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Considerations of correlated fertility between genders on genetic diversity: the *Pinus densiflora* seed orchard as a model

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Abstract The correlation between 99 clone female and male fertilities in a first generation seed orchard of *Pinus densiflora* was studied over 6 years. The effective number of the parent (N_p) and the variance effective population number [$N_e^{(v)}$] were used to assess the impact of total (Ψ_T), female (ψ_f) and male (ψ_m) fertility variation. A theoretical framework was developed to account for female and male fertility correlations as well as the impact of possible pollen contamination. Total fertility variation was described by the sibling coefficient (Ψ_T: the probability that two genes randomly chosen from the gamete gene pool originate from the same parent), which was further subdivided into ψ_f and ψ_m. These parameters were compared under various conditions including the total seed harvest, imposing on equal seed harvest among the orchard's clones and two contamination scenarios (M = 0 and 20%). Fertility variations among females, males and clones were observed within and among years. Sibling coefficients (Ψ_T) were lower, but the effective number of parent (N_p) and variance effective population number ($N_e^{(v)}$) were higher in years with moderate female and good male strobilus production. N_p for female and male reproductive outputs varied from 49 to 82 and from 57 to 93, respectively. N_p was higher for males than females. When the crop of the 6 years was pooled, N_p for female, male and the clone were 73, 87 and 85, respectively. The impact of female-male fertility correlation for conditions with no-, positive- and negative-correlations were assessed and their impact on Ψ_T, N_p and $N_e^{(v)}$ was also evaluated. It was demonstrated that the practice of equal seed harvesting from every clone, or the mixing of seeds from several years, would substantially improve the genetic diversity and the genetic representation of the seed orchard population when a positive correlation between gender fertilities was observed. The relevance of these results to supplemental-mass-pollination was discussed under two cases where equal- and un-equal amounts of pollen from clones were included in the pollen mixes.

Keywords Fertility variation · Sibling coefficients · Effective number of parent · Equal seed harvest · Pollen contamination · Seed orchard management

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Introduction

Conifers, like *Pinus densiflora* Sieb. et Zucc., are among the most genetically variable of plants (Mitton 1983), thus the maintenance of this diversity is a major concern in reforestation and breeding programs. As seed orchards become a predominant seed source, the reproductive output of orchard parents and its role on genetic diversity merit increased scientific and managerial attention.

If seed orchards are to reach their maximum genetic efficiency, they should perform as a close, perfect population. This efficiency is also described as the degree to which the parental clones transfer their genetic superiority and diversity to their seed crops. To reach this goal, it was assumed that orchard parents' gametic contribution should reach near equality. However, in most cases, orchards do not fulfill this condition (Muona and Harju 1989; Kang and Lindgren 1998).

Crow and Denniston (1988) introduced the concept of effective population number (N_e) to assess the levels of genetic diversity and relatedness of natural populations. Similarly, Kjær and Wellendorf (1997) and Lindgren and Mullin (1998) used N_e and status number (N_s) to assess genetic diversity and relatedness in forest seed-orchard populations. Differences among orchard clones/families in fertility have been observed and it is reported that unequal contribution is very common (Eriksson et al. 1973; El-Kassaby and Cook 1994; Kang and Lindgren 1999). Thus, fertility variation among orchard genotypes should be taken into account when effective population number and relatedness are estimated.

It should be emphasized that a clonal gametic contribution is the function of its female (seed-cone) and male (pollen-cone) strobilus production. Assuming that female and male strobilus production count is a good representative of their gametic contribution (i.e. reproductive energy equals reproductive success), then this count could be used to estimate potential gamete contribution and hence fertility (Gregorius 1989).

The genetic makeup of a seed orchard's crop can be manipulated by selective seed-cone harvesting methods (Lindgren and El-Kassaby 1989; Kang et al. 2001), but the result will depend on the direction and significance level of the correlation between female and male fertility. Thus, the correlation between female and male fertility represents an important attribute in determining the genetic makeup of the resultant seed crop and should affect the methods used for selective seed-cone harvesting. This important correlation (i.e. gender correlation) has not yet been considered or evaluated in seed orchard genetics and management.

The objectives of this study are to: (1) investigate the correlation between female and male fertilities, and (2) develop the theoretical framework that accounts for this correlation when the effective number of parent and gene diversity are being estimated.

