n increases, the corresponding values of  $T_u$  must first increase, attaining a maximum near p=u/S, and then decrease. Since n takes only integer values, there may be no value such that p(n) exactly equals u/S. But, there does exist an integer  $n_u$  such that  $T_u$  is increasing to the left of  $n_u$  and decreasing to the right. The number  $n_u$  is the maximum likelihood estimate of n.

Because of the computational difficulty of solving for  $n_u$ , it is more convenient in practice to take as our estimate the value of n which makes p(n) closest to u/S. This is easily accomplished using the columns headed 1-5 in  $Table\ 1$ , in which values of p have been computed for various combinations of n and f. For instance, if f=2 and a sample shows 63 percent empty seed, the number of lethal alleles is estimated as n=5. If f=2 and u/S=.88, then we estimate n as either 9 or 10. Generally this "closest" estimate coincides with the maximum likelihood estimate. An ambiguous choice may occur when the interpolated value from the table is near the midpoint between two integers. In such instances the approximate procedure gives an estimate which either coincides with the maximum likelihood estimate or differs from it by one unit.

## Number of Fertilizations per Ovule Assumed Variable

As in the preceding section, suppose that u unsound seeds are found in a sample of S seeds. When the number of fertilizations per ovule is assumed variable, the number n of heterozygous lethal loci is estimated by choosing that number which makes the theoretical probability q in equation (2) closest to the observed frequency u/S. This procedure, identical to that described above except that q replaces p, again yields a maximum likelihood estimate of n

(or, at most, differs from the maximum likelihood estimate by one unit). The proof of this fact follows exactly the same lines as that for the constant case, and will be omitted.

Equation (2) computes a weighted average of the terms in columns 1—5 of a given row of the table, the weights being the numbers P(F=f). Empirical weights from data given by Sarvas (1962, 1968) are presented below for Norway Spruce and Scotch Pine:

Table 1. — Probabilities of Unsound Seed¹)

| Lethal Numb<br>Alleles(n) l |                 | r of Fe | ertiliza<br>3 | ations<br>4 | (f)<br>5 | Norway Spruce | Scotch Pine |
|-----------------------------|-----------------|---------|---------------|-------------|----------|---------------|-------------|
| 1                           | 0.25            | 0.13    | 0.06          | 0.03        | 0.02     | 0.19          | 0.17        |
| 2                           | 0.44            | 0.27    | 0.17          | 0.11        | 0.08     | 0.32          | 0.33        |
| 3                           | 0.58            | 0.40    | 0.29          | 0.22        | 0.16     | 0.44          | 0.46        |
| 4                           | 0.68            | 0.52    | 0.41          | 0.33        | 0.27     | 0.55          | 0.57        |
| 5                           | 0.76            | 0.62    | 0.52          | 0.44        | 0.38     | 0.64          | 0.67        |
| 6                           | 0.82            | 0.70    | 0.61          | 0.54        | 0.48     | 0.71          | 0.74        |
| 7                           | 0.87            | 0.77    | 0.69          | 0.63        | 0.58     | 0.78          | 0.80        |
| 8                           | 0,90            | 0.82    | 0.76          | 0.71        | 0.66     | 0.83          | 0.85        |
| 9                           | 0.92            | 0.86    | 0.81          | 0.77        | 0.73     | 0.86          | 0.88        |
| 10                          | 0.94            | 0.90    | 0.86          | 0.82        | 0.79     | 0.90          | 0.91        |
| 11                          | 0.96            | 0.92    | 0.89          | 0.86        | 0.83     | 0.92          | 0.93        |
| 12                          | 0.97            | 0.94    | 0.91          | 0.89        | 0.87     | 0.94          | 0.95        |
| 13                          | 0.98            | 0.95    | 0.93          | 0.92        | 0.90     | 0.95          | 0.96        |
| 14                          | 0.98            | 0.97    | 0.95          | 0.94        | 0.92     | 0.97          | 0.97        |
| 15                          | 0.99            | 0.97    | 0.96          | 0.95        | 0.94     | 0.97          | 0.98        |
| 16                          | 0.99            | 0.98    | 0.97          | 0.96        | 0.95     | 0.98          | 0.98        |
| 17                          | 0.99            | 0.99    | 0.98          | 0.97        | 0.97     | 0.99          | 0.99        |
| 18                          | 0.99            | 0.99    | 0.98          | 0.98        | 0.97     | 0.99          | 0.99        |
| 19                          | 1.00 <u>2</u> / | 0.99    | 0.99          | 0.98        | 0.98     | 0.99          | 0.99        |
| 20                          | 1.00 <u>3</u> / | 0.99    | 0.99          | 0.99        | 0.98     | 0.99          | 0.99        |

<sup>1/</sup> Columns 1 - 5, which verify and extend the Bramlett-Popham figures, list values of p for a constant number of fertilizations per ovule. The last two columns assume a random number of fertilizations per ovule and are based on estimated values of p(F = f) given in Sarvas (1962, 1968).

