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Number of Lethal Loci and Lethal Equivalents in Willow, Salix viminalis

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Abstract

Two methods of estimating lethal equivalents have been examined in this paper: A combinatorial method (COMB) and a method developed by Morton, Crow and Muller (MCM). Both methods produce similar estimates of lethal equivalents. However, the 2 methods differ in 2 respects: (1) COMB makes inferences to particular individual(s) in the population, while MCM makes inferences to the entire population; and (2) COMB estimates the number of lethal loci which is translated into lethal equivalents, while MCM directly estimates lethal equivalents. In a previous paper Kang et al. (1992) failed to recognize the second difference between COMB and MCM, and overestimated lethal equivalents in *Salix viminalis*. The revised estimate of lethal equivalents using COMB is 1.8, which is similar to that (1.69) estimated by MCM previously.

Key words: lethal equivalent, inbreeding, selfing, full-sib crossing, willow, *Salix viminalis*.

FDC: 165.3; 165.41; 161.6; 176.1 *Salix viminalis*.

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Introduction

Two different methods of estimating lethal equivalents have been widely used in forest genetics literature. Some authors (Sorensen, 1969; Fowler and Park, 1983; Park and Fowler, 1984) used a method (MCM) developed by Morton et al. (1956). Others (Koski, 1971; Bramlett and Pepper, 1974; Bishir and Pepper, 1977; Bishir and Namkoong, 1987) used a combinatorial approach (COMB). There are different variations of these 2 methods. For example, using MCM, Sorensen (1969) removed the proportion of mortality due to environmental effects and outcrossing by taking the ratio between the viable seeds of selfed vs outcrossed. Bishir and Namkoong (1987) devised a least square method to remove environmental/maternal effects when using COMB. Salvolainen et al. (1992) also proposed a model which extends COMB to incorporate environmental causes of death. A general conclusion one can draw from these different variations of COMB and MCM is that both methods result in similar estimates of lethal equivalents.

More important distinctions that should be made between COMB and MCM are: (1) in COMB inferences are made to particular individuals, while in MCM inferences are made to the entire population; and (2) COMB estimates the number of lethal loci in the particular individual(s), while MCM estimates the lethal equivalents of the entire population. In case of selfing, the number of lethal loci in a parent is the same as the lethal equivalents of the

parent, when the parent is considered to represent a population. For other crossing schemes, the number of lethal loci is not the same as the lethal equivalents. In a previous paper, KANG et al. (1992) used COMB to estimate the lethal equivalents using full-sib crossings. They failed to distinguish the number of lethal loci and the lethal equivalents and overestimated the lethal equivalents. The objectives of this paper are to: (1) discuss the differences between COMB and MCM, and (2) present revised values of lethal equivalents in *Salix viminalis* based on the data from KANG et al. (1992).

MCM and Lethal Equivalents

The most important assumption used in MCM is that all the factors that cause death of an individual are independent in action. This makes it possible to define a multiplicative expression for the survival probability (S) of an individual such that:

$$S = (1-w)\prod_{i=1}^{M}(1-v_i) \qquad [1]$$

where w represents the probability of death due to environmental causes,
M represents the total number of loci involved in causing genetic death,
v_i represents the probability of death due to genetic causes at the i^{th} locus,
$v_i = Fs_iq_i + (1-F)s_iq_i^2 + 2(1-F)s_ih_iq_i(1-q_i)$,
F represents inbreeding coefficient,
q represents frequency of deleterious allele,
s represents selection coefficient, and
h represents the coefficient of dominance.

MORTON et al. (1956) also defined lethal equivalents of a zygote as:

$$2\varepsilon = 2\sum_{i=1}^{M} s_iq_i . \qquad [2]$$

The lethal equivalents can be determined by using the survival probability S as defined in *equation [1]*. In forest genetics literature where proportions of viable seeds from selfing and outcrossing were used, the lethal equivalents were frequently estimated as (SORENSEN, 1969):

$$2\varepsilon = -4\ln\left(\frac{S_I}{S_O}\right), \qquad [3]$$

where S_I represents the proportion of viable seeds from selfing and S_O represents that from outcrossing.

COMB and Number of Lethal Loci

The combinatorial method (COMB) was originally developed for selfing individuals where the frequency of lethal allele is either 0 or 0.5 for all the loci that are mutable to lethal genes. This method is particularly useful for estimating lethal equivalents of some conifers with multiple archegonia in ovules that can be fertilized by different pollen (BISHIR and PEPPER, 1977). The resulting expression for the probability that a selfed seed is unsound in a tree carrying m lethals is (BISHIR and NAMKOONG, 1987):

$$Q = \sum_{j=1}^{z} p(y=j \mid y>0)\sum_{i=0}^{m}\binom{m}{i}\left(\frac{1}{2}\right)^m\left[1-\left(\frac{1}{2}\right)^i\right]^j ,$$

where y represents the number of fertilizations, and
z represents the maximum possible number of fertilizations.