Materials and methods

Seed orchard and flowering assessment

A clonal seed orchard of *P. densiflora* located at Anmyun island, Republic of Korea (latitude 36°30′N, longitude 126°20′E), provided the material for this study. The seed orchard is surrounded by a pollen dilution zone approximately 2 km wide to avoid outside gene migration. This zone was not effective in eliminating pollen contamination, as seed yield was high at an early age when pollen production within the orchard was rather low. Thus, pollen migration was factored when the effective numbers of parent and fertility variation were estimated (see below). For more detailed information regarding the seed orchard design, the number of clones, the material source, the date of establishment and the data collection, see Kang (2000).

The number of female and male strobili (reproductive output estimates) was counted for six ramets from a sample of 99 clones in the seed orchard over 6 consecutive years (1994–1999). Additionally, two rates of pollen contamination were assumed to allow for possible fluctuation. These rates were 0 and 20% (i.e. gene migration, $M = 0.0$ and 0.1, respectively). It was also assumed that contaminating pollen arrived from a large population, thus it is not related to itself and not related to the orchard clones either.

Fertility estimation

Fertility variation can be described by the sibling coefficient (Ψ: the likelihood that two genes randomly chosen from the gamete gene pool originate from the same parent) of Kang and Lindgren (1998, 1999). Additionally, the sibling coefficient is related to the fertility coefficient of variation [*CV*: Kang and Lindgren (1999)] and to female and male fertility (see below). The sibling coefficient of clonal fertility can be described as female (ψ_f) and male (ψ_m) sibling coefficients as follows:

$$\psi_f = N\sum_{i=1}^{N} f_i^2 = CV_f^2 + 1, \quad \text{and} \quad \psi_m = N\sum_{i=1}^{N} m_i^2 = CV_m^2 + 1, \tag{1}$$

where f_i and m_i are the proportional contributions of female and male, and N is the census number of clones in the seed orchard. Thus, ψ_f and ψ_m could be expressed as CV_f and CV_m (coefficients of variation in female and male fertilities), respectively.

Total fertility variation (Ψ_T) in the seed orchard can be calculated by adding the two components of equation (1), assuming no correlation between female and male fertilities (Kang and Lindgren 1999):

$$\begin{aligned}\Psi_T &= N\sum_{i=1}^{N} p_i^2 = N\sum_{i=1}^{N}\left(\frac{f_i + (1-2M)m_i}{2}\right)^2\\ &= 0.25\left(\psi_f + (1-2M)^2\psi_m\right) + 0.5(1-2M),\end{aligned} \tag{2}$$

where p_i^2 is the total fertility of the *i*-th clone and M is the gene migration (i.e. half the pollen contamination). With no correlation, selfing will be $1/N$ (i.e. $\sum m_i p_i = 1/N$).

If there is a correlation between female and male fertilities, then a covariance between them should be considered for estimating the total fertility variation (Ψ_T). The covariance can be replaced without loss of information by the coefficient of determination or its square root, the coefficient of correlation (r). When the contamination effect (M) is considered, the variance of total fertility (V) can be expressed as follows:

$$\begin{aligned}V &= V_{(f)} + (1-2M)^2 V_{(m)} + (1-2M)2Cov_{(f,m)}\\ &= \frac{\begin{gathered}N\sum f_i^2 - 1 + (1-2M)^2\left(N\sum m_i^2 - 1\right)\\ + 2r(1-2M)\sqrt{\left(N\sum f_i^2 - 1\right)\left(N\sum m_i^2 - 1\right)}\end{gathered}}{N^2}\\ &= \frac{\begin{gathered}\psi_f + (1-2M)^2\psi_m - 1 - (1-2M)^2\\ + 2r(1-2M)\sqrt{(\psi_f - 1)(\psi_m - 1)}\end{gathered}}{N^2},\end{aligned} \tag{3}$$

where $V_{(f)}$ and $V_{(m)}$ are the variances of female and male fertilities, and $Cov_{(f,m)}$ is the covariance and r is the correlation coefficient between female and male fertilities. Thus, the coefficient of variation (CV) of the total fertility can be expressed as:

$$\begin{aligned}CV &= \frac{\sqrt{V}}{2\bar{K}} = \frac{N\sqrt{V}}{2(1-M)}\\ &= \frac{\begin{gathered}\sqrt{\psi_f + (1-2M)^2\psi_m - 1 - (1-2M)^2 + 2r(1-2M)}\cdot\\ \sqrt{\sqrt{(\psi_f - 1)(\psi_m - 1)}}\end{gathered}}{2(1-M)},\end{aligned} \tag{4}$$

where $\bar{K}$ is the average contribution of each parent to total gamete production (female+male). Note that the male contribution is affected by pollen contamination.