<sup>2/</sup> Rounded to 1.00; actual value = .9958.

<sup>3/</sup> Rounded to 1.00; actual value = .9968.

#### Norway Spruce

Fertilization per ovule (f) 0 1 2 3 4 5 Proportion of ovules 0.0852 0.1407 0.4704 0.2481 0.0519 0.0037 Mean (2.0519)

Pollen Catch: 200-245 grains/mm<sup>2</sup>

#### Scotch Pine

 Fertilization per ovule (f)
 1
 2
 3
 4
 5

 Proportion of ovules
 0.40
 0.50
 0.10
 0.00
 0.00

 Mean (1.7)

Pollen Catch: 238-300 grains/mm<sup>2</sup>

Application of equation (2) for computing the probability q of unsound seed results in two columns of probabilities, one for each species, as shown in *Table 1*.

Norway spruce differs slightly from Scotch pine in its seed development. Nonpollinated ovules of spruce do not wither and develop into mere wings as do nonpollinated ovules of Scotch pine; they generally grow to the archegonial stage like pollinated ovules and develop into full-sized empty seeds (Sarvas, 1968). For spruce, therefore, nonpollinated seeds are included in the category of empty seed, and the result may be an overestimation of the importance of embryonic lethal alleles.

Despite the fact that nonpollinated ovules were counted in the data for Norway spruce, the average number of fertilizations per ovule is larger than the corresponding average for Scotch pine. Accordingly, the probabilities in  $Table\ 1$  are generally smaller for Norway Spruce. However, estimates of n do not differ by more than one unit from those obtained when f is assumed constant (f = 2). Thus, for these data the estimation procedure is relatively insensitive to the nonconstant number of fertilizations per ovule.

General Comparison of Estimates Obtained with the Two Models

The assumption that F remains constant always produces values of n larger than corresponding estimates which assume variation in F. This occurs because equating f in equation (1) to the observed average of the frequency distribution of F used in equation (2) always makes q larger than p (see Appendix for proof).

The phenomenon described above is easily illustrated by both equations (1) and (2) with an hypothetical example where small values of F have high frequencies. Suppose 30 percent of the seeds in a sample obtained from selfed Norway spruce are empty due to fertilization failure; 40 percent resulted from one fertilization per ovule and 30 percent from two fertilizations per ovule. The average number of fertilizations per ovule is 0.30 (0) + 0.40 (1) +0.30(2) = 1.0. An observed empty seed percentage of 44 gives an estimate of n = 2 if we use column 1 in Table 1 to correspond to the observed average of 1.0. Using the weights of 0.30, 0.40, and 0.30 to obtain a weighted average of 0.44 with equation (2) can only be accomplished with the first row of Table 1. (If f = 0, the probability of unsound seed is unity.) Therefore, the more exact procedure gives an estimate of n = 1.

Even greater discrepancy between the two estimates is possible when the distribution of F is concentrated in the low and high values. For instance, if 69 percent of the seeds in a sample obtained from Norway spruce are empty due to fertilization failure, while all the remaining 31 percent have 5 fertilizations per ovule, the estimates of n are 5 when F is assumed constant as opposed to 1 with the more exact procedure. Of course, it is unlikely that an observed sample will produce such an extreme distribution of F. (For the Sarvas data reported above, estimates using  $\mathbf{f}=\mathbf{2}$  in

Table 1 never differ by more than one unit from those obtained using the more exact values in the last two columns.) Still, the potential danger exists, and the researcher needs to be aware of the possibility of overestimation of n.

#### Interval estimation

Equation (3) shows that the assumed distribution for the observed number (U) of empty seeds is binomial with parameters S and p. A 0.99 or 0.95 confidence interval for p can be determined using charts given by Pearson and Harrley (1966, pages 204—205). For a given sample size and observed proportion u/S, two values,  $p_A$  and  $p_B$ , of p are read from the charts so that P ( $p_A \leqslant p \leqslant p_B$ ) = 1 —  $\alpha$  where  $\alpha = 0.01$  or 0.05.

