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

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;

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

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;

$$Q=\sum_{i=0}^{m}\binom{m}{i}(q)^{i}\,(1-q)^{m-i}\left[1-\left(1-q^{*}\right)^{i}\right] \qquad [A3]$$

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 $m_1, m_2, m_3, \ldots, m_x$ loci with allele frequencies of $q_1, q_2, q_3, \ldots, q_x$ in the female gamete pool, and $q^*_1, q^*_2, q^*_3, \ldots, q^*_x$ in the male gamete pool. Let $i = j_1 + j_2 + j_3 + \ldots + j_x$, $u_0 = i$, 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

$$\sum_{j_1=0}^{u_0}\sum_{j_2=0}^{u_1}\sum_{j_3=0}^{u_2}\cdots\sum_{j_{X-1}=0}^{u_{X-2}}\prod_{k=1}^{X}\binom{m_k}{j_k}(q_k)^{j_k}\,(1-q_k)^{m_k-j_k},\ \text{where}$$

the last j_k — i.e. j_x — is replaced by u_{x-1}.

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

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

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

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

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

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

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.

Table 1. — Clonal variation in seed and pollen productivity, as well as phenological synchrony of some seed orchards in British Columbia.

Seed Orchard					
Species	**No. of Clones (N)**	**PSCV[1]**	**PMCV[2]**	**MRD[3]**	**RDCV[4]**
Coastal Douglas-fir	71	0.98	0.86	5.81	0.57
Coastal Douglas-fir	94	2.14	1.05	0.77	0.55
Interior Spruce	114	2.48	4.65	-	-
Interior Spruce	174	-	-	3.63	1.15
Lodgepole Pine	103	-	-	1.72	1.38
Western Red Cedar	100	0.82	0.73	5.67	0.49
Ranges of Values Used for Simulation					
	10-200	**0-2.50**	**0-5.00**	**0.5-8.0**	**0-1.50**

[1] PSCV = coefficient of variability of seed productivity.

[2] PMCV = coefficient of variability of pollen productivity.

[3] MRD = average number of days of reproductive phenological overlap between male and female clones in the orchard.

[4] RDCV = coefficient of variability of the number of days of reproductive phenological overlap among clones in the orchard.

Parameters of interest related to the genetic quality of orchard seedlots include predicted genetic gain and effective population size (Ne). Genetic gain evaluates the potential improvement that may be achieved in the traits of interest. It is usually calculated as the average breeding value of orchard clones weighted by their proportional contribution of gametes to the seedlot. In the absence of correlations between productivity and breeding value, the unweighted average breeding value of the orchard clones provides an unbiased prediction of genetic gain of an orchard seedlot.

The effective population size of an orchard seedlot, or the effective number of orchard clones which contribute gametes to the seedlot, is equivalent to the number of clones of an idealized seed orchard population in which all clones have an equal expectation of being the parents of any progeny individual (Hedrick, 1983). Information on Ne is useful in evaluating the attributes of individual seedlots. Unlike genetic gain, however, Ne drops as variation in the proportional gamete contribution of orchard clones increases. Without knowledge of clonal gamete contributions, reliable estimation of Ne is impossible. Seed and pollen productivity, as well as reproductive phenological synchrony are three major determinants of the proportional gamete contributions of orchard clones (Askew, 1988) and, therefore, the effective population sizes of orchard seedlots. Variation in these factors will result in changes in the proportional gamete contribution of orchard clones and a reduction in effective population size. Since collecting these data may involve considerable cost and effort, understanding which factors are the critical drivers of changes in Ne estimates is essential to ensure spending is focused and efficient.

In this study, a computer simulation was performed to investigate the sensitivity of Ne to changes in the variability of seed and pollen productivity, as well as reproductive phenological synchrony among orchard clones. The accuracy of estimating Ne with different seed orchard input is examined, and critical data needs for estimating Ne for seed orchard seedlots are recommended.

Methods

Calculation of proportional gamete contributions

The methodology used in this study for calculating the proportional gamete contributions of orchard clones was modified from that developed by Askew (1988). Let

S_i = the seed productivity of clone i,
M_j = the pollen productivity of clone j, and
RD_{ij} = the number of receptive days of clone i during which clone j is shedding pollen,

Table 2. — Regression models of Ne on the 3 input variables and the predicted changes in Ne per unit change in each variable (Δ'Ne^{a}) ($N=100$, $MRD=3.5$).

Independent Variable / Conditions	Regression Model	R^2	Prob. > F	Δ'Ne^{a}
PSCV				
PMCV=0.00, RDCV=0.00	$102.27-21.95PSCV-1.21PSCV^2$	0.99	0.0001	-24.43
PMCV=0.50, RDCV=0.15	$95.95-21.93PSCV-0.97PSCV^2$	0.99	0.0001	-25.39
PMCV=2.50, RDCV=0.75	$33.99-8.95PSCV+0.76PSCV^2$	0.98	0.0001	-20.74
PMCV=5.0, RDCV=1.50	$14.94-3.00PSCV+0.16PSCV^2$	0.72	0.0065	-17.40
			Average:	**-21.99**
PMCV				
PSCV=0.00, RDCV=0.00	$106.17-34.30PMCV+3.25PMCV^2$	0.99	0.0001	-17.01
PSCV=0.25, RDCV=0.15	$101.27-33.07PMCV+3.13PMCV^2$	0.99	0.0001	-17.20
PSCV=1.25, RDCV=0.75	$64.85-20.16PMCV+1.86PMCV^2$	0.99	0.0001	-16.75
PSCV=2.50, RDCV=1.50	$34.96-8.27PMCV+0.54PMCV^2$	0.98	0.0001	-15.75
			Average:	**-16.68**
RDCV				
PSCV=0.00, PMCV=0.00	$102.38-20.48RDCV+9.76RDCV^2$	0.75	0.0041	-5.70
PSCV=0.25, PMCV=0.50	$92.01-16.39RDCV+5.82RDCV^2$	0.63	0.0184	-8.33
PSCV=1.25, PMCV=2.50	$27.09-5.71RDCV+3.78RDCV^2$	0.17	0.4790	0
PSCV=2.50, PMCV=5.00	$11.03-9.02RDCV+5.19RDCV^2$	0.37	0.1547	0
			Average:	-3.51