The sibling coefficient for total fertility (Ψ_T) is thus calculated as follows:

$$\begin{aligned}\Psi_T &= CV^2 + 1\\ &= \frac{\begin{gathered}\psi_f + (1-2M)^2\psi_m + 2(1-2M)\\ + 2r(1-2M)\sqrt{(\psi_f - 1)(\psi_m - 1)}\end{gathered}}{4(1-M)^2}.\end{aligned} \tag{5}$$

Under the assumption of *no contamination* with (1) ***no correlation*** between female and male fertilities (Kang and Lindgren 1999), the above equation is simplified to $\Psi_T = 0.25(\psi_f + \psi_m) + 0.5$, (2) ***a perfect positive correlation*** ($r = 1$), the sibling coefficients for female, male and total fertility variation are all equal ($\Psi_T = \psi_f = \psi_m$), and (3) ***a perfect negative correlation*** ($r = -1$), the sibling coefficient for total fertility variation equals one ($\Psi_T = 1$) and $\psi_f = \psi_m$.

When ***no correlation*** between female and male fertilities exist ($r = 0$) and equal seed harvest is practiced ($\psi_f = 1$) to mitigate the effect of parental imbalance (i.e. differential reproductive output among the orchards clones), then the sibling coefficient (Ψ_E) will depend only on the male fertility variation (ψ_m) and pollen contamination (M) as:

$$\Psi_E = \frac{(1-2M)^2\psi_m - 4M + 3}{4(1-M)^2}. \tag{6}$$

The relative effect of equal seed harvest [i.e. equation (5)/equation (6)] is as follows:

$$\frac{\Psi_T}{\Psi_E} = \frac{\psi_f + (1-2M)^2\psi_m + 2(1-2M) + 2r(1-2M)\sqrt{(\psi_f - 1)(\psi_m - 1)}}{(1-2M)^2\psi_m - 4M + 3}. \tag{7}$$

Equation (7) describes the relative improvement in fertility variation after imposing an equal seed harvest as compared to the natural situation (i.e. the total seed harvest when both female and male fertilities vary). The relative improvement in fertility variation after an equal seed harvest under various ranges of correlations is presented in the Appendix.

Effective population numbers

The effective number of the parent (N_p) was calculated from the sibling coefficient (Ψ_T) of Kang and Lindgren (1999), i.e.

$$N_p = \frac{N}{\Psi_T}. \tag{8}$$

Under equal fertility, N_p equals N [i.e. the population is "ideal" and the progeny are distributed in Poisson fashion (Kimura and Crow 1963)]. The N_p depends only on the fertility variation among clones and does not depend on how clones are related or their degree of inbreeding (e.g. selfing is regarded as producing two offspring; more sibs). The N_p is often identical to the classical "inbreeding effective number" (e.g. Kimura and Crow 1963; Crow and Denniston 1988). The relative effective number of the parent (N_r) is the inverse of the sibling coefficient (i.e. $N_r = 1/\Psi$) (Kang and Lindgren 1999). The effective number of female ($N_{p(f)}$) and male ($N_{p(m)}$) parents can be estimated from equation (8) by substituting female (ψ_f) and male (ψ_m) sibling coefficients in place of total fertility variation (Ψ_T).

The variance-effective population number ($N_e^{(v)}$) was estimated based on the total fertility variation of the seed orchard genotypes with slight modification, as has been done by Kang and Lindgren (1998) as follows:

$$N_e^{(v)} = \frac{N}{\Psi_T - 1}. \tag{9}$$

Under equal fertility, the $N_e^{(v)}$ becomes infinite, as it should, because there is no gene frequency change (Kimura and Crow 1963). It was assumed that the number of seeds harvested was infinitive. Thus, $N_e^{(v)}$ can be interpreted as a variance in the change of N_p between generations. As indicated above, the variance-effective numbers of female [$N_{e(f)}{}^{(v)}$] and male [$N_{e(m)}{}^{(v)}$] parents can be estimated from equation (9) by substituting female (ψ_f) and male (ψ_m) sibling coefficients in place of total fertility variation (Ψ_T).