In many tree species such as those in *Salix* and in *Pinus* multiple archegonia are of little concern. For these species, z can be set to 1, which makes it easy to develop a generalized expression of Q for mating systems other than selfing. To develop the generalized expression of Q, we will first follow the traditional logic used to define COMB. Then we will discuss an alternative interpretation of the resulting expression and the number of lethal loci.

Genenral expression for Q

Consider a population with m independent loci with lethal alleles (selection coefficients s = 1 and coefficient of dominance h = 0). In case of selfing, frequency of lethal alleles for all lethal loci is 0.5 in both male and female gamete pools. To obtain the general expression for Q, we allow the allele frequency to vary over different loci and gamete pools. Suppose there are X groups with m_1, m_2, m_3, ..., m_x loci with allele frequencies of q_1, q_2, q_3, ..., q_x in the female gamete pool, and q^*_1, q^*_2, q^*_3,..., q^*_x in the male gamete pool. Let $i = j_1 + j_2 + j_3 + ... + j_X$, $u_0 = i$, and $u_k = u_{k-1} - j_k$ for $k \geq 1$. The resulting expression for the probability that a selfed seed is unsound in a tree (or group of trees) carrying lethals at $m = m_1 + m_2 + m_3 + ... + m_x$ loci is in [4] (Appendix A).

The expression of Q as shown in *equation [4]* can be applied to various mating systems. When selfing, q and q* in [A3] may be replaced with 1/2 to produce the well-known expression for $Q|_{Selfing}$ (KOSKI, 1971; BRAMLETT and PEPPER, 1974):

$$Q|_{Selfing} = \sum_{i=0}^{m}\binom{m}{i}\left(\frac{1}{2}\right)^m\left[1-\left(\frac{1}{2}\right)^i\right]. \qquad [5]$$

When 2 individuals, A and B, are crossed to produce a full-sib family, 3 combinations of lethal loci arrangement between the parents are possible: (1) AB -- for m_1 loci, both A and B have a lethal allele (heterozygous loci); (2) AO -- for m_{21} loci, only A has lethal alleles but B has no lethal alleles, thus denoted by O; and (3) OB--for m_{22} loci, only B has lethal alleles. In AB, the frequency of lethal alleles in the full-sibs is 1/3 ($=q_1=q^*_1$), and for both AO and OB, the frequency is 1/4 ($=q_2=q^*_2$). We may combine AO and OB and let $m_2=m_{21}+m_{22}$. Given q_1, q_2, m_1, and m_2, we can use *equation [4]* to determine the probability ($Q|_{Fullsib}$) that the zygote formed by 2 gametes randomly chosen from the full-sib gamete pool is not viable:

$$Q = \sum_{i=0}^{M}\sum_{j_1=0}^{u_0}\sum_{j_2=0}^{u_1}\sum_{j_3=0}^{u_2}\cdots\sum_{j_{x-1}=0}^{u_{x-2}}\prod_{k=1}^{X}\binom{m_k}{j_k}(q_k)^{j_k}(1-q_k)^{m_k-j_k}\left[1-\prod_{k=1}^{X}(1-q_k^*)^{j_k}\right]. \qquad [4]$$

$$Q|_{Fullsib} = \sum_{i=0}^{m} \sum_{j_1=0}^{i} \binom{m_1}{j_1}\binom{m_2}{j_2}\left(\frac{1}{3}\right)^{j_1}\left(\frac{2}{3}\right)^{m_1-j_1}\left(\frac{1}{4}\right)^{j_2}\left(\frac{3}{4}\right)^{m_2-j_2}\left[1-\left(\frac{2}{3}\right)^{j_1}\left(\frac{3}{4}\right)^{j_2}\right], \quad [6]$$

which is the same as *equation [7]* in KANG et al. (1992).

An alternative expression for Q

It is possible to express Q in *equation* [4] in an alternate form such that (LEE et al., submitted):

$$Q = 1-\prod_{i=1}^{X}(1-q_i q_i^*)^{m_i} \quad [7]$$

Consequently, $Q|_{Selfing}$ and $Q|_{Fullsib}$ can be expressed in concise and closed forms:

$$Q|_{Selfing} = 1-\left(\frac{3}{4}\right)^{m}, \text{ and} \quad [8]$$

$$Q|_{Fullsib} = 1-\left(\frac{8}{9}\right)^{m_1}\left(\frac{15}{16}\right)^{m_2}. \quad [9]$$

From [7] we may also define the probability of survival:

$$S = 1-Q$$

$$= \prod_{i=1}^{X}(1-q_i q_i^*)^{m_i}. \quad [10]$$

The expression of Q in *equation* [4] was defined based on the number and location of lethal alleles sampled in the uniting gametes. However, the expression of Q in *equation [7]* means that the probability of death of a zygote is one minus the product of the probabilities of the individual surviving mortality due to all the loci with lethal alleles. The equality between *equation [4]* and *equation [7]* is due to the assumption that gene action among different loci is independent. The expression of S in *equation* [10] is essentially of the same form as that in *equation [1]* used in MCM. The main difference is that the product of the lethal allele frequencies in the male and female gamete pools ($q_i q_i^*$) replaces the v_i in *equation [1]*, with an additional assumption that w=0. This is also a result of having identical assumptions of independence of different loci in both methods, and explains why past estimates of lethal equivalents obtained by using COMB and MCM resulted in similar values.