[a] Δ'Ne = difference between the predicted values of Ne at the highest and lowest input CV values of the corresponding variable divided by the range of the CV values.

then, the proportional seed (female gamete) contribution by clone i (PS_i) relative to the total orchard seed production and the proportional pollen (male gamete) contribution by clone j (PM_j) relative to the total within orchard pollen production are

$$PS_i = S_i / \Sigma_j S_j \text{ and}$$

$$PM_j = M_j / \Sigma_j M_j,$$

respectively. Similarly, the proportion of clone i's total pollen capture days accounted for by clone j is

$$RDP_{ij} = RD_{ij} / \Sigma_j RD_{jj}.$$

If data on seed and pollen productivity, as well as reproductive phenology are available, the proportional gamete contribution to the seedlot from matings between clones i and j can be calculated as

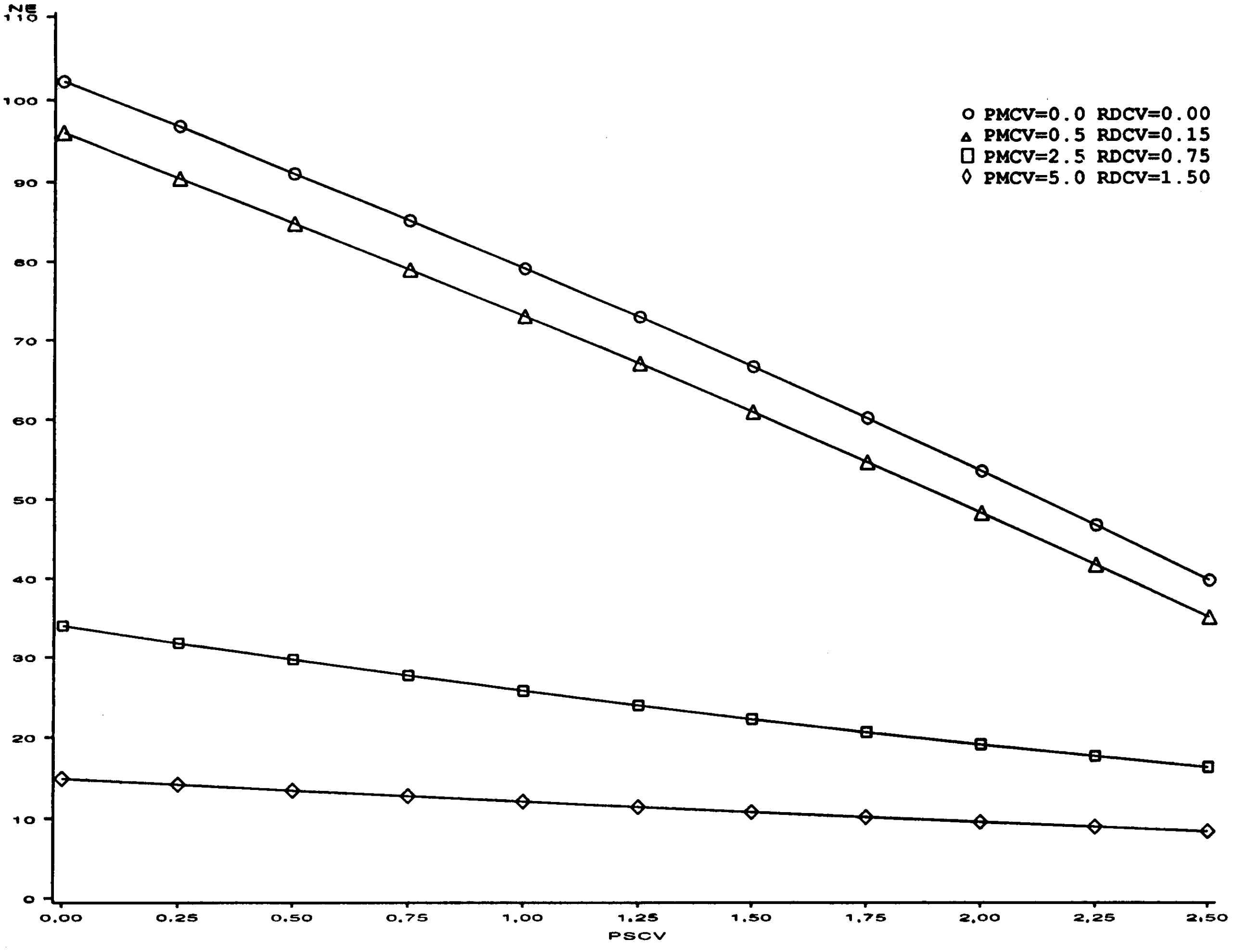
$$GC_{ij}(I) = \frac{(RDP_{ij} \text{ x } PM_i)}{\Sigma_j (RDP_{ij} \text{ x } PM_i)} \text{ x } PS_i.$$