Since p=p(n) is a monotone increasing function of n, it follows that there are numbers  $n_A$  and  $n_B$  (the solutions for n in  $p=p_A$  and  $p=p_B)$  such that  $p_A\leqslant p\leqslant p_B$  if and only if  $n_A\leqslant n\leqslant n_B.$  Therefore,  $P\left(n_A\leqslant n\leqslant n_B\right)=1-\alpha$  and the numbers  $n_A$  and  $n_B$  provide  $1-\alpha$  confidence limits for n.

If the number of fertilizations is assumed to be variable, the distribution is binomial, but with parameters S and q. The procedure described above, with q replacing p, will again provide  $1-\alpha$  confidence limits for n.

In practice the end points of the confidence interval for n will be determined by interpolation in columns 1—5 of Table 1 or, for empirical data, in columns like those for Norway Spruce and Scotch Pine. For illustration, suppose  $u=30,\,S=60,\,$  and  $\alpha=0.05$  in data for Scotch pine. Then  $P(0.37\leqslant p\leqslant 0.63)=0.95$  (Pearson and Hartley, 1966; page 204). Using f=2 in Table 1 we find that the end points of the confidence interval for n are 2.8 and 5.1. Since the only integer values in this interval are 3, 4, and 5, we would be 95 percent confident that the parent tree sampled has either 3. 4. or 5 lethal alleles.

Similar use of the Pearson-Hartley charts, together with the column for Scotch pine gives P (0.37  $\leqslant$  q  $\leqslant$  0.63), so we are 95 percent confident that n=3 or n=4.

If u=54 and S=60, the observed frequency is 0.9. Ninety-five percent confidence limits for p are 0.78 and 0.95, leading to the 0.95 confidence interval of  $8\leqslant n\leqslant 13$  for n (again using f=2 in Table 1). The same limits for q lead to the 0.95 confidence interval  $7\leqslant n\leqslant 12$ . Thus, the precision of the estimate for n is much more affected by the length of the interval estimate for p (or q) when p is large, resulting in an unacceptably wide confidence interval for n. Since average estimates of n from 8 to 10 are quite common in reported studies of conifers (Koski, 1971), it would appear that S=60 is an inadequate sample size for most cases of practical interest.

Table 3 in Koski (1971) reports empty seed percentages in 80 Scotch pines. Sample sizes of S=400 are not uncommon. Taking the report for tree number E88, we find that of the 400 seeds examined, 80 percent were empty. Pearson and Hartley (1966, page 204) gives 0.95 confidence limits for p of 0.76 and 0.84. Interpolating in Table 1 with f=2, we find that n is either 7 or 8 with 95 percent confidence.

Similar computations using q and "the column for Scotch pine" give the estimate n=7 and the 0.95 confidence interval n=7.

The above calculations show that interval estimates of satisfactory precision can be obtained for n using sample sizes commonly reported in the literature. For values of  $\alpha$  other than 0.05 and 0.01 an approximate procedure involving the normal distribution can be used for large samples (Freund, 1971; pages 275—277).

## Appendix 1

For our estimation procedure we need to establish the facts that p and q are increasing functions of n, varying from zero at n = 0 to unity as  $n \to \infty$ . Consider p first. To emphasize the dependence of p upon n, we rewrite equation (1):

$$p = p_n = \sum_{r=0}^{n} {n \choose r} \frac{1}{2^r} (1 - 2^{-r})^{r}.$$
 (4)

Then

$$p_{n+1} = \sum_{r=0}^{n+1} {n+1 \choose r} \frac{1}{2^{n+1}} (1-2^{-r})f.$$

Using the binomial identit

$$\binom{n+1}{r} = \binom{n}{r} + \binom{n}{r-1}$$

and dividing  $p_{n+1}$  by  $p_n$  we find, after some manipulation,

$$\frac{p_{n+1}}{p_n} = \frac{1}{2} + \frac{1}{2} \frac{\sum_{r=1}^{n+1} {n \choose r-1} (1-2^{-r})^{f}}{\sum_{r=0}^{n} {n \choose r} (1-2^{-r})^{f}}.$$