Number of lethal loci

COMB directly estimates the number of loci with lethal alleles in the individual(s) of interest. In the selfing case, *equation* [8] can be rewritten such that m = ln(1—Q)/ln (3/4). This clearly shows that for a given proportion of unsound seeds, one can directly estimate the number of parental loci (m) with lethal alleles. In the full-sib case, both m_1 and m_2 cannot be readily estimated with a single value of Q. However, it is possible to define the range of values m_1 and m_2 can take. If we assume that all the grandparental laci are AB types, m_{min} = ln(1—Q)/ln (8/9). If we assume that all the grandparental loci are AO or OB types, m_{max} = ln(1—Q)/ln(15/16). *Figure 1a* shows the probability of mortality for different number of lethal loci. It also shows the probability of mortality at different lethal equivalents as determined by MCM. This figure is equivalent to *figure 1* in KANG et al. (1992), which erroneously designated the number of lethal loci as the lethal equivalents.

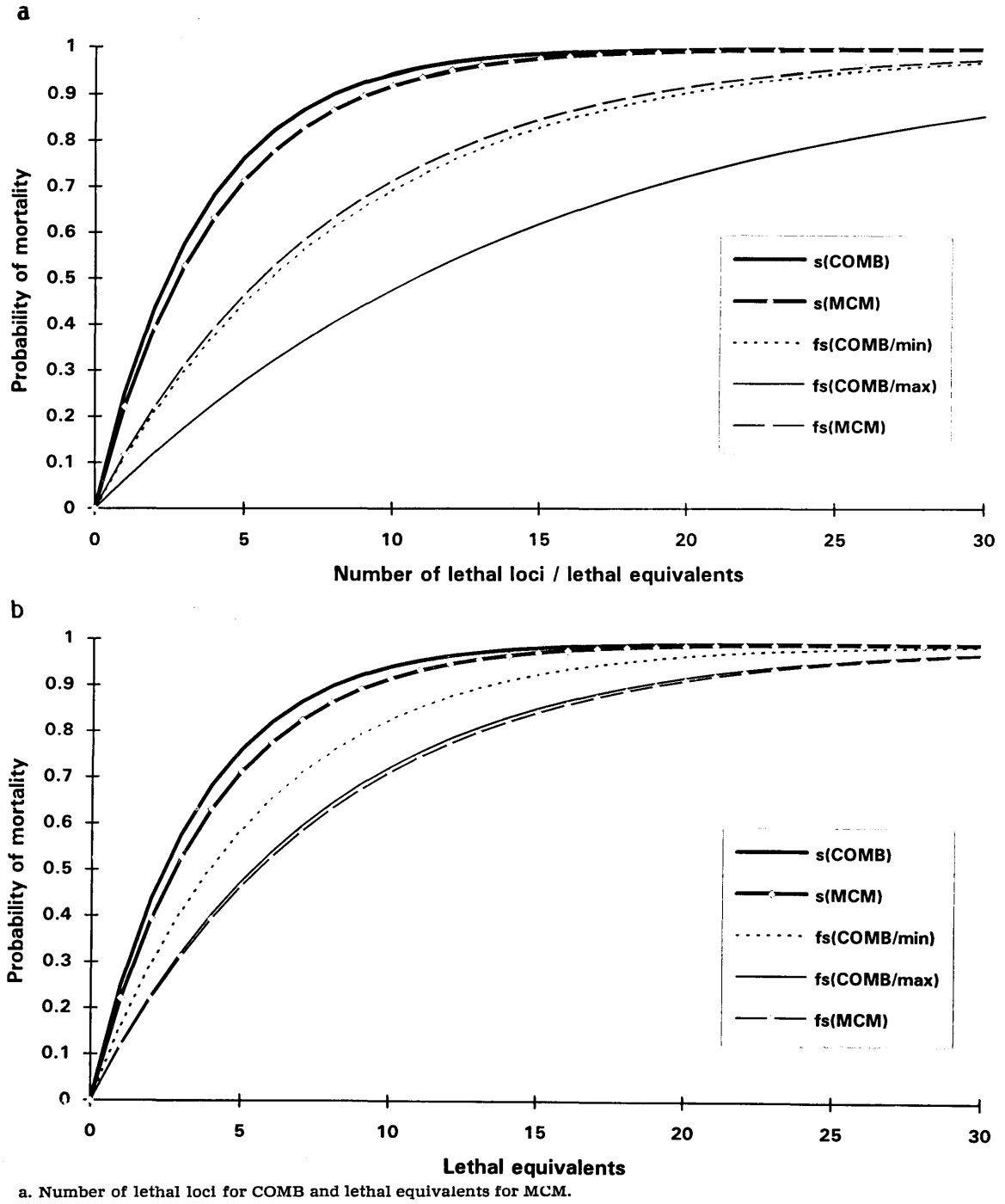
In the selfing case, the lethal equivalent (E) estimated by COMB is E = 2 m (1/2) = m, where 1/2 is the lethal allele frequency of the parent. Therefore, the number of lethal loci is the same as the lethal equivalents. This equality does not hold for the full-sib case because E_{min} = 2 m_{min} (1/3) = 2 m_{min}/3, where 1/3 is the frequency of lethal alleles in the progeny population of AB type grandparents. Similarly E_{max} = 2 m_{max} (1/4) = m_{max}/2. *Figure 1b* shows the probability of mortality for the 3 cases of different lethal equivalents. It also shows the probability of mortality at different lethal equivalents as determined by MCM. The lethal equivalent for selfing estimated by MCM for a given Q is similar to that estimated by COMB. In the case of full-sib, the ε estimated by MCM is similar to the E_{max} estimated by COMB for a given Q. The similarity between 2ε and E_{max}, instead of E_{min}, is due to the low probability that the AB type is likely to occur in a pair of individuals sampled from a population. This point will be discussed further in the following section.