If only seed and pollen productivity data are available, the corresponding proportional gamete contribution can be simplified as

$$GC_{ij}(II) = PM_j \text{ x } PS_i.$$

This is the proportion of the seedlot made up by the specific cross between clone i as a female and clone j as a male. The total proportion of gametes (female and male) contributed to the effective gamete pool of the seed orchard by clone i can be calculated as follows:

1), if data on both seed and pollen productivity, as well as reproductive phenology are available,


NE
110
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1.00
1.25
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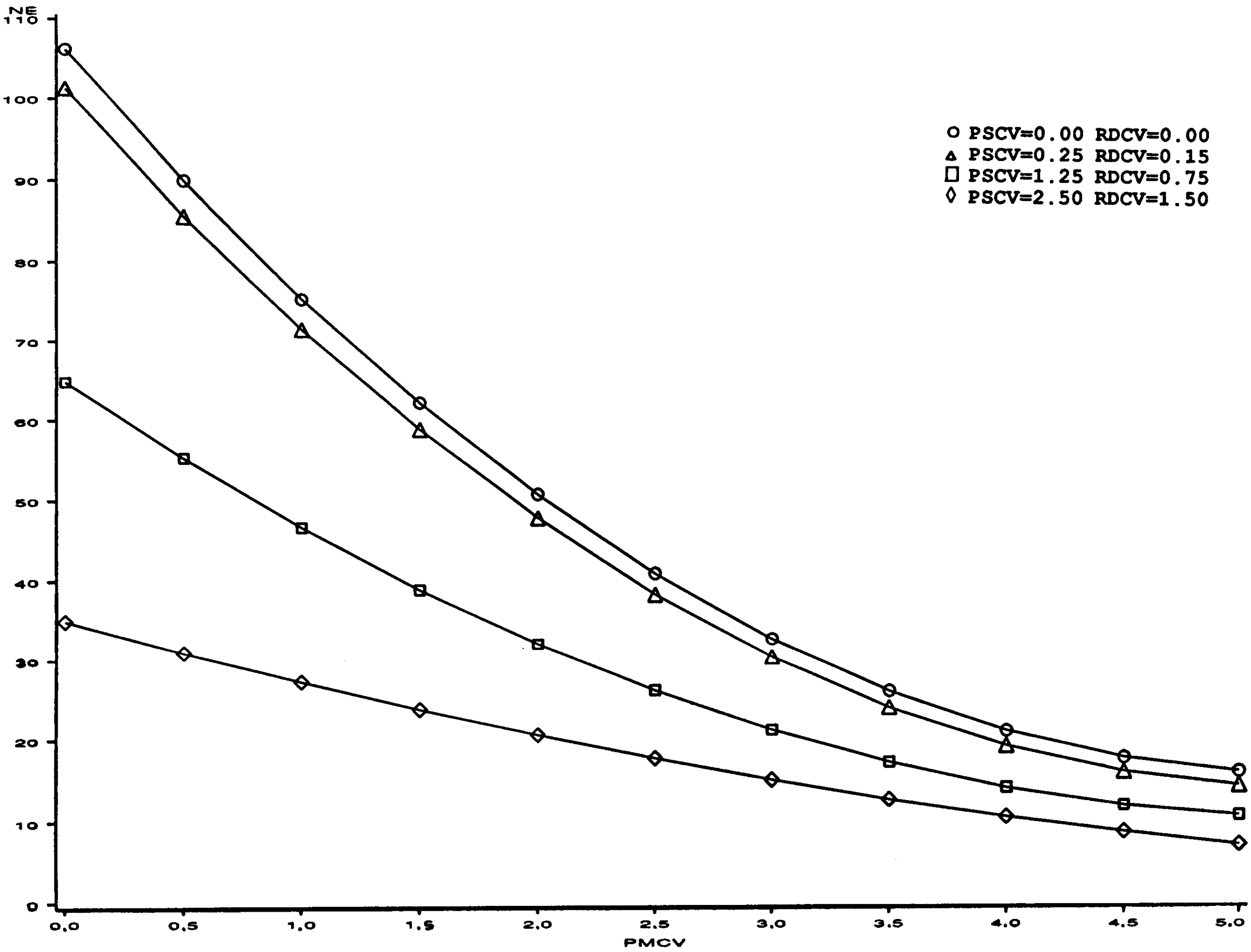
1.75
2.00
2.25
2.50
PSCV
○ PMCV=0.0 RDCV=0.00
△ PMCV=0.5 RDCV=0.15
□ PMCV=2.5 RDCV=0.75
◊ PMCV=5.0 RDCV=1.50

(a)