Results

Variation of flower production

Differences in female and male strobilus production were observed among clones. The highest and lowest average numbers of female strobili per clone were observed in 1994 ($\bar{X} = 49.5$) and 1999 ($\bar{X} = 16.5$), respectively (Table 1). While the male strobili was highest and lowest in 1996 ($\bar{X} = 735.5$) and 1999 ($\bar{X} = 264.0$), the remaining years showed intermediate and low female and male strobilus production, respectively.

In general, coefficients of variation of male strobili were smaller than those of females in most studied years (Table 1). The *CV* of female strobili was highest in 1994 (1.019) and lowest in 1996 (0.449), while the *CV* of male strobili was highest in 1999 (0.856) and lowest in 1995 (0.259). The difference in *CV* between female and male strobilus production became smaller over time (i.e. the differences were reduced as the orchard gets older). Phenotypic correlations between female and male strobilus production were positive for all assessed years, and statistically significant ($r = 0.358$, $p < 0.05$) in 1997.

Based on the studied 6 years, the mean numbers of female and male strobili were 34.2 and 572.2, respectively, and the coefficient of variation in female strobilus production was higher than that in the male. Thus, over time female strobilus production could be divided into three groups such as good (1994 and 1998), moderate (1995 and 1996) and poor (1997 and 1999). The years with moderate female production coincided with good male production.

Table 1 Average cone production, coefficient of variation (CV_f and CV_m) and correlation coefficient (r) between female and male output over a 6-year assessment period in a clonal seed orchard of *Pinus densiflora*

Item	1994		1995		1996		1997		1998		1999		Average	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Average	49.5	664.9	30.9	688.8	34.4	735.7	25.2	627.5	48.9	452.5	16.5	264.0	34.2	572.2
CV_f and CV_m	1.019	0.578	0.503	0.259	0.449	0.270	0.941	0.644	0.727	0.676	0.853	0.856	0.593	0.377
$CV_f - CV_m$[a]	0.441		0.245		0.179		0.297		0.050		–0.003		0.216	
r[b]	0.305		0.207		0.200		0.358*		0.318		0.185		0.323	

[a] Difference in *CV* between seed- (CV_f) and pollen-cone (CV_m) production

[b] Correlation coefficient between the number of female and male cones per clone

* Statistically significant at the 0.05 probability level

Table 2 Female and male sibling coefficient (ψ_f and ψ_m), effective number of parent ($N_{p(f)}$ and $N_{p(m)}$), relative effective number of parent ($N_{r(f)}$ and $N_{r(m)}$) and variance effective population number [$N_{e(f)}^{(v)}$ and $N_{e(m)}^{(v)}$] for gamete contribution. Pollen contamination was considered to be 20% (i.e. gene migration, $M = 0.1$)

Item	Female fertility						Male fertility					
	1994	1995	1996	1997	1998	1999	1994	1995	1996	1997	1998	1999
ψ_f and ψ_m[a]	2.04	1.25	1.20	1.88	1.53	1.73	1.33	1.07	1.07	1.41	1.46	1.73
$N_{p(f)}$ and $N_{p(m)}$	48.6	79.0	82.4	52.5	64.8	57.3	74.2	92.8	92.3	70.0	67.9	57.1
$N_{r(f)}$ and $N_{r(m)}$	0.49	0.80	0.83	0.53	0.65	0.58	0.75	0.94	0.93	0.71	0.69	0.58
$N_{e(f)}^{(v)}$ and $N_{e(m)}^{(v)}$	95.3	390.7	490.1	111.9	187.4	136.1	296.4	1,480.8	1,353.2	239.0	216.3	135.1

[a] *f* and *m* represent female and male reproductive outputs, respectively

Table 3 Clone sibling coefficient (Ψ_T and Ψ_E), effective number of parents (N_p), relative effective number of parents (N_r), and variance effective population number [$N_e^{(v)}$] for the gamete gene pool in the case where both female and male fertilities vary and female fertility is kept constant. $M = 0.1$

