

FERTILITY VARIATION AMONG CLONES OF KOREAN PINE (*PINUS KORAIENSIS* S. et Z.) AND ITS IMPLICATIONS ON SEED ORCHARD MANAGEMENT

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ABSTRACT

Variation in production of female and male strobili among 180 clones was investigated in a Korean pine (*Pinus koraiensis* S. et Z.) clone bank for 5 consecutive years. The strobilus production varied among clones and years. When averaged for 5 years, the most productive 25% of the clones produced 52.3 and 90.4% of total female and male strobili, respectively. Maleness index (M_i) indicated that the 73% orchard clones contributed to reproductive success as maternal parents than paternal. Based on the fertility estimated by variation in female and male strobilus production, the effective numbers of parents (N_p) were calculated to be 38, 44, 52, 66 and 39 (i.e., 21, 24, 29, 37 and 21% of the census number) for the 5 years, respectively. The effective number of parents was increased when seeds from different years were pooled and when an equal amount of seeds was collected from each clone. Expected inbreeding (selfing) in the seeds increased due to the differential fertility, but relative gene diversity remained high. The impacts of fertility variation on the genetic diversity of seed crops and possible management options are discussed.

Key words: fertility variation, effective parent number, group coancestry, inbreeding, maleness index, *Pinus koraiensis*

INTRODUCTION

Korean pine (*Pinus koraiensis* S. et Z.) occurs at elevations from 100 to 1,900m in all regions of Korea and is also distributed in China, Japan and Siberia (CHO 1990, POTENKO & VELIKOV 1998). It is an economically important native species in Korea because of its edible pine nuts and wood production. Seed supply of *P. koraiensis* for the reforestation program in Korea has not been satisfactory due to low seed production in seed orchards.

Seed orchards are the link between breeding programs and plantation establishment. They are designed and managed to produce seeds of superior genetic quality compared to those obtained from seed production areas or unimproved stands (MUONA & HARJU 1989, ASKEW 1988, CHAISURISRI & EL-KASSABY 1993). However, it has been reported that seed orchards often deviate from their ideal expectations because of differences in floral phenology, fertility and reproductive output among parents (ERICKSON & ADAMS 1989, EL-KASSABY & ASKEW 1991), which causes seed orchard clones to contribute differently to the seed crop (EL-

KASSABY & REYNOLDS 1990, MATZIRIS 1993, BURCZYK & CHALUPKA 1997).

The genetic diversity of seeds is influenced by the level of kinship (LINDGREN & MULLIN 1998) and the differences in gamete production among orchard clones (O' REILLY *et al.* 1982, KJER 1996). Uneven production of female and male strobili reduces the status effective number in the seed crop (KANG & LINDGREN 1998). To use the seeds from seed orchards with a low effective number may lead to a loss of genetic diversity in the plantations (LINDGREN *et al.* 1996). Thus, the effects of unequal contribution to gamete production should be taken into account in monitoring genetic diversity of seed crop and on the management of seed orchards (REYNOLDS & EL-KASSABY 1990, LINDGREN & KANG 1997).

The objectives of the present study were: to develop a means of calculating the effective number based on female and male fertility; to describe fertility variation and maleness index by strobilus assessment; and to estimate expected inbreeding in the seed crop. Implications of fertility variation on the management of seed orchards were also discussed.

THEORETICAL FRAMEWORK

Fertility and sibling coefficient

The fertility of a clone is its expected number of offspring, thus the expected number of successful gametes. Here this is assumed to be proportional to the amount of reproductive structures produced. Fertility variation can be described by parameter *A*, which is the square integral of the probability density function of fertility (KANG & LINDGREN 1998). The parameter *A* refers to the probability that two gametes randomly chosen from the gamete gene pool originate from the same parent. The fertility of an individual can be described as its ability to produce sibs, so we suggest calling *A* as "sibling coefficient". The sibling coefficient (*A*) is related to the coefficient of variation (*C.V.*) of parental fertility (see KANG & LINDGREN 1998, for details) as

$$A = (C.V.)^2 + 1 \tag{1}$$

A is a standardised measure that does not depend on the census number of parent genotypes (*N*), but only on how variable their fertility is. The fertility of each parent is given as a fraction of all gametes and thus the sibling coefficient (*A*) can also be calculated

$$A = N \sum_{i=1}^N p_i^2 \tag{2}$$

where *p_i* is the fertility of orchard genotype *i*, and *N* is the census number of genotypes in the seed orchard.