The difference, although small, in the estimates of lethal equivalents between COMB and MCM exists because of the differences in the inferences made in the two methods. In COMB, inferences are made about particular individuals, while in MCM, inferences are made about the entire population. For example, in the selfing case, COMB defines Q = (prob. of unsound seed|m, 1/2) without any regard to M and p_i, where M represents the total number of loci at which lethal mutations can occur and p_i represents the lethal allese frequency at i^{th} locus. When M and p_i are considered in COMB, the resulting estimates of lethal equivalents of the entire population are identical to those obtained by MCM (LEE et al., in preparation). The same is true for the full-sib case.

Number of Lethal Loci and Lethal Equivalents in *Salix viminalis*

In this section, the data used in KANG et al. (1992) are reexamined to revise the lethal equivalents reported in their *table 2*. Grandparents of *Salix viminalis* in this experiment originated from many different locations in Sweden, Finland, and France (*Figure 2*). Although these individuals were sampled in naturally regenerated populations, most of those populations are not located in the natural range of the species. *Salix viminalis* was introduced to Sweden about 200 years ago from unknown origins. Therefore, there is a good possibility that some of the populations share those origins.

From the 10 progeny groups, full-sib crossing within the group, as well as outcrossing between different groups, was made. The observed fraction (u) of mortality in the full-sib crossing was adjusted for environmental/maternal effects ($\hat{b}$) to obtain the estimated probability of mortality of an offspring ($\hat{Q}$). The environmental/maternal effects (b) were estimated by using *equation [11]* in KANG et al. (1992). Using $\hat{Q}$, 4 parameters, m_{min}, m_{max}, E_{min}, and E_{max}, were estimated (*Table 1*). This table replaces *table 2* in



a. Number of lethal loci for COMB and lethal equivalents for MCM.
b. Lethal equivalents.
s = selfing.
fs = full-sib crossing.

Figure 1. — Number of lethal loci and lethal equivalents.

KANG et al. (1992). Values of the above parameters are 0 for 19 of 61 cases. *Figure 3a* shows the distribution of $\hat{Q}$. Although $\hat{Q}$ is broadly distributed between 0 and 1, the distribution is definitely reverse J-shaped, and there is another peak between 0.35 and 0.45. In 5 cases which appear to be outliers, $\hat{Q}$ is $\geq$ 0.79. These could be results of unknown experimental errors. This is in contrast to the case of *Pseudotsuga menziesii* (SORENSEN, 1969) where the distribution of $\hat{Q}$ is compact and J-shaped (*Figure 3b*). The broad distribution of $\hat{Q}$, and consequently that of lethal equivalents (E), appears to be the result of the widecrosses made to create the full-sib families (*Figure 2*).

Overall means and variances (in parentheses) of E_{min} and E_{max} are [2.38 (16.99), 3.26 (31.82)], while the variance-mean ratios are (7.14, 9.76). These ratios are much greater than theoretical expectations. BISHIR and NAMKOONG (1987) showed that the variance of lethal equivalents in expected to be less than or equal to the mean. The ratios between variance and mean in other species are: 0.78 (FRANKLIN, 1972) and 1.45 (BISHIR and NAMKOONG, 1986) in *Pinus taeda*, 0.5 in *Picea glauca* (FOWLER and PARK, 1983), 2.81 in *Pseu-*

Table 1. — Estimates of individual lethal equivalents (E).