Item	Female and male fertilities vary						Female fertility constant (equal seed harvest)					
	1994	1995	1996	1997	1998	1999	1994	1995	1996	1997	1998	1999
Ψ_T and Ψ_E	1.48	1.10	1.09	1.46	1.33	1.44	1.07	1.01	1.01	1.08	1.09	1.14
N_p	67.1	89.6	90.9	67.7	74.4	69.0	92.9	97.7	97.6	91.5	90.8	86.5
N_r	0.68	0.91	0.92	0.68	0.75	0.70	0.94	0.99	0.99	0.92	0.92	0.87
$N_e^{(v)}$	208.3	945.5	1,114.7	2,14.4	299.5	227.2	1,500.5	7,496.4	6,850.6	1,209.9	1,095.2	684.1

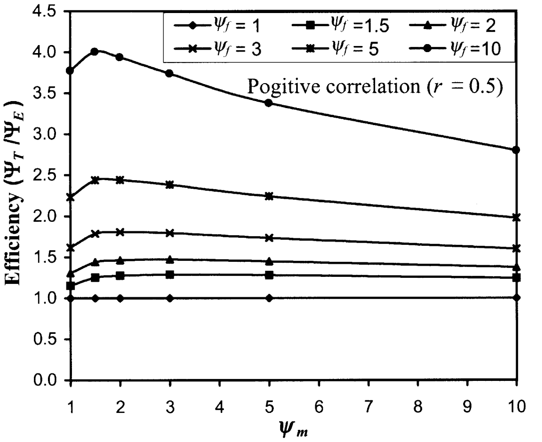

Fig. 1 Efficiency (Ψ_T/Ψ_E) of equal seed harvest among parents across the seed orchard under different female (ψ_f) and male (ψ_m) fertility variation when the female and male output correlation coefficient is $r = 0.5$, and gene migration is $M = 0.1$ (i.e. pollen contamination is 20%)

Both female and male fertility variations (ψ_f and ψ_m) were small in the moderate female-production years (Table 2).

Estimating fertility variation over the study period (i.e. observing the genetic variation of the seed orchard crop over time) produced ψ_f and ψ_m of 1.35 and 1.14, respectively, with a correlation coefficient of 0.323. When equal seed harvest was practiced, the sibling coefficient (Ψ_E) was smaller than Ψ_T for all surveyed years (Table 3). The effect of imposing female-fertility equality was considered to be positive on fertility variation (Table 3 and Fig. 1): i.e. the equal seed collection among clones was estimated to be 114% better than the total seed harvest [$\Psi_T/\Psi_E = 1.17/1.03$ from equation (7)].

Effective population numbers

As expected, higher effective number of parents (N_p) and variance-effective population number ($N_e^{(v)}$) were found in years with low and intermediate fertility variation (see Table 3). With the exception of 1999, generally the effective number of the male parent, $N_{p(m)}$ was higher than that of females $N_{p(f)}$ (Table 2).

The effective number of the parents (N_p) varied between 67.1 (1994) and 90.9 (1996) (Table 3), while the effective numbers of the female ($N_{p(f)}$) and male ($N_{p(m)}$) varied from 48.6 (1994) to 82.4 (1996) and from 57.1 (1999) to 92.8 (1995), respectively (Table 2). These results indicated that female fertility was slightly more variable than male fertility in the studied seed orchard. The relative effective number of the parents (N_r) when all seeds were harvest varied between 0.68 (1994 and 1997) and 0.92 (1996) (Table 3). Additionally, N_p, $N_{p(f)}$ and $N_{p(m)}$ were higher under moderate female and good male production (Tables 2 and 3).

On average over the study period combined, female, male and clone total sibling coefficients were $\psi_f = 1.35$, $\psi_m = 1.14$ and $\Psi_T = 1.17$. Thereafter, the effective numbers of parents were $N_{p(f)} = 73.2$, $N_{p(m)} = 86.7$ and $N_p = 84.5$. If an equal amount of seed harvest from each clone was practiced, the effective number of the parent ($N_p = 96.3$) would have been improved by 114% (= 96.3/84.5).

Over years, the variance effective population number ($N_e^{(v)}$) was higher in males than in females (Table 2).

$N_{p(f)}^{(v)}$ was higher in the moderate, compared to good or poor, flowering years. On average over the 6 years, under total seed harvest, the variance-effective numbers of the female, male and clones were 281.5, 698.1 and 574.9, respectively. On the other hand, under equal seed harvest, the variance-effective numbers of the female, male and clones over the 6 years were infinity, 698.1 and 3534.0, respectively (data not given). Under an equal seed harvest, male fertility remains uncontrolled and thus $N_{e(m)}^{(v)}$ was kept equal.