The sum of squared fertilities describes the expected inbreeding in the seed crop. Thus, the sibling coefficient can be given both a probabilistic and a variance interpretation.

The sum of squared fertilities will be calculated

$$\begin{aligned} \sum_{i=1}^N p_i^2 &= \sum_{i=1}^N \left[\frac{m_i + f_i}{2} \right]^2 \\ &= 0.25 \sum_{i=1}^N m_i^2 + 0.25 \sum_{i=1}^N f_i^2 + 0.5 \sum_{i=1}^N m_i f_i \end{aligned} \tag{3}$$

where *m_i* and *f_i* are the male and female fertilities, respectively, for genotype *i*.

The numbers of male and female gametes produced by an individual are male fertility and female fertility, respectively (GREGORIUS 1989). For the case where there is no correlation between female and male fertility, the last term in the expansion of formula [3] is 1/*N* and the sibling coefficient (*A*) can be described as

$$\begin{aligned} A &= 0.25N \sum_{i=1}^N m_i^2 + 0.25N \sum_{i=1}^N f_i^2 + 0.5N \sum_{i=1}^N m_i f_i \\ &= 0.25(N \sum_{i=1}^N m_i^2 + N \sum_{i=1}^N f_i^2) + 0.5 \\ &= 0.25(C.V._m^2 + C.V._f^2) + 1 \end{aligned} \tag{4}$$

where *C.V._m* and *C.V._f* are the coefficients of variation for male fertility and female fertility, respectively, in the seed orchard.

When an equal amount of seed is collected from each clone, the female fertility is kept constant. Fertility variation will then be a function of variation in pollen production and the sibling coefficient (*A*) can be described as

$$A = 0.25(C.V._m^2) + 1 \tag{5}$$

The sibling coefficient cannot be smaller than 1 because the minimum value of the *C.V.* is 0. If there is equal fertility among genotypes, the sibling coefficient will be 1.

Effective number of parents and group coancestry

It is practical to have a unique term for effective number based only on fertility variation among parents. We will call it "effective number of parents" (*N_p*), defined as the number of genotypes divided by the sibling coefficient.

$$N_p = \frac{N}{A} = \frac{1}{\sum_{i=1}^N p_i^2} \tag{6}$$

N_p is equivalent to the status number (*N_s*) of a seed orchard where clones are unrelated and non-inbred (LINDGREN & MULLIN 1998). Whereas *N_p* is independent of how parents are related or inbred, the status number depends on the relatedness of the parents. Average relatedness among members of a population is described by "group coancestry" (Θ), which is the probability that two randomly sampled gametes contain the same gene (COCKERHAM 1967). Following LINDGREN & MULLIN (1998), this probability is given by

$$\Theta = \sum_{i=1}^N p_i \sum_{j=1}^N p_j \theta_{ij} = \sum_{i=1}^N \sum_{j=1}^N p_i p_j \theta_{ij} \tag{7}$$

where *p_i* and *p_j* are the probabilities that genes sampled at random from the gamete pool originate from genotypes *i* and *j*, respectively; and θ_{ij} is the probability that genes sampled from genotypes *i* and *j* are identical by descent (*i.e.*, coancestry between genotypes *i* and *j*).

If different sexes among the parents are considered, this expression can be divided into a paternal, a maternal components and an interaction term, so that

$$\Theta = \sum_{i=1}^N (m_i + f_i) \sum_{j=1}^N (m_j + f_j) \theta_{ij} \quad [8]$$

$$= \sum_{i=1}^N m_i \sum_{j=1}^N m_j \theta_{ij} + \sum_{i=1}^N f_i \sum_{j=1}^N f_j \theta_{ij} + 2 \sum_{i=1}^N m_i \sum_{j=1}^N f_j \theta_{ij}$$

For the case where there is no correlation between genders in fertility, the last term in equation [8] is zero. Assuming that genotypes are unrelated and non-inbred, all pair-wise coancestries are equal to zero, and all self-coancestries equal to 0.5, so that group coancestry is given by

$$\Theta = 0.5 \sum_{i=1}^N p_i^2 = \frac{0.5A}{N} \quad [9]$$

and thus the sibling coefficient, $A = 2\Theta N$.