Family	u	$\hat{b}$	#	$\hat{Q}$	m_{min}	m_{max}	E_{min}	E_{max}
1	0.06	0.07	1	0	0	0	0	0
	0.35	0.07	1	0.3	3.0	5.5	2.0	2.8
7	0.09	0.08	4	0.01	0.1	0.2	0.1	0.1
	0.03	0.08	4	0	0	0	0	0
	0	0.08	4	0	0	0	0	0
	0.44	0	0	0.44	4.9	9.0	3.3	4.5
	0.11	0	0	0.11	1.0	1.8	0.7	0.9
	0.05	0	0	0.05	0.4	0.8	0.3	0.4
	0.71	0.38	1	0.54	6.6	12.0	4.4	6.0
	0.03	0.38	1	0	0	0	0	0
	0.16	0.38	1	0	0	0	0	0
	0.04	0.06	0	0	0	0	0	0
	0.11	0.06	0	0.05	0.4	0.8	0.3	0.4
104	0.67	0.39	2	0.45	5.1	9.3	3.4	4.6
	0.98	0.39	2	0.97	29.8	54.3	19.8	27.2
	0.65	0.29	2	0.51	6.1	11.1	4.0	5.5
	0.47	0.29	2	0.25	2.4	4.5	1.6	2.2
	0.6	0.29	2	0.44	4.9	9.0	3.3	4.5
	0.3	0.51	2	0	0	0	0	0
	0.75	0.51	2	0.49	5.7	10.4	3.8	5.2
19	0.62	0.9	1	0	0	0	0	0
	0.74	0.9	1	0	0	0	0	0
	0.07	0.33	2	0	0	0	0	0
	0	0.33	2	0	0	0	0	0
	0.03	0.33	2	0	0	0	0	0
	0.81	0.45	3	0.65	8.9	16.3	5.9	8.1
	0.62	0.45	3	0.31	3.2	5.7	2.1	2.9
20	0.45	0	0	0.45	5.1	9.3	3.4	4.6
	0.95	0.64	2	0.86	16.7	30.5	11.1	15.2
26	0.56	0.31	2	0.37	3.9	7.2	2.6	3.6
	0	0.31	2	0	0	0	0	0
	0.88	0	0	0.88	18.0	32.9	12.0	16.4
	0.09	0	0	0.09	0.8	1.5	0.5	0.7
	0.01	0.1	1	0	0	0	0	0
	0.98	0.1	1	0.97	29.8	54.3	19.8	27.2
27	0.15	0	0	0.15	1.4	2.5	0.9	1.3
	0.58	0	0	0.58	7.4	13.4	4.9	6.7
	0.09	0	0	0.09	0.8	1.5	0.5	0.7
	0.35	0.37	2	0	0	0	0	0
	0.05	0.37	2	0	0	0	0	0
	0.39	0.37	2	0.04	0.3	0.6	0.2	0.3
	0.23	0	0	0.23	2.2	4.0	1.5	2.0
	0.03	0	0	0.03	0.3	0.5	0.2	0.2
	0.07	0	0	0.07	0.6	1.1	0.4	0.6
30	0.4	0.1	3	0.33	3.4	6.2	2.3	3.1
	0.23	0.1	3	0.14	1.3	2.3	0.9	1.2
	0.49	0.1	3	0.43	4.8	8.7	3.2	4.4
	0.44	0	0	0.44	4.9	9.0	3.3	4.5
	0.07	0	0	0.07	0.6	1.1	0.4	0.6
	0.45	0	0	0.45	5.1	9.3	3.4	4.6
	0.33	0.18	1	0.19	1.8	3.3	1.2	1.6
38	0.69	0.52	3	0.35	3.7	6.7	2.4	3.3
	0.38	0.52	3	0	0	0	0	0
	0.9	0.52	3	0.79	13.3	24.2	8.8	12.1
	0.83	0.76	1	0.28	2.8	5.1	1.9	2.5
	0.2	0	0	0.2	1.9	3.5	1.3	1.7
104	0.28	0.04	3	0.25	2.4	4.5	1.6	2.2
	0.11	0.04	3	0.08	0.7	1.3	0.5	0.6
	0.18	0.04	3	0.15	1.4	2.5	0.9	1.3
	0.63	0.72	2	0	0	0	0	0
	0.33	0.72	2	0	0	0	0	0

u = observed fraction of mortality of inbreds, # = number of outcross families used in estimating b,

$\hat{b}$ = estimated maternal effects, and $\hat{Q}$ = estimated probability of mortality of an offspring

Underlines represent putative outliers.