Discussion

Fertility variation

Correlation between female and male fertilities may increase or decrease total fertility variation and subsequently the reproductive success of seed orchard's clones (Askew 1985). Positive correlation will lead to increase in the total fertility variation, and thus reduce effective population numbers when compared to no correlation. On the other hand, high negative correlation will reduce total fertility variation and increase the effective population number [Equation (5)]. The effect of negative correlation on gene diversity is stronger when pollen contamination is present and where ψ_m is larger than ψ_f (see Fig. 3). If there is no correlation between female and male fertilities, the last term of the numerator in equation (5) equals zero (Kang and Lindgren 1999). It is certainly relevant to the dioecious species.

Equal seed harvest as a seed orchard crop management option (i.e. equal contribution among clones) considerably reduces relatedness of the seed crop, and thus it is proven to be an effective option in maintaining high genetic diversity (Table 3). However, imposing an equal contribution may lead to loss of seed production in the presence of low seed-producing clones or when seed is in high demand. It should be noted that the developed algorithm would not work in the presence of at least one non-seed-producing clone.

The efficiency of equal seed harvesting is dependent on the magnitude of female and male fertility variation and the direction and strength of their correlation (Figs. 1 and 2). In the case of a positive correlation, the effect of this option will be mirrored by the female fertility (Scots pine: Nikkanen and Velling 1987; Norway spruce: Kjær 1996; black spruce: Caron and Powell 1989; and white spruce: Schoen et al. 1986). Under no correlation, the magnitude of equal seed harvesting is marginal due to their independence. When a high and negative correlation between female and male fertilities exits, the effect will substantially reduce the genetic diversity and this reduction will be accentuated when fertility variation of the female is considerably low but the male is high (see Appendix). In cases of low and negative correlation, the effect is marginal but it is applicable to germplasm collections from natural populations for gene-conservation purposes (Savolainen et al. 1993; unpublished results).

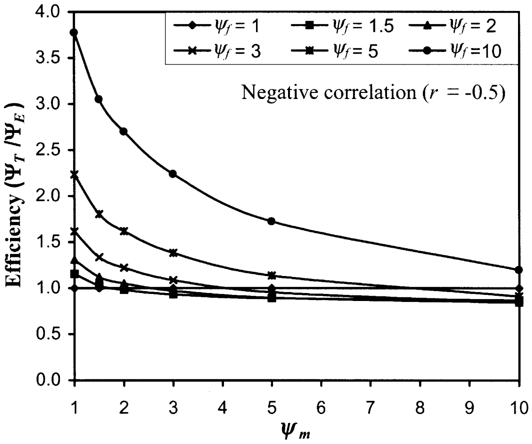

Fig. 2 Efficiency (Ψ_T/Ψ_E) of equal seed harvest under various ψ_f and ψ_m, $r = -0.5$ and $M = 0.1$. Note: under high and negative correlation, the effect of equal seed harvest is negative especially when the female fertility variation is considerably low and male fertility is high. Equal seed harvest is not superior when Ψ_T/Ψ_E is less than one

The sibling coefficient (Ψ_T) refers to the probability that two genes randomly chosen from the gamete gene pool originate from the same parent (Kang and Lindgren 1999). When the data over the 6 years were pooled, Ψ_T was estimated to be 1.17, indicating that the parental contribution is almost balanced. However, if Ψ_T equals two, this indicates that some clones contribute twice as much as others. This in turn increases relatedness and inbreeding within the established populations from this seed source, and the use of seed from this plantation is not recommended due to the build up of inbreeding.

In this study, it was assumed that the number of seed- and pollen-cones is an indication of gamete contribution among the clones. This assumption could be affected by other factors such as reproductive phenology, pollen viability, pollen dispersal, pollen competition, male–female complementarity, self-compatibility and frequency-dependent male reproductive success (Eriksson et al. 1973; Apsit et al. 1989; El-Kassaby and Reynolds 1990; El-Kassaby and Ritland 1992). Thus, the reproductive energy could be a poor indicator of reproductive success (El-Kassaby and Askew 1991; Roberds et al. 1991; El-Kassaby and Cook 1994). However, Gregorius (1989) indicated that this count (i.e. reproductive energy) could be used to estimate potential gamete contribution and hence fertility (Kang and Lindgren 1998).