Inbreeding and gene diversity

Coancestry of the parental generation becomes inbreeding in the offspring generation if the parents mate at random (FALCONER & MACKAY 1996). When seeds are harvested, the group coancestry of orchard clones will be the expected inbreeding in the seeds. Thus, the expected inbreeding (\hat{F}) in the next generation following random mating in a seed orchard can be calculated as a function of fertility variation and parent number.

$$\hat{F}_{offspring} = \Theta_{parents} = \frac{A_{parents}}{2N_{parents}} \quad [10]$$

Relative gene diversity of seed crop (GD) is a direct function of the effective number of parents (LINDGREN & KANG 1997, KANG & LINDGREN 1998) so that

$$GD = 1 - \frac{0.5}{N_p} \quad [11]$$

Inbreeding and gene diversity of seed crop from first-generation seed orchards can be related to the group coancestry of a reference population. The reference population is defined as having an infinite number of unrelated individuals, and therefore a group coancestry of 0. The inbreeding of the reference population is also considered to be 0. For idealised populations, inbreeding is reduced by a constant proportion in each generation (FALCONER & MACKAY 1996).

Maleness index

In this study, maleness index (M_i) is defined as the proportion of a clone's reproductive success that is transmitted through its pollen (*i.e.*, male parents). The maleness index represents the sexual asymmetry among clones in their contributions to the seed crop (LLOYD 1979). The maleness index based on strobilus production is calculated as

$$M_i = \frac{pm_i}{pf_i + pm_i} \quad [12]$$

where pm_i and pf_i are the proportions of male and female strobilus production, respectively, of the i -th clone.

A high maleness index for a clone indicates that the clone is contributing more as a male than as a female parent, when compared to other clones in the seed orchard (BURCZYK & CHALUPKA 1997). A femaleness index can also be calculated as $1 - M_i$, and describes the seed production success of female parents.

MATERIALS AND METHODS

Clonal archive considered as a hypothetical seed orchard

A clone bank for *P. koraiensis* is located at the Gomae Experiment Forest at latitude 37° 70'N, longitude 127° 20'E and elevation 100m in Suwon, Korea, and contains a total of 180 clones. It was established by the Forest Genetics Research Institute (now a part of Forest Research Institute) of Korea in 1983. Clones originated from plus trees selected in natural stands or, less commonly, in plantations in Korea. Planting design of the clone bank was a row plantation with 5 ramets per clone at a 4 × 4m spacing.

For this study, we assumed that all 180 clones would form a hypothetical clonal seed orchard with an equal number of ramets per clone. Thus, the seed orchard would have the same clone composition and gamete contributions as in the clone bank. We also assumed that there was no pollen contamination in the seed orchard.

Flowering assessment and maleness index

For each clone in the clone bank, the numbers of female and male strobili were counted in early June for 5 consecutive years, from 1991 through 1995. The counts were made for all female and male strobili over the entire crown on all 5 ramets of each clone. The

ramets in the clone bank were considered reproductively mature to produce seeds during the study period.

The maleness index (M_i) for each clone was calculated based on the 5-year average of the female and male strobilus production.

Sibling coefficient, effective parent number and inbreeding

The sibling coefficient (A), group coancestry (Θ), effective parent number (N_p), expected inbreeding (\hat{F}) and relative gene diversity (GD) were calculated based on fertility variation estimated for each of the 5 years as described earlier. For comparison between census number (N) and effective number of parents (N_p), relative effective parent number (N_r) was calculated as N_p / N .

RESULTS

Strobilus production and maleness index

Average strobilus production and coefficient of variation over the 5-year assessment period, and the correlation coefficient between genders are presented in Table 1. The production of female and male strobili was found to vary among clones. Also, the number of female and male strobili varied considerably from year to year; production of female strobili peaked in 1993 with an average of 8.1, while that of male strobili was highest in 1994 with an average of 75.2.