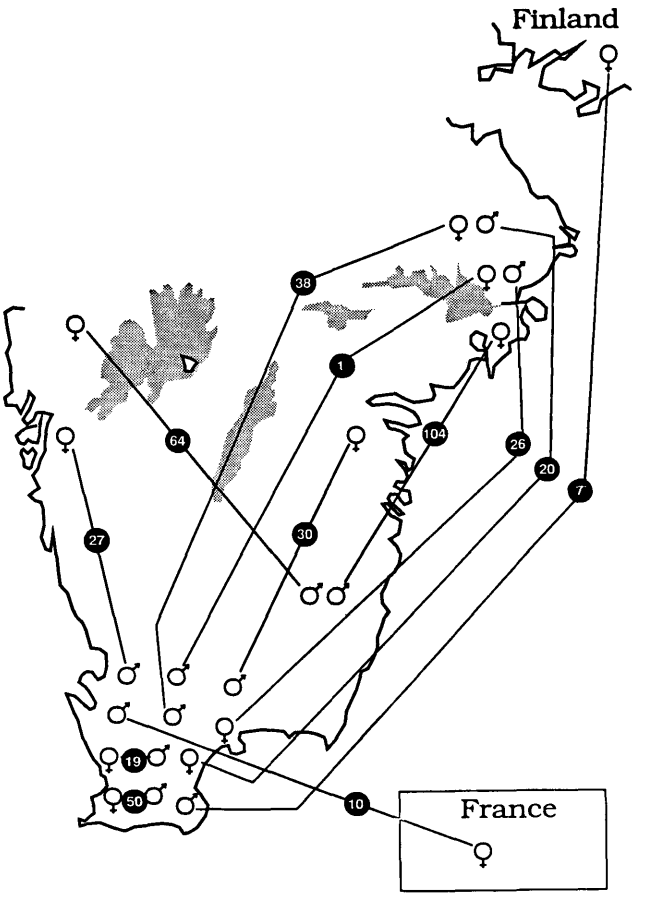


Figure 2. — Origins and crossing patterns of grandparents used in this experiment.

dotsuga menziesii (SORENSEN, 1969), and 3.03 in *Pinus virginia* (BISHIR and NAMKOONG, 1987). The ratio observed in our study far exceed the values from other studies. When the 5 putative outliers are eliminated from the data of 61 observations, means and variances of E_{min} and E_{max} are [(1.31 (2.44), 1.80 (4.58)], while the variance-mean ratios are (1.86, 2.54). Eliminating the 5 putative outliers not only reduces the lethal equivalents by about half, but also reduces the variances drastically. The resulting variance-mean ratios are well within the values observed in other studies. The lethal equivalents in *Salix viminalis* (E_{max} = 1.8) is substantially smaller than that observed in most conifers with 8+ lethal equivalents. This value is comparable to the lethal equivalents observed in *Abies procera* (1.8 to 3.4, SORENSEN et al., 1976), many diploid ferns (HEDRICK, 1987), and many mammals (RALLS et al., 1988), but is smaller than that in humans (3 to 5, MORTON et al., 1956).

The mean value of E_{max} (=1.80) obtained after deleting the 5 extreme cases is similar to the lethal equivalents ($2\varepsilon = 1.69$) obtained by MCM using the same data, as suggested by *figure 1b*. The reason why E_{max}, rather than E_{min}, resembles 2ε can be traced to the likelihood that the frequency of lethal alleles in a large population will be extremely small. The mean allele frequency is $\bar{p}=\varepsilon/M$, where M represents the total number of loci at which lethal mutations can occur. NAMKOONG and BISHIR (1987) concluded that in a forest tree population at a steady state (mutation-selection), M is likely to range between 5×10^4 and 5×10^5. In a population with $\varepsilon = 5$, the allele frequency would be less than 10^{-4}. CROW and SIMMONS (1983) estimated M for *Drosophila* to range between 5,000 and 6,000. *Figure 1b* also suggests that the allele frequency would be very small, say less than 10^{-3}. In the full-sib crossing, E_{min} corresponds to the case where both grandparents have lethal alleles at the same locus -- i. e., AB case. If the frequency of lethal alleles is as small as indicated above, the probability of obtaining AB is nearly zero. Consequently, E_{max} would represent the realistic estimate and resemble 2ε. It is unclear if this is true for *Salix viminalis* populations in general, but the fact that the crosses were made between individuals from populations located widely apart assures a low probability of sampling two lethal alleles at the same locus in this experiment.

When the population from which samples were drawn is small to begin with or the population was created from a small number of individuals, the allele frequency is likely to be fairly large. In this case, we can no longer claim that $\bar{p}$ is small and we may not be able to ignore E_{min}. Many *Salix viminalis* populations tend to exist in small clumps. The species is insect-pollinated and will not have broad gene flow as is the case with conifers. Furthermore, the number of clones could have been small when this species was imported to Sweden some 200 years ago. Therefore, when experiments were made using individuals from a single location, E_{max} could only mean the maximum possible value rather than the realistic estimate.