NE
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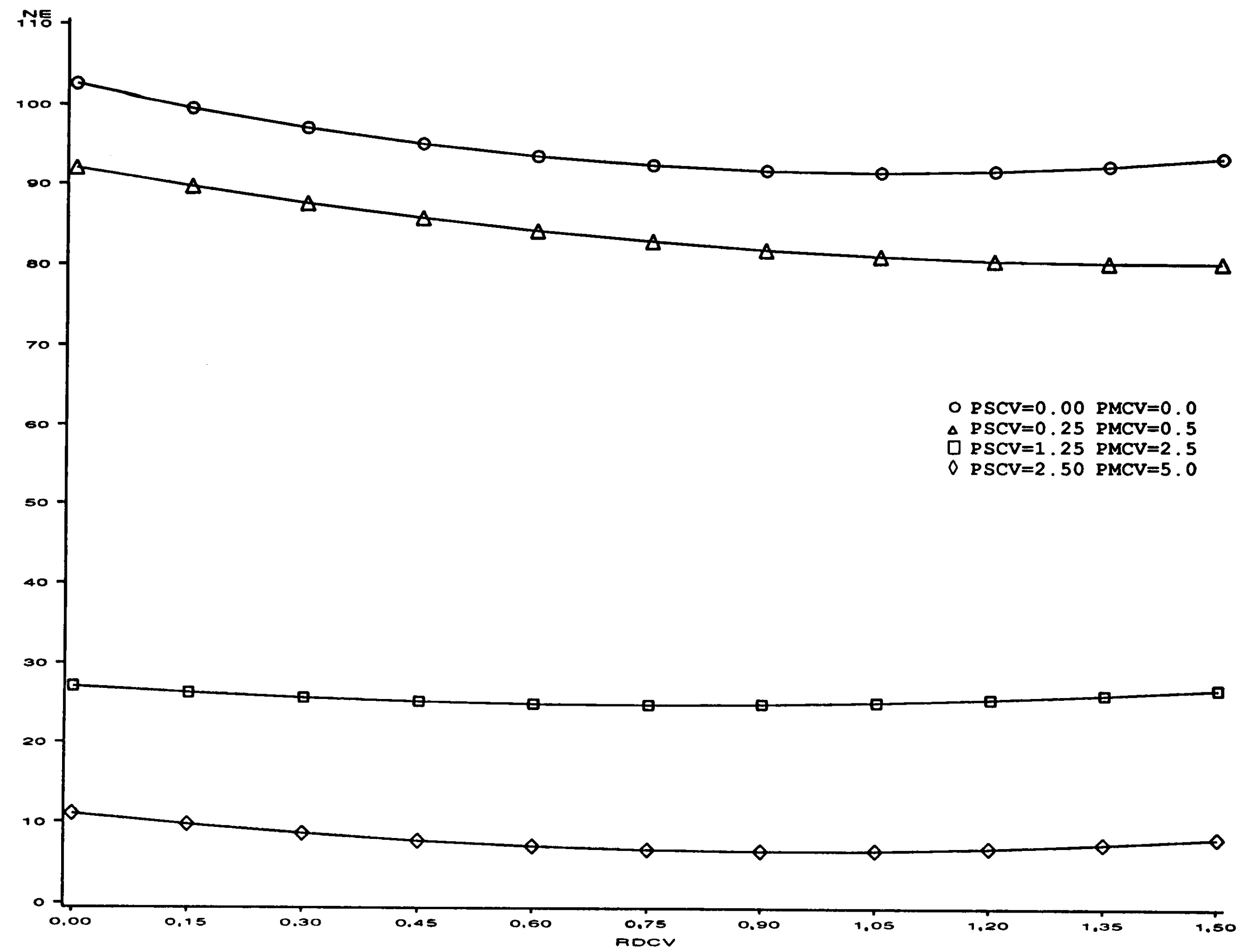
2.5
3.0
3.5
4.0
4.5
5.0
PMCV
○ PSCV=0.00 RDCV=0.00
△ PSCV=0.25 RDCV=0.15
□ PSCV=1.25 RDCV=0.75
◊ PSCV=2.50 RDCV=1.50

(b)



(c)

Figure 1. — Predicted trends of Ne estimates with changes in the variability of seed productivity (PSCV) (a), pollen productivity (PMCV) (b) and reproductive phenological synchrony among orchard clones (RDCV) (c) (N=100, MRD=3.5).

$G_i(I) = [\Sigma_j GC_{ij}(I) + \Sigma_i GC_{ij} (I)] / 2$;

2), if only data on seed and pollen productivity are available,

$G_i(II) = [\Sigma_j GC_{ij}(II) + \Sigma_i GC_{ij}(II)] / 2$;

3), if only data on seed productivity are available,

$G_i(III) = PS_i$.

There are a few assumptions for the above methodology: 1), pollen produced by each clone is equally viable, 2), the probability of a successful pollination event is equal for all possible combinations of clones i and j, 3), all days during the pollination period are equally suitable for pollen shed, distribution and pollination, 4) self-fertilization and outbreeding occur with the same probability, and 5), no pollen contamination from outside the orchard.

The first 3 assumptions may be violated. However, the deviations from the assumptions, if any, are likely randomly distributed throughout the orchard population, and would have a limited effect upon parameters calculated from the gamete contribution values. Assumptions 4 and 5 are known to be violated (see Adams and Birkes, 1990, for references), but with information on the rates of selfing and pollen contamination, G_i can be adjusted.