When averaged over the 5 years, the production of female strobili by the clones varied from 0 to 26.5, and that of male strobili ranged from 0 to 1,241. Twenty-eight clones did not produce any male strobili. Based on the 5-year average, the 25% most productive clones provided 52.3% of the total female and 90.4% of the total male strobili (Figure 1). The top 25% of clones produced 71.6, 63.6, 62.8, 56.6 and 66.1% of total female strobili, and produced 98.6, 94.7, 93.8, 92.4 and

96.9% of total male strobili in 1991, 1992, 1993, 1994 and 1995, respectively. Thus, the strobilus production by clone was slightly more uniform over the 5 years, compared to production in any single year. The top producing quartile, on average, was not the same set of clones as that for a single year result. Also, if the worst 25% of clones was discarded on the basis of the strobilus production using the 5-year average, the top 25% clones provided 46.4 and 84.9% of the total female and male strobilus production, respectively.

Correlation coefficients (r) between female and male strobilus production were weak and negative in all years (Table 1). These were not statistically significant in 1991, 1993 and 1995, but significant at the 5% level in 1992 and 1994. For the average 5-year production, the correlation was also negative and non-significant. None of the correlations were greatly different from zero during the study period.

The maleness index (M_i) describing sexual asymmetry of clones is presented in Figure 2. The highest maleness was obtained from clone KG55 ($M_i = 1.0$). The lowest maleness index was obtained from 28 clones that never produced male strobili, although they produced some female strobili during the study period. A portion, 27% of orchard clones, produced more male strobili than female strobili, while the remaining 73% of clones produced more female strobili than male strobili.

Sibling coefficient, effective parent number and inbreeding

The sibling coefficient (A), group coancestry (Θ), effective parent number (N_p), relative effective parent number (N_r) and expected inbreeding (\hat{F}) are presented of variation in the strobilus production (see also Table 1).

Estimates of the effective number of parents varied between genders and among years. N_p was high in female fertility and in the year with a small A where

Table 1. Average number of strobili per clone, coefficient of variation (*C.V.*) and coefficient of correlation (r) for female and male strobilus production in a *Pinus koraiensis* clone bank..

	1991		1992		1993		1994		1995		Average	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Average	2.2	49.7	3.5	25.6	8.1	44.1	5.8	75.2	3.4	43.9	4.6	47.7
<i>C.V.</i>	1.46	3.67	1.23	3.33	1.17	2.78	0.89	2.49	1.130	3.77	0.85	2.75
$r^{1)}$	-0.053 ^{ns}		-0.025 [*]		-0.109 ^{ns}		-0.017 [*]		-0.095 ^{ns}		-0.037 ^{ns}	

¹⁾ Pearson's product-moment correlation coefficients between female and male.

^{ns} non-significant, ^{*}: statistically significant at the 0.05 probability level, $df = 178$.

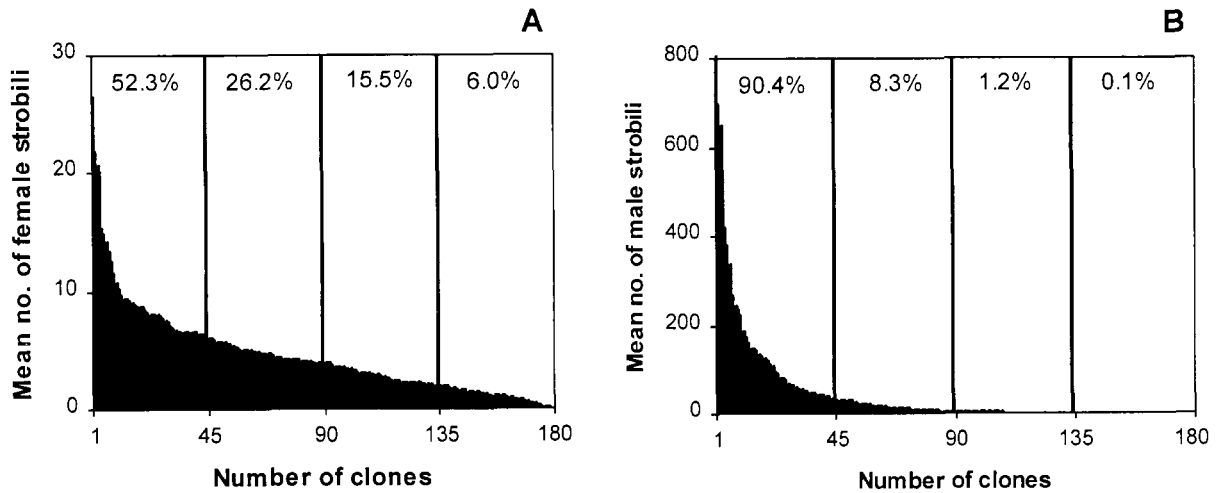


Figure 1. The contributions of individual clones ranked for female (A) and male (B) strobilus production based on the 5-year average.