Effective population numbers

The effective number of the parent (N_p) is equivalent to the status number (N_s) if the seed orchard parents are non-inbred and unrelated. Lindgren and Mullin (1998) formulated the concept of effective population number for seed orchard crops as the status effective number, and pointed out that this should be viewed as a characteristic of the seed orchard crop. The concept of the effective number of the parents is also identical to some earlier work on first-generation seed orchards (e.g. Chaisurisri and El-Kassaby 1993; Fries 1994). This case can be extended to related clones in advanced generation seed orchards because N_p does not depend on the relatedness of the parent, but the relatedness may also affect the gene diversity of seed orchards' crops.

In the studied seed orchard, the inbreeding by self-pollination is theoretically expected to be equal to N/N^2 ($99/9801 \times 100 = 1.01\%$). Predicted inbreeding is inversely proportional to the effective number of the parents as $1/(2N_p)$, following random mating (Kang and Lindgren 1999). The effective number of the parents (N_p) in the present study varied between 67 and 91 (Table 3). It is calculated, using the effective number of the parents, that the inbreeding in the seed crop varied between 0.55 and 0.75%, lower than the expected value. Thus, it is expected that the inbreeding will be higher in advanced generation seed orchards due to the reduced effective number of the parents and the presence of common parentage (i.e. relatedness among clones).

In this study, N_p was higher in the years with the moderate female and good male cone production (Tables 2 and 3). This indicates that seed quality in terms of relatedness and gene diversity may be improved in such years. As the number of clones decreases due to genetic thinning, the average relatedness within sibships may increase, the genetic variation within sibships may decrease, and the variation among sibships may increase (Levin 1988). Therefore, it is recommended that seed orchard mangers continue monitoring future cone crops and be proactive in implementing selective cone harvesting to increase the genetic diversity as well as genetic gain in their seed crops (Kang et al. 2001).

The effective number of parents (N_p) varies among years and orchards, depending on the fertility variation of parents. Unless a high and negative correlation is present, equal seed harvest has shown a considerable increase in N_p relative to the total seed harvest. Thus, under the proper conditions, equal seed harvesting from each clone has proven to be an effective factor in increasing gene diversity in the seed-orchard crops.

Pollen contamination

Pollen contamination, in general, increases the gene diversity of seed crops (Lindgren and Mullin 1998). However, the effect of contamination was difficult to assess due to the observed fluctuations in fertility variation. Under various fertility variation scenarios, pollen contamination could decrease the relative effective number of the parents (N_r) compared to no contamination (Fig. 3). When female and male fertilities were equal (i.e. $\psi_f = \psi_m$) or the fertility variation among female parents was larger than that among males, pollen contamination could give a lower N_r. Conversely, when the fertility variation of males was larger than that of females, the pollen contamination gave a higher N_r.

Pollen contamination will tend to dampen the effect of male fertility variation (Fig. 4). As the pollen contamination increases, the effect of male fertility decreases and female fertility variation begins to dominate (Askew 1985). However, it should be emphasized that contamination is not desired in seed orchards due to its negative impact on the genetic gain and adaptation.

When equal seed harvest was practiced, pollen contamination increased N_r and improved Ψ_T in the present study (Fig. 4). The results indicate that equal seed harvest under pollen contamination can improve the gene diversity of seed crops, especially when a positive correlation between female and male fertilities exists. It also implies that supplemental-mass-pollination with an equal amount of pollen from different parents could be considered as a good option in crop management. In cases where male fertility differences are high among clones, then adjusting the pollen mixes to over- and/or under-emphasize the low and high pollen-producing clones, respectively, is recommended.