Calculation of Ne for orchard seedlots

Two basic methods, inbreeding and variance effective population size, are available for calculating effective population size (Crow, 1954). They are generally either identical or quite similar, but deal with different reference populations (Crow and Kimura, 1970; Hedrick, 1983; Kang and Namkoong, 1988). In this study, the definition of inbreeding effective population size presented by Kang and Namkoong (1988) is employed. It is a modification of Robertson's (1961) definition of effective population size, and is most useful for determining an Ne value which relates to the effective number of clones in a seed orchard which contribute gametes to a seed crop. Using the G_i values derived above, the effective population size of an orchard seedlot can be calculated as

$$Ne = 1 / \Sigma_i G_i^2,$$

where, $G_i = G_i(I)$, $G_i(II)$, and $G_i(III)$, and the corresponding formulas as referred to as Model 1, Model 2 and Model 3, respectively.

Simulation

A PC based computer program was developed in SAS (SAS Institute Inc., 1988). This program uses random number generators to produce data with normal distributions of specified means and standard deviations. Three sets of data were generated in each run: proportional seed production of orchard clones (PS_i), proportional pollen production of orchard clones (PM_j), and the number of receptive days for clone i during which clone j is shedding

Table 3. — Bias (%)[1]) of Ne estimated from Model 3 campared to that from Model 1 (N=100, MRD=3.5).

		Bias (%) Compared to Ne from Model 1				
PSCV	**Ne from Model 3**	**PMCV=0.00 RDCV=0.00**	**PMCV=0.50 RDCV=0.15**	**PMCV=2.50 RDCV=0.75**	**PMCV=5.00 RDCV=1.50**	**|Average|**
0.00	100.00	0.00 (ns)[2]	+ 5.29 (*)[3]	+65.30 (*)	+84.54 (*)	38.78
0.25	93.82	- 4.53 (*)	+ 2.91 (ns)	+67.02 (*)	+85.05 (*)	39.87
0.50	78.81	- 16.89 (*)	- 11.34 (*)	+62.87 (*)	+82.76 (*)	43.47
0.75	64.88	- 37.79 (*)	- 19.39 (*)	+56.70 (*)	+79.52 (*)	48.35
1.00	49.19	- 56.89 (*)	- 49.38 (*)	+47.25 (*)	+79.33 (*)	58.20
1.25	37.76	- 83.05 (*)	- 82.28 (*)	+38.19 (*)	+74.89 (*)	69.60
1.50	31.67	-111.90 (*)	- 79.44 (*)	+24.60 (*)	+58.95 (*)	68.70
1.75	29.90	- 99.70 (*)	- 84.18 (*)	+31.77 (*)	+60.37 (*)	69.00
2.00	21.17	-157.01 (*)	-130.94 (*)	+15.73 (ns)	+58.48 (*)	90.55
2.25	17.16	-177.21 (*)	-144.58 (*)	- 7.93 (ns)	+42.19 (*)	93.01
2.50	13.75	-186.98 (*)	-156.73 (*)	-17.96 (ns)	+46.98 (*)	102.18
Average	48.92	- 84.72	- 68.93	+37.23	+68.46	65.61

[1]) $$\text{Bias (\%)} = \frac{\text{Ne (model 3)} - \text{Ne (model 1)}}{\text{Ne (model 3)}} \times 100\ \%.$$

[2]) ns: Ne estimates from Model 1 and Model 3 are not significantly different ($p > 0.05$).

[3]) *: Ne estimates from Model 1 and Model 3 are significantly different ($p < 0.05$).

pollen (RD_{ij}). These data were used to generate values for Ne following the above models.

The input data for simulation were the means of proportional seed and pollen production of orchard clones, the average number of days of reproductive phenological overlap between male and female clones and the standard deviations of these 3 variables. Available data from 6 seed orchards located in both the coast and interior of British Columbia, which are believed to bracket the seed orchard conditions in the province were used to determine operationally relevant values for these input variables (*Table 1*).

Seed orchard size (number of clones) and the average length (days) of reproductive phenological overlap between female and male clones were fixed at 100 and 3.5, respectively, which are the average conditions of the 6 orchards (*Table 1*). The observed ranges of variability, as measured by the coefficient of variation (CV), of seed and pollen productivity, as well as reproductive phenological synchrony (i. e. PSCV, PMCV and RDCV, respectively) were equally divided into 10 levels. Standard deviations were calculated from the corresponding CV values and specified means, which were used as 10 sets of input data.

For each set of input data 50 independent runs were performed. Means of Ne estimates over independent runs were calculated for the three models described above and analysis of variance (ANOVA) was employed to test the siginificance of their differences. The trends in Ne with changes in the variability of seed and pollen productivity, as well as reproductive phenological synchrony (i. e. PSCV, PMCV and RDCV) were examined by regression analysis. The sensitivity of Ne to changes in the variability of these factors was quantified by changes in Ne% per unit change in the coefficients of variation of the corresponding factors.

The effects of seed orchard size and the average length of reproductive phenological overlap among seed orchard trees on the accuracy of Ne estimation from different models were also investigated.

Results

Trend and sensitivity of Ne with changes in the variability of input variables

As expected, the effective population size (Ne) of an orchard seedlot decreases as the variability of seed and pollen productivity (PSCV and PMCV, respectively), as well as reproductive phenological synchrony among orchard clones (RDCV) increases (*Figure 1* and *Table 2*).

Table 4. — Bias (%)[1] of Ne estimated from Model 2 compared to that from Model 1 (N=100, MRD=3.5).