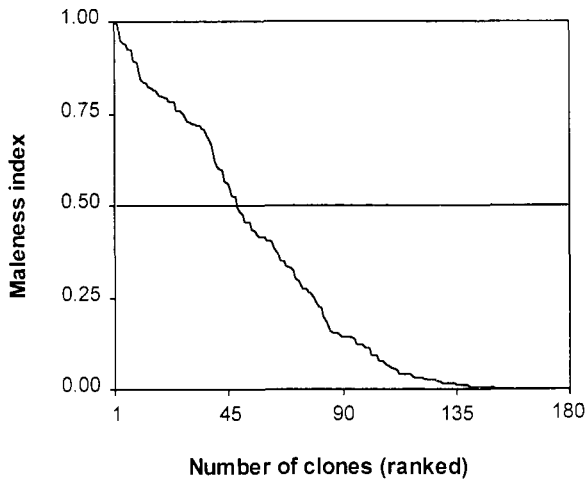


Figure 2. Maleness indices (M_i) calculated for individual clone based on 5-year mean strobilus production. The straight horizontal line represents sexual symmetry among clones, *i.e.*, an equal maleness index.

group coancestry was also low. N_p was 38 (21% of census number, N_c), 44 (24%), 52 (29%), 66 (37%) and

39 (21%), respectively for each of the 5 years. For the 5-year average, N_p was 105, 21 and 60 for female, male and total fertility, respectively. If only good years in strobilus production were considered (*i.e.*, 1993 and 1994), N_p for female, male and total fertility was 106, 27 and 69, respectively. Thus, N_p was slightly higher during good years for strobilus production.

When the worst 25% clones was discarded based on the 5-year average, N_e was 0.70 and 0.16 for female and male fertility, respectively. When the worst 50% were removed, N_e increased from 0.58 to 0.77 and from 0.12 to 0.17, for both genders, respectively. However, at 25 and 50% simulated thinning, the N_e for total fertility remained the same at $N_e = 0.43$.

The sibling coefficient (A), group coancestry (Θ), effective parent number (N_e), relative effective parent number (N_r) and expected inbreeding (\hat{F}) are presented in Table 3 for the case where female fertility variation was held constant. N_p in this case was a little higher in all years studied than was the case when both genders had varying fertilities (see Table 2). This case is analogous to collecting or mixing an equal amount of

Table 2. Sibling coefficient (A), group coancestry (Θ), effective parent number (N_e), relative effective parent number (N_r) and expected inbreeding (\hat{F}) based on the fertility variation estimated by female and male strobilus production.

	1991			1992			1993			1994			1995			Average		
	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total	♂	♀	Total
A	3.12	14.43	4.75	2.52	12.09	4.10	2.36	8.71	3.45	1.79	7.22	2.73	2.27	15.18	4.66	1.71	8.53	3.02
Θ	.0086	.0399	.0131	.0070	.0334	.0114	.0065	.0241	.0095	.0050	.0199	.0076	.0063	.0420	.0129	.0095	.0472	.0167
N_p	58	12	38	71	15	44	76	21	52	101	25	66	76	12	39	105	21	60
N_r	0.32	0.07	0.21	0.40	0.08	0.24	0.42	0.11	0.29	0.56	0.14	0.37	0.44	0.07	0.21	0.58	0.12	0.33
\hat{F}	-	-	0.013	-	-	0.011	-	-	0.010	-	-	0.008	-	-	0.013	-	-	0.008

Table 3. Sibling coefficient (A), group coancestry (Θ), effective parent number (N_p), relative effective parent number (N_r) and expected inbreeding (\hat{F}) in the case where female fertility was held constant.

	1991	1992	1993	1994	1995
A	4.359	3.773	2.928	2.554	4.545
Θ	0.01206	0.01044	0.00810	0.00707	0.01257
N_p	41	48	61	70	40
N_r	0.23	0.27	0.34	0.39	0.22
\hat{F}	0.012	0.010	0.008	0.007	0.013

seeds from each clone. Also, N_p was higher when male fertility was held constant than was the case when female fertility was constant (data not shown).