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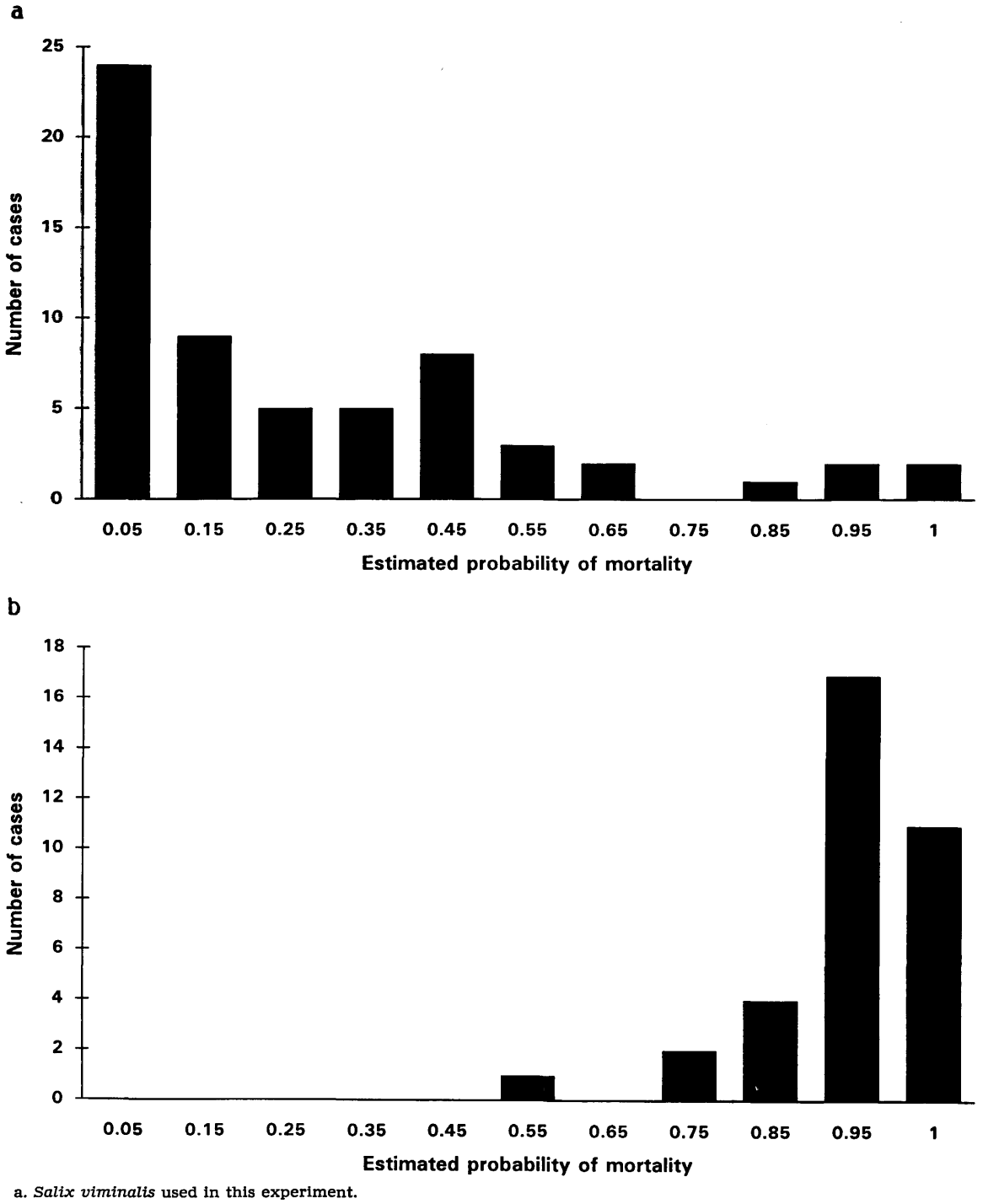
Appendix A: General Expression for Q

Consider a population with m independent loci with lethal alleles (selection coefficient s=1 and coefficient of



a. *Salix viminalis* used in this experiment.
b. *Pseudotsuga menziesii* (data from Sorensen, 1969).