			Bias (%) Compared to Ne from Model 1				
PSCV	**PMCV**	**Ne from Model 2**	**RDCV=0.00**	**RDCV=0.15**	**RDCV=0.75**	**RDCV=1.50**	**|Average|**
0.00	0.00	100.00	0.00(ns)[2]	+ 0.02(ns)	+11.07(*)[3]	+11.38(*)	5.62
0.25	0.50	90.10	- 0.69(ns)	+ 0.59(ns)	+ 6.97(*)	+11.24(*)	4.87
0.50	1.00	72.56	+ 2.26(ns)	+ 1.35(ns)	+12.51(*)	+10.82(*)	6.74
0.75	1.50	59.65	+ 9.61(*)	+14.20(*)	+20.97(*)	+35.46(*)	20.07
1.00	2.00	46.89	+11.86(*)	+16.40(ns)	+31.20(*)	+42.89(*)	25.59
1.25	2.50	35.37	+25.05(*)	+11.14(ns)	+39.41(*)	+31.04(*)	26.67
1.50	3.00	28.47	+19.53(ns)	+21.22(ns)	+18.83(ns)	+37.86(*)	24.34
1.75	3.50	19.33	+ 0.31(ns)	+ 0.67(ns)	+30.32(*)	+26.59(ns)	14.49
2.00	4.00	19.16	+19.31(ns)	+25.84(ns)	+43.37(*)	+36.12(*)	31.16
2.25	4.50	14.66	+11.12(ns)	+15.42(ns)	+51.71(*)	+44.61(*)	30.70
2.50	5.00	13.29	+24.00(ns)	+33.03(ns)	+58.99(*)	+47.86(*)	40.93
Average		45.41	+11.12	+12.72	+29.58	+30.53	20.99

[1] $\text{Bias (\%)} = \frac{\text{Ne (model 2)} - \text{Ne (model 1)}}{\text{Ne (model 2)}} \times 100\ \%$.

[2] ns: Ne estimates from Model 2 and Model 1 are not significantly different ($p > 0.05$).

[3] *: Ne estimates from Model 2 and Model 1 are significantly different ($p < 0.05$).

However, the sensitivity of Ne to changes in various variables was quite different. As indicated in *table 2*, when the number of clones in the seed orchard equals 100 and the average length of reproductive phenological overlap among orchard clones is 3.5 days, per unit change in the variability of seed productivity (PSCV) results in an average Ne reduction of about 22%, while per unit change in the variability of reproductive phenological synchrony (RDCV) only causes an average reduction of less than 4 %. It is also evident that the effect of each variable on Ne tends to decline as the variability of the other variables increases (*Figure 1* and *Table 2*).

Accuracy of Ne estimation with different seed orchard input

I. Model 3 vs. Model 1

As *table 3* and *figure 2a* indicate, when the variability of pollen productivity (PMCV) and phenological synchrony (RDCV) is low, Ne deived from Model 3 tends to be an underestimate compared to that from Model 1. Also the bias increases with the variability of seed productivity (PSCV). However, when PMCV and RDCV are near the averages or higher, Ne from Model 3 tends to be an overestimate, and the bias declines as PSCV increases. With a seed orchard size of 100 clones and an average length of reproductive phenological overlap of 3.5 days, the bias of Ne estimated from Model 3, compared with that from Model 1, could be as high as 187 %. In most cases, it is statistically significant (*Table 3*). The bias increases as the variability of pollen productivity and reproductive phenological synchrony approaches the extremes. Estimating Ne using only information on seed productivity may result in substantial error, and the error increases with variability in seed productivity.

II. Model 2 vs. Model 1

Model 2 consistently overestimates Ne compared to Model 1 (*Table 4* and *Figure 2b*). When the variability of reproductive phenological synchrony is low, the upward bias is negligible (statistically nonsignificant in most cases). But as RDCV nears the average or higher, the bias becomes significant (*Table 4*). Without information on the variation of reproductive phenological synchrony, one may expect an average upward bias of 21% in Ne estimation in a seed orchard of 100 clones and with average reproductive phenological overlap of 3.5 days. The bias tends to increase with the variability of seed and pollen productivity.

Effect of orchard size on Ne estimation

The effect of orchard size on the estimation of Ne using Model 2 was investigated. For a wide range of orchard sizes, Ne estimates consistently show the following trends:

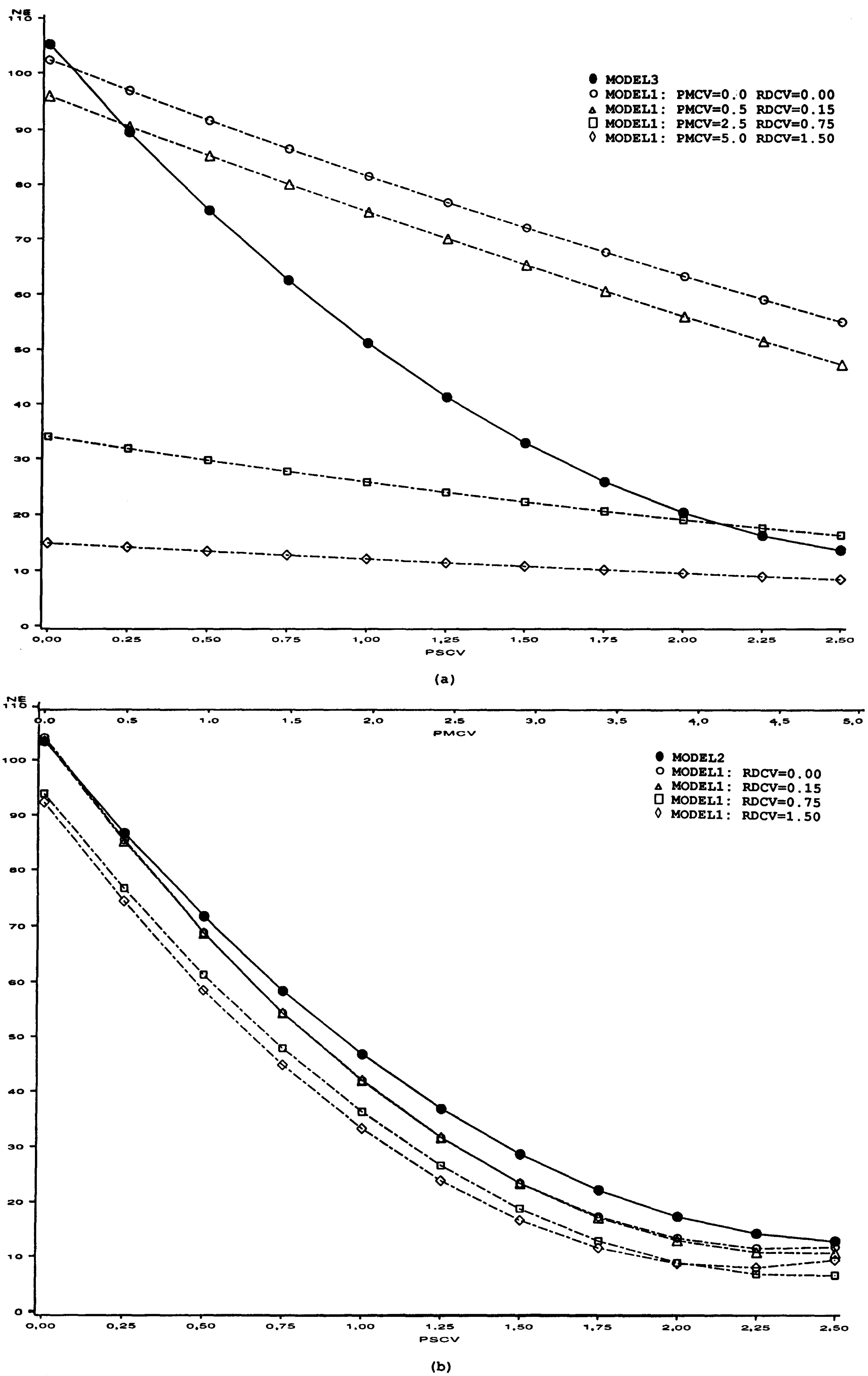
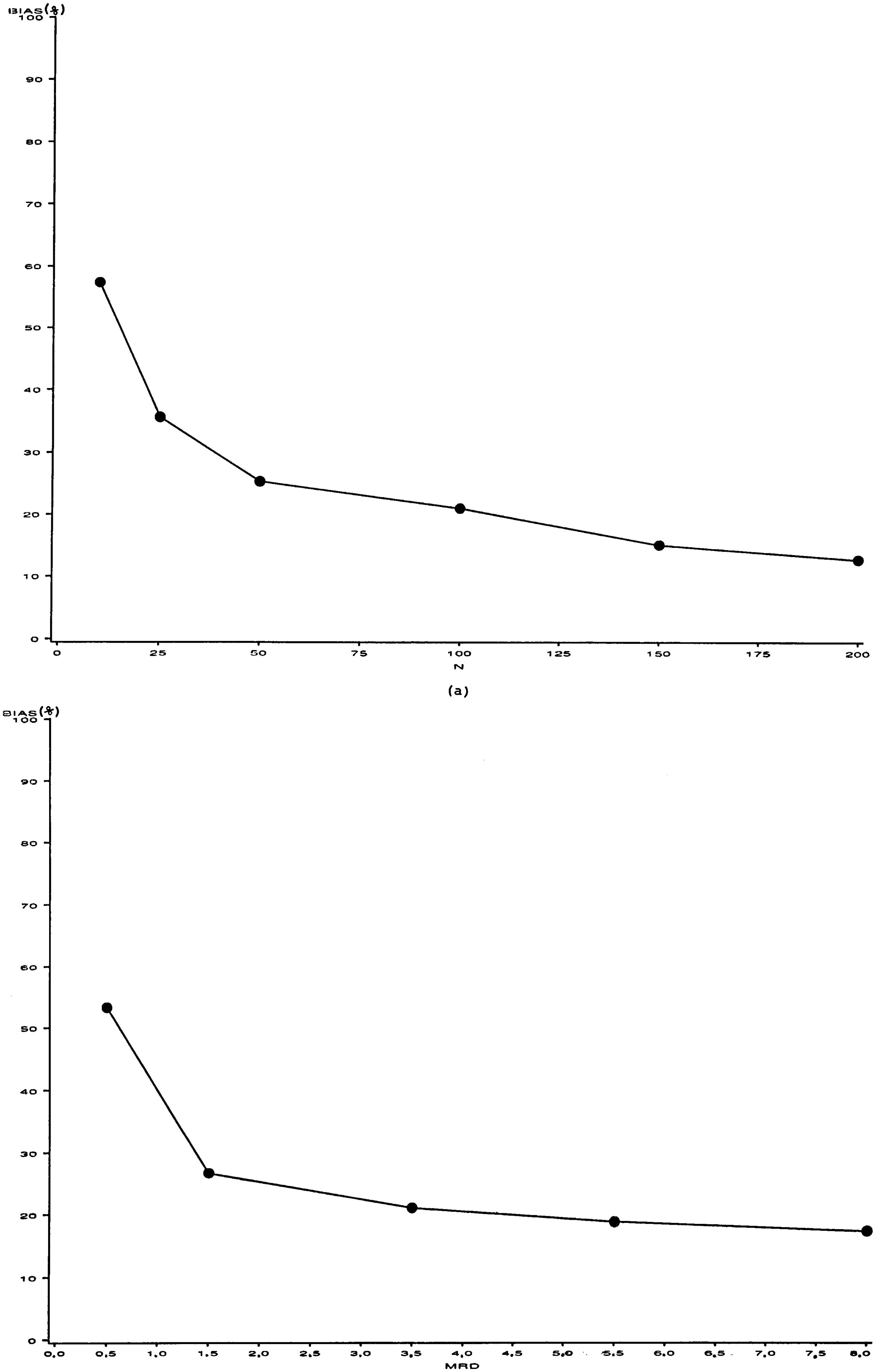