When female fertility was equal among clones, the expected inbreeding (\hat{F}) was slightly lower than when fertility varied in both genders (Tables 2 and 3). Expected inbreeding in the orchard seeds increased in all years studied, compared to that in the reference population, but the reduction of gene diversity was very small. It was illustrated that relative gene diversity (GD) of the seed crop remained high when compared to the reference population assuming random mating (*i.e.*, average $GD = 0.992$).

DISCUSSION

This paper discusses mainly two related concepts, sibling coefficient (A) and effective number of parents (N_p) which are newly established. We believe that additional or alternative measures are needed in addition to the conventional ones, and we now consider status number and group coancestry as conventional. Sibling coefficient and effective number of parents can be regarded as additions to this discussion.

Fertility variation and sibling coefficient

There was a general lack of flower production in this species and seed production in the seed orchards was low over the study period. With the variation in the amount of flower production among clones and the relative contribution of each clone to seed crops, the clones in the seed orchard of *P. koraiensis* were not expected to be under panmixia. Also, there was a large difference in gamete contributions to the seed crop among clones. The difference in male strobilus production among the clones was very large. Similar differences in the strobilus production have been reported in *Pseudotsuga menziesii* (REYNOLDS & EL-KASSABY 1990), *Pinus nigra* (MATZIRIS 1993) and *Pinus sylvestris* (BURCZYK & CHALUPKA 1997) seed orchards. This differential gamete production may have important impact on genetic diversity of seeds from an orchard, as

uneven production will cause a reduction of the N_p .

Differences in reproductive phenology were not evaluated in this study. It is difficult to compare the consequences of phenology versus flower production for reproductive success; however, differences in flower production or reproductive output are often found to be of much greater consequence than phenology when considering reproductive balance in a seed orchard (O'REILLY *et al.* 1982, ADAMS & KUNZE 1996). But, if there is a large difference in pollination period among parents and female strobili become receptive before pollen is shedding, early flowering male parents may represent more contributions than late flowering male parents (*e.g.*, YAZDANI *et al.* 1995, BURCZYK & CHALUPKA 1997) and *vice versa* (*e.g.*, EL-KASSABY *et al.* 1984, ASKEW 1988). Thus, the sibling coefficient and effective number of male parents would be less accurate than those of female parents.

We found that some clones were consistently poor in strobilus production during the study period. It has been reported that the differences in strobilus production among orchard clones are largely dependent on genetic factors, and that poor cone producers in one year are consistently poor in other years (ERIKSSON *et al.* 1973, JONSSON *et al.* 1976). ERIKSSON *et al.* (1973) pointed out that direct or indirect influence of climate factors like temperature and precipitation during the formation of the generative organs in the grafts was certainly of great importance. The seed collection of pine species was poor in Korea during 1995, and this was probably due to such interactions between climatic factors and vegetative status of the grafts.

Sexual asymmetry is common among monoecious plants (ROSS 1990). Maleness index provides a quantitative measure of gender. Clones with high maleness index will have relatively high male fertility. One clone (KG55) did not produce any female strobili for the 5 consecutive years, indicating that this clone was contributing only as a pollen parent in the gamete gene pool. On the other hand, 28 clones did not provide male strobili for the 5 years. Such clones having extremely high or low maleness index should be considered in the practice of orchard management such as genetic thin-

ning and selective cone harvest. The presence of sexual asymmetry, however, may be considered advantageous for the reduction of probability of self-fertilisation (BURCZYK & CHALUPKA 1997). Also, it is noted that the clones, which do not produce strobili, will not influence gene diversity of seeds.

Genetic thinning based on fertility by truncation selection could be impractical for balancing gamete frequencies among clones (LINDGREN & MATHESON 1986). If genetic thinning of seed orchards for this species is based only growth performance, some desirable pollen producers could be eliminated because there was a large variation in fertility and maleness index among clones. In fact, when genetic thinning was simulated by discarding one quarter or one half of the lowest-ranking clones for strobilus production, female and male fertilities were improved slightly but total fertility was not.