A change of variable in the top summation shows it to be the same as

$$\sum_{r=0}^{n} {n \choose r} (1 - 2^{-(r+1)})^{r}$$

 $\sum_{r=0}^{n} \binom{n}{r} \ (1-2^{-(r+1)})f.$  Since  $1-2^{-(r+1)} > 1-2^{-r}$ , this upper sum is, term by term, larger than the corresponding sum in the denominator. We conclude that

$$\frac{p_{n+1}}{p_n} > \frac{1}{2} + \frac{1}{2} = 1$$

or that

$$p_{n+1} > p_n$$

for all n. Thus, p is a strictly increasing function of n. It is obvious from (4) that p = 0 when n = 0. To see what happens as  $n\to\infty,$  let  $\epsilon$  be any positive number. In

$$p_n = \sum_{r=0}^{n} {n \choose r} \frac{1}{2^n} (1 - 2^{-r})^f$$

first choose a number z such that  $(1-2^{-r})^{f} > 1-\varepsilon$  when  $r \geqslant z$ . Then choose n large enough that

$$\frac{1}{2^n}\sum_{r=z}^n\binom{n}{r}>1-\varepsilon.$$

(This is possible because  $\frac{1}{2^n} \sum_{r=0}^n \binom{n}{r} = 1$ . As n increases,

the first z terms of this sum decrease to zero.) Putting these two choices together, we find

$$\begin{aligned} \mathbf{p}_{\infty} &= \frac{\lim_{n \to \infty} \frac{1}{2^{n}} \sum_{\mathbf{r} = \mathbf{0}}^{n} \binom{n}{\mathbf{r}} \quad (1 - 2^{-\mathbf{r}})^{\mathbf{f}} \\ &\geq \lim_{n \to \infty} \frac{1}{2^{n}} \sum_{\mathbf{r} = \mathbf{z}}^{n} \binom{n}{\mathbf{r}} \quad (1 - 2^{-\mathbf{r}})^{\mathbf{f}} \\ &\geqslant (1 - \varepsilon) \lim_{n \to \infty} \frac{1}{2^{n}} \sum_{\mathbf{r} = \mathbf{z}}^{n} \binom{n}{\mathbf{r}} \\ &\geqslant (1 - \varepsilon)^{2} \text{ for every } \varepsilon. \end{aligned}$$

Since  $p_{\infty}\geqslant (1-\varepsilon)^2=1-(2\varepsilon-\varepsilon^2)$  is true for any  $\varepsilon>0$ , we conclude that  $p_{\infty} = 1$ .

To show that q is an increasing function of n, varying from q=0 at n=0 to q=1 as  $n\to\infty,$  we rewrite equation (2) emphasizing the dependence of q upon n:

$$\mathbf{q}_{n} = \sum_{\mathbf{f}=\mathbf{0}}^{\mathbf{m}} \mathbf{P} \left( \mathbf{F} = \mathbf{f} \right) \mathbf{p}_{n}. \tag{5}$$

It has been shown above that for a given value of f, the sequence  $p_n$  satisfies the monotonicity property and has the specified limiting values. To establish that  $q_n$  possesses the same properties we need only observe that  $\mathbf{q}_n$  is a linear combination of terms  $\boldsymbol{p}_{\boldsymbol{n}}$  with non-negative coefficients, P(F = f), which add to unity.

### Appendix 2

The probability p of unsound seed, given in equation (1), depends on the number n of embryonic lethals and the number f of fertilizations. In the following discussion, we write  $p = p_f$  to emphasize the dependence on f, but omit n since here we will always be working with the values in a single row of Table 1.

The probability q, given in equation (2), is a weighted average of the numbers pf, and depends only upon n. What we wish to prove is that if the average, or expected, value of the random variable F is an integer e, then  $q \geqslant p_{\rm e}.$  The weighted average must be at least as large as the particular entry.

We are assuming that

$$\sum_{f=0}^{m} f P (F = f) = e.$$

Since

$$\sum_{\mathbf{f}=\mathbf{0}}^{\mathbf{m}}\mathbf{P}\left(\mathbf{F}=\mathbf{f}\right)=\mathbf{1},$$

it is true that  $e = \sum_{f=0}^{m} e P(F = f)$ , so that  $\sum_{f=0}^{m} (e - f) P(F = f)$ 

f) = 0, a fact we will need later.