Figure 2. — Comparison of Ne estimates from model 1 to those from models 3 (a) and 2 (b) under different seed orchard conditions (N=100, MRD=3.5).



(a)

(b)

Figure 3. — Effect of seed orchard size (N) (a) and average level of reproductive phenological synchrony among orchard clones (MRD) (b) on Ne estimation.

1) Ne derived from Model 2 always tends to be an overestimate compared to that from Model 1; and 2) the bias increases with the variability of pollen and seed productivity, as well as reproductive phenological synchrony. However, Ne estimates become more accurate as the number of clones in the seed orchard increases. *Figure 3a* illustrates the trend of average bias of Ne estimates with changes in seed orchard size when the average length of reproductive phenological overlap between orchard clones is 3.5 days. It is obvious that the effect of orchard size on Ne estimation is most significant for orchards with less than 50 clones.

Effect of average level of reproductive phenological synchrony on Ne estimation

The effect of average length of reproductive phenological overlap between orchard clones on Ne estimation using Model 2 was examined. Regardless of the level of reproductive phenological synchrony among seed orchard clones, Ne estimates have the following common features: 1) Ne derived from Model 2 always tends to be an overestimate compared to that from Model 1; and 2) the upward bias increases with the variability of seed and pollen productivity as well as reproductive phenological synchrony. However, the accuracy of Ne estimates declines as the average length of reproductive phenological overlap among orchard clones decreases. *Figure 3b* shows the trend of average bias of Ne estimates with changes in the average length of reproductive phenological overlap in a seed orchard of 100 clones. When the average length of reproductive phenological overlap is 0.5 days (the lowest level of the screened data), the average bias of Ne estimates from Model 2 is as high as about 55 % compared to that from Model 1. However, as the average length of reproductive phenological overlap increases to 8.0 days, the bias lowers to about 17 %. It is also clear that the effect of reproductive phenological synchrony on Ne estimation is most significant when its levels are low. When the average length of reproductive phenological overlap among orchard clones is over 1.5 days, variation in the level of reproductive phenological synchrony does not seem to strongly affect the accuracy of Ne estimation *(Figure 3b).*

Conclusions

Results from this study demonstrate that variation in seed and pollen productivity, as well as reproductive phenological synchrony has significant influence on the estimation of effective population size (Ne) of an orchard seedlot, and that Ne decreases as the variability of these factors increases. However, different factors may have differing effects on Ne estimation, and their relative importance may change with different seed orchard conditions. For example, information on reproductive phenological synchrony is more important to Ne estimation in seed orchards of smaller sizes, and/or with shorter periods of average reproductive phenological overlap among orchard clones. In addition, the effect of an individual factor on Ne estimation tends to decrease as the variability of the other factors increases.

Estimating Ne for an orchard seedlot by using only information on seed productivity may result in either a positive or a negative bias, depending on the levels of variation in pollen productivity and reproductive phenological synchrony. On average, a bias as high as 66 % may be expected in a seed orchard with 100 clones and with an average length of reproductive phenological overlap of 3.5 days. For seed orchards with smaller sizes and lower levels of reproductive phenological overlap the bias may be much higher. Adding information on pollen production can greatly improve the estimation of effective population size of an orchard seedlot. The bias could not only be reduced drastically (more than 3 times under the same seed orchard conditions) but also be predictable (always upwards).

Reproductive phenological information further improves the accuracy of Ne estimates. Such improvement is limited in seed orchards with a large number of clones and with moderate to long periods of average reproductive phenological overlap. However, for seed orchards with small numbers of clones (<50) and/or with low levels of reproductive phenological overlap (<1.5 days), information on reproductive phenology is important to reliably estimate the effective population size of an orchard seedlot.

On a practical level, collecting the data needed to accurately estimate the effective population size of an orchard seedlot (seed and pollen productivity plus reproductive phenology) may be expensive. In many orchards, however, these data are at least partly available through other activities such as seed collection by clone, phenological monitoring for supplemental mass pollination and contaminant pollen, and pollen surveys to estimate orchard viability. Effective collection and use of these data may provide information necessary for reliable estimation of Ne with minimum cost.

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