The sibling coefficient (A) describes the fertility variation in the seed orchard because it is derived from the variance of fertility, and it is not dependent on how parents are related (KANG & LINDGREN 1998). When the sibling coefficient is known, it is advantageous to describe the parental cumulative contribution using the power function, $F(x) = x^a$ (see BILA & LINDGREN 1998; KANG & LINDGREN 1998), where a comes from $A(1 + \sqrt{1 - 1/A})$. Theoretically, if all 180 clones contribute equally ($A = 1$), each clone will contribute about 0.56% of the total fertility. Based on the 5-year average, however, the estimated clonal contributions varied from 0 to 3.2% for female and from 0 to 14.5% for male, indicating unequal representations of both maternal and paternal parents in the orchard seeds.

The sibling coefficient can also describe the expected increment of inbreeding (*i.e.*, loss of gene diversity) in the next generation following random mating. If there is no pollen contamination, inbreeding in the next generation will be $A/(2N)$, which is the probability that uniting gametes carry identical genes in a random mating population (FALCONER & MACKAY 1996).

Effective number of parents

The effective number of parents (N_p) describes what proportion of parents is involved in the production of the progeny. N_p expresses the accumulated genetic drift raised by fertility variation from the reference population. Whereas N_s cannot be described for a future generation, without knowledge of the pedigree because of the relatedness among parents, N_p is defined solely by their contributions as parental genotypes, without reference to pedigree.

N_p can also describe that an orchard behaves as if it

were that many unrelated and non-inbred clones. Assuming that the orchard consists of unrelated clones, N_p shown that, due to variation in fertility, the simulated seed orchard was expected behave as if it had unrelated clones that amounted to 38, 44, 52, 66 and 39 for the successive 5 years (Table 2).

N_p will be larger when female and male fertilities among clones are more balanced. Thus, N_p based only on one gender (*e.g.*, seed production) may not be adequate to describe genetic diversity of seeds if there is a large difference between genders in fertility. The loss of diversity is proportional to the fertility variation in seed orchards. Therefore, a small effective number of parents in the seed orchard will reduce the genetic diversity of orchard seeds.

Information about the different gamete contributions of orchard clones and the effective number of parents is important when breeders make assumptions about expected genetic diversity in orchard seed crops used for reforestation (BURCZYK 1996). In the present study, N_p was 29% ($N_p = 52$) and 37% (66) in the abundant flowering years (1993 and 1994) with small *C.V.*, while N_p was 21% (38) and 21% (39) during the poor and intermediate flowering years (Table 2). This implies that it would be desirable to collect seeds in good flowering years to obtain improved genetic diversity in the seed crop.

It may be debated what the desired level of diversity in a seed orchard crop should be. From a commercial and managerial point of view, uniformity (thus lack of diversity of a seed crop) can usually be seen as desirable. There are legal and public relations, and safety views that are the most important reasons to demand high diversity. It is likely that some diversity is beneficial for the following reasons: biological production, pest resistance (LINDGREN 1993), flexibility to change the genetic characteristic of the seed crop when the seed orchard grows older (LINDGREN & EL-KASSABY 1989), and the ability of a plantation derived from the seed orchard to support new forest after self-generation (KJÆR 1999). Even if low diversity is desired, it may be difficult to obtain because of selfing (LINDGREN & EL-KASSABY 1989) or pollen contamination (LINDGREN & MULLIN 1998). Independent on the view of genetic diversity, some quantitative description of its size is needed for management of any production population that consists of more than one genotype.

If there is a strong correlation between female and male fertility, other statistics ought to be used for calculating N_p based on total fertility as calculated by formula [4]. Phenotypic correlations between female and male fertility were consistently weak, even if those in 1992 and 1994 were statistically significant. These calculations were from the whole population of the

hypothetical seed orchard consisting of equal number of ramets. But if clones are represented by differing numbers of ramets and grafts are sampled from the clones to estimate fertility variation, genetic correlation will give better information in relationship between female and male fertility than phenotypic correlation. The lack of good correlation between female and male flowering indicated that flowering capacity was clone specific, and that the traits were independent (FRIES 1994).

Collection of scions from different parts of the crowns of plus trees may cause negative correlations between female and male strobilus production. It may also increase maleness variation among ramets (BURCZYK & CHALUPKA 1997) due to topophysis (WRIGHT 1964). In general, seed cones of *P. koraiensis* are concentrated in the upper crown. If one scion is collected from the female flowering portion of the crown and another lower in the male portion, this may increase inter-clonal variation causing negative genetic correlations (DORMLING 1970).