Equation (2), together with  $p_e = \sum_{f=a}^{m} p_e P(F = f)$ , gives

$$\mathbf{q} - \mathbf{p}_{e} = \sum_{f=0}^{m} (\mathbf{p}_{f} - \mathbf{p}_{e}) \cdot \mathbf{P} (\mathbf{F} = \mathbf{f}). \text{ When } \mathbf{f} = \mathbf{e}, \ \mathbf{p}_{f} - \mathbf{p}_{e} = \mathbf{0}.$$

Omit this term, and break the rest into two parts (the first is non-existent if e=0, the second if e=m):

$$\begin{aligned} \mathbf{q} - \mathbf{p}_e &= \sum_{\mathbf{f} = \mathbf{0}}^{\mathbf{e} - \mathbf{1}} \left( \mathbf{p}_\mathbf{f} - \mathbf{p}_e \right) \mathbf{P} \left( \mathbf{F} = \mathbf{f} \right) + \sum_{\mathbf{f} = \mathbf{e} + \mathbf{1}}^{\mathbf{m}} \left( \mathbf{p}_\mathbf{f} - \mathbf{p}_e \right) \ \mathbf{P} \left( \mathbf{F} = \mathbf{f} \right). \end{aligned}$$
 Now note, for instance, that  $\mathbf{p}_\mathbf{0} - \mathbf{p}_\mathbf{2}$  can be written as

 $(p_0 - p_1) + (p_1 - p_2).$ 

Similar expansion of the general term  $p_f - p_e$  gives

In columns 1—5 of Table 1, we see that the terms  $p_k - p_{k+1}$ are positive but decreasing as we move to the right. This can be shown algebraically, but we omit the proof. In particular, if k < e,  $p_k - p_{k+1} > p_e - p_{e+1}$  (call this  $\delta_e$ , for short). Similarly, if  $k \ge e$ ,  $p_{k+1} - p_k$  is negative, but greater than or equal to  $-\delta_e$ .

$$\begin{aligned} \mathbf{q} - \mathbf{p}_{e} \geqslant & \overset{\text{e-1}}{\overset{f}{\varSigma}} \left( \mathbf{e} - \mathbf{f} \right) \delta_{e} \, \mathbf{P} \left( \mathbf{F} = \mathbf{f} \right) - \underbrace{\overset{m}{\overset{f}{\varSigma}}}_{\mathbf{f} = \mathbf{e} + 1} \left( \mathbf{f} - \mathbf{e} \right) \, \delta_{e} \, \mathbf{P} \left( \mathbf{F} = \mathbf{f} \right) \\ &= \delta_{e} \, \overset{m}{\overset{f}{\varSigma}} \left( \mathbf{e} - \mathbf{f} \right) \, \mathbf{P} \left( \mathbf{F} = \mathbf{f} \right) = \mathbf{0} \, \left( \mathbf{from above} \right). \end{aligned}$$

That is,  $q \geqslant p_e$ , which is what we wanted to prove.

## Summary

The customary procedure for estimating the number of embryonic lethal alleles (n) in selfed conifers (Bramlett and Popham, 1971; Koski, 1971) is examined and compared with a more exact procedure. It is shown that the estimates obtained with both procedures generally coincide with the maximum likelihood estimates obtained with the two corresponding models. The customary procedure used heretofore produces estimates of n larger than those obtained with the exact procedure, but no evidence was found to indicate that the discrepancy is serious in practice.

Sufficiently precise confidence intervals can be obtained for n. Such intervals are unacceptably wide only when sample sizes are small. e.g., S=60. However, sample sizes this small appear to be uncommon in practice.

Key words: Lethal allele, self-pollination, point estimation, interval estimation.

## Zusammenfassung

Die herkömmliche Methode zur Schätzung der Zahl embryonaler Letalallele (n) in selbstbefruchteten Koniferen (Bramlett und Popham, 1971; Koski, 1971) wird untersucht und mit einer genaueren Methode verglichen. Es wird gezeigt, daß die mit den beiden Methoden erhaltenen Schätzwerte im allgemeinen mit den von den beiden entsprechenden Modellen erhaltenen maximum likelihood-Schätzwerten übereinstimmen. Die nach der herkömmlichen Methode berechneten Schätzwerte von n sind größer als die mit der genauen Methode erhaltenen Schätzwerte. Jedoch wird keine Anweisung dafür gefunden, daß die Abweichung in der Praxis erheblich sein dürfte.

Es ist möglich, genügend genaue Mutungsintervalle für nzu finden. Nur wenn der Stichprobenumfang klein ist, z.B. wenn S=60, sind solche Intervalle unannehmbar lang. Solche kleinen Stichprobenumfänge kommen in der Praxis, wie es scheint, nur selten vor.

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