Figure 3. — Distribution of estimated probability of mortality ($\hat{Q}$).

dominance h =0). Assume that the frequency of the lethal allele, q, in the gamete pool(s) is the same for all the loci. If we randomly sample a female gamete from the gamete pool, the probability of sampling exactly i loci with lethal alleles in the female gamete is

$$\binom{m}{i}(q)^i(1-q)^{m-i} \qquad [A1]$$

Suppose we randomly sampled a gamete from a male gamete pool with lethal allele frequency q*. This male gamete pool may or may not be the same as the female gamete pool. If this male gamete has a lethal allele in at least one of the above i loci, then the zygote formed by these two gametes will not be viable. We first determine the probability of the complementary event -- i.e., none of the i loci will have the lethal allele in the male gamete; $(1-q^*)^i$, and

$$(1-q^*)^i, \text{ and}$$

the probability that at least one of the i loci in the male gamete will have a lethal allele is

$$1-(1-q^*)^i \qquad \text{[A2]}$$

By multiplying [A1] and [A2], we get the probability ($Q|i$) that the zvgote will not be viable when the female gamete has i lethal alleles;

$$Q|i = \binom{m}{i}(q)^i(1-q)^{m-i}\left[1-(1-q^*)^i\right]$$

By summing $Q|_i$ for all i values between 0 and m, we get the probability (Q) that the zygote formed by 2 gametes randomly sampled from the gamete pool will not be viable;

[A3]

$$Q = \sum_{i=0}^{m}\binom{m}{i}(q)^i(1-q)^{m-i}\left[1-(1-q^*)^i\right]$$

We may extend the Q for situations where the lethal allele frequency, q, is not the same for all the loci. Suppose there are X groups with m_1, m_2, m_3, ..., m_x loci with allele frequencies of q_1, q_2, q_3, ..., q_x in the female gamete pool, and q^*_1, q^*_2, q^*_3, ..., q^*_x in the male gamete pool. Let $i = j_1 + j_2 + j_3 + ... + j_x$, $u_o = i$, and $u_k = u_{k-1} - j_k$ for $k \geq 1$. Then the probability of obtaining exactly i loci with lethal alleles in a female gamete randomly sampled from the gamete pool is

$$\sum_{j_1=0}^{u_0}\sum_{j_2=0}^{u_1}\sum_{j_3=0}^{u_2}\cdots\sum_{j_{x-1}=0}^{u_{x-2}}\prod_{k=1}^{X}\binom{m_k}{j_k}(q_k)^{j_k}(1-q_k)^{m_k-j_k}$$ where the last j_k — i.e. j_x — is replaced by u_{x-1}.

The probability ($Q|_i$) that the zygote is not viable when male gamete randomly sampled from the male gamete pool will have a lethal allele is

$$1-\prod_{k=1}^{X}(1-q_k^*)^{j_k}$$

The probability ($Q|_i$) that the zygote is not viable when the female gamete has i lethal alleles is

$$Q|i = \sum_{j_1=0}^{u_0}\sum_{j_2=0}^{u_1}\sum_{j_3=0}^{u_2}\cdots\sum_{j_{x-1}=0}^{u_{x-2}}\prod_{k=1}^{X}\binom{m_k}{j_k}(q_k)^{j_k}(1-q_k)^{m_k-j_k}\left[1-\prod_{k=1}^{X}(1-q_k^*)^{j_k}\right], \text{ and}$$

the probability (Q) that the zygote formed by 2 gametes randomly sampled from the gamete pool is

$$Q = \sum_{i=0}^{M}\sum_{j_1=0}^{u_0}\sum_{j_2=0}^{u_1}\sum_{j_3=0}^{u_2}\cdots\sum_{j_{x-1}=0}^{u_{x-2}}\prod_{k=1}^{X}\binom{m_k}{j_k}(q_k)^{j_k}(1-q_k)^{m_k-j_k}\left[1-\prod_{k=1}^{X}(1-q_k^*)^{j_k}\right]. \qquad \text{[A4]}$$

Effects of Seed Orchard Inputs on Estimating Effective Population Size of Seedlots – A Computer Simulation

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Abstract

The effects of clonal variation in seed and pollen productivity and reproductive phenological synchrony on estimating effective population size (Ne) of orchard seedlots were examined by a computer simulation. Results indicate that Ne decreases as the variability of these factors increases. The relative importance of these factors on Ne estimation changes with seed orchard conditions, and the effect of an individual factor decreases as the variability of the others increases.

Estimating Ne using only information on clonal seed production may result in a large bias in either direction. By adding information on pollen production, the bias of Ne estimates may not only be greatly reduced but be predictable (always upward). Improvement in the accuracy of Ne estimation by including reproductive phenological information is limited in seed orchards of more than 50 clones and with an average of more than 1.5 days of phenological overlap between male and female clones. However, information on reproductive phenology is important if seed orchards are small and/or the levels of reproductive phenological synchrony are low.

Key words: Seed orchard, seed qutlity, effective population size, computer simulation.

FDC: 232.311.3; 232.311.1; 165.441.

Introduction

Seed orchards are commonly used to produce mass quantities of genetically improved seed for reforestation (Andersson, 1960). The genetic composition, and therefore genetic quality, of annual seed crops from an orchard varies with changes in many factors, including female (seed) and male (pollen) productivity, as well as reproductive phenology among orchard clones (Woessner and Franklin, 1973). As more orchard seed is being used for reforestation, the genetic quality of orchard seedlots is of increased concern.