Group coancestry and inbreeding

The group coancestry of parents in the orchard under study is 0.0028 ($= 0.5/N$), if we assume the orchard consists of unrelated clones. Under panmixia, this value will be the expected group coancestry of seed crop. Due to the fertility variation, however, the group coancestry of seed crops was greater than that of the parents (Table 2). In all 5 years, a large variation in the contribution of clones to the seed crop had a significant impact on relatedness, although the group coancestry in the crop remained low. The impact of fertility variation which lowered the N_p was more pronounced. Thus, despite variation in flowering, if the clones are assumed to be unrelated, the group coancestry was maintained at a low value, and high gene diversity and low levels of inbreeding were maintained in the seed crops.

Group coancestry among successful gametes becomes inbreeding in the next generation if these unite at random (BILA & LINDGREN 1998), so that group coancestry among parents will be the expected inbreeding in the seed crop. Inbreeding of clones in first-generation seed orchards is normally considered to be zero, as plus trees are assumed to have been selected from a reference population consisting of unrelated and non-inbred individuals (KANG & LINDGREN 1998). Under assumptions of random mating and viable seed from selfing, seed crops produced in 1991, 1992, 1993, 1994 and 1995 would have expected inbreeding of 0.013, 0.011, 0.010, 0.008, and 0.013, respectively.

Inbreeding and reduction of diversity in seed crops are influenced by the relatedness and fertility variation

of orchard clones. When orchard genotypes contribute differently to the gamete gene pool in different years, inbreeding may vary from year to year. KJÆR (1996) reported that inbreeding was high when the flowering was poor and unbalanced among clones. The loss of genetic variability in the planting stock can thus be somewhat moderated if parental contributions to the seed crop can be balanced or when one gender has a constant fertility.

Implications in seed orchard management

Our study indicates potential problems in seed orchards of *P. koraiensis* due to differential fertility variation among clones and years, including inadequate pollen supply, panmictic disequilibrium and parental unbalance. These problems relate to both the amount of seeds produced and the diversity of crop. HAN *et al.* (1997) reported that broad-sense heritabilities for female and male flowering of *P. koraiensis* were 0.37 to 0.56 and 0.68 to 0.81, respectively, for different years. The high heritability values indicate that female and male strobilus production is under strong genetic control. Therefore, it would be worthy that orchard managers apply some managerial options to obtain an increased amount of seeds with desirable diversity from seed orchards.

Seed production in a seed orchard can be increased by supplemental mass pollination (SMP). SMP has been reported to increase seed yield in young *Pseudotsuga menziesii* (DANIELS 1978), *Pinus taeda* (BRIDGWATER & BRAMLETT 1982) and *Pinus sylvestris* (ERIKSSON *et al.* 1994) seed orchards. EL-KASSABY and REYNOLDS (1990) reported a significant difference in the average number of filled seeds per cone between SMP and control trees in a *Pseudotsuga menziesii* seed orchard. SMP might therefore be proposed as a management option in *P. koraiensis* orchards to alleviate the effects of parental imbalance and to increase seed production.

Clones with low fertility should be stimulated to flower, especially for male strobili, through the use of cultural treatment such as top- or root-pruning, girdling, fertiliser, heat and drought (PHILIPSON 1985, ROSS 1988), and/or hormonal treatments such as exogenous gibberellins (MARQUARD & HANOVER 1985, CHALUPKA 1991). It must be cautioned, however, that all flower-induction treatments are stress treatments and their application might generate serious and eternal genetic change in the resulting seed crop (EL-KASSABY & REYNOLDS 1990). ADAMS and KUNZE (1996) reported that *Picea mariana* and *Picea glauca* clones which produced more cones per tree tended to produce fewer seed per cone, and their seeds were smaller than

those produced by clones with more moderate levels of cone production.

Collecting equal amounts of seed from each clone is one possible management option in seed orchards. This will increase the effective number of parents, because N_p in the case where female parents have constant fertility will be greater than the case where fertility varies for both genders at the seed orchard. If orchard managers of *P. koraiensis* wish to increase the N_p , more genotypes may be needed to establish new seed orchards because there was a large variation in female and male fertilities among clones.

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