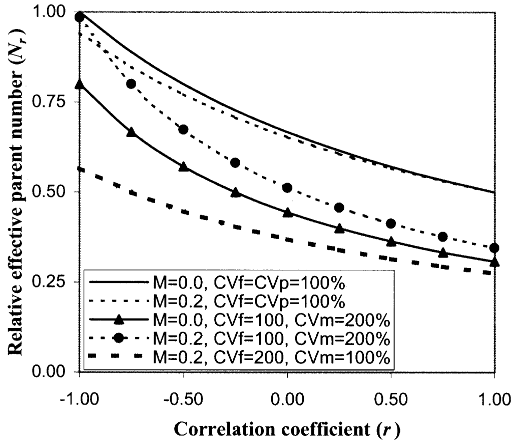

Fig. 3 Relationship between the relative effective number of the parents (N_r) and female and male output correlation coefficient (r) at different levels of fertility variation (CV_f and CV_m) and gene migration (M). The curve for $M = 0$, $CV_f = 200$ and $CVm = 100\%$ is the same as the situation with $M = 0$, $CV_f = 100$ and $CV_m = 200\%$ (*triangle marked line*) in this example

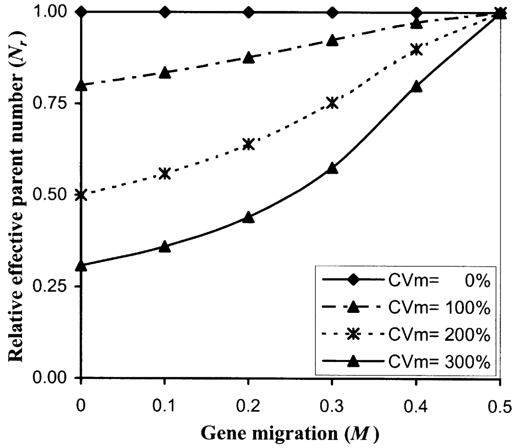

Fig. 4 Relative effective number of parents (N_r) at the different levels of gene migration (M) and male fertility (CV_m; ψ_m) in an equal seed harvest when the fertility variation of the female parent is kept at zero ($CV_f = 0$; $\psi_f = 0$) and with no correlation between genders ($r = 0$)

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Appendix

The relative effect of equal seed harvest compared to total seed collection is given, based on Equation (7) for Ψ_T/Ψ_E. Pollen contamination is set to be 20% ($M = 0.1$). Note: when Ψ_T/Ψ_E is < 1, the option of equal seed harvest is not effective for improving fertility variation and the effective number of parents (i.e. gene diversity) compared to the total seed collection method.

r[a]	ψ_m	ψ_f					
		1	1.5	2	3	5	10
0.75	1	1.00	1.15	1.31	1.62	2.23	3.78
	1.5	1.00	1.31	1.52	1.90	2.60	4.24
	2	1.00	1.35	1.57	1.95	2.65	4.25
	3	1.00	1.38	1.60	1.97	2.64	4.12
	5	1.00	1.38	1.59	1.93	2.52	3.79
	10	1.00	1.34	1.51	1.79	2.24	3.20
0.50	1	1.00	1.15	1.31	1.62	2.23	3.78
	1.5	1.00	1.25	1.44	1.79	2.44	4.00
	2	1.00	1.27	1.46	1.81	2.44	3.94
	3	1.00	1.29	1.47	1.80	2.39	3.74
	5	1.00	1.28	1.45	1.73	2.24	3.38
	10	1.00	1.24	1.38	1.60	1.98	2.80
0.25	1	1.00	1.15	1.31	1.62	2.23	3.78
	1.5	1.00	1.20	1.36	1.67	2.28	3.77
	2	1.00	1.20	1.36	1.66	2.24	3.63
	3	1.00	1.20	1.35	1.62	2.14	3.37
	5	1.00	1.18	1.31	1.54	1.97	2.97
	10	1.00	1.15	1.24	1.41	1.71	2.40
–0.25	1	1.00	1.15	1.31	1.62	2.23	3.78
	1.5	1.00	1.08	1.20	1.45	1.96	3.29
	2	1.00	1.06	1.15	1.37	1.82	3.01
	3	1.00	1.02	1.10	1.27	1.63	2.62
	5	1.00	0.99	1.03	1.15	1.41	2.14
	10	1.00	0.96	0.98	1.03	1.18	1.60
–0.50	1	1.00	1.15	1.31	1.62	2.23	3.78
	1.5	1.00	1.03	1.12	1.34	1.81	3.05
	2	1.00	0.98	1.05	1.22	1.62	2.70
	3	1.00	0.93	0.97	1.09	1.38	2.24
	5	1.00	0.89	0.90	0.95	1.14	1.72
	10	1.00	0.87	0.84	0.85	0.91	1.20
–0.75	1	1.00	1.15	1.31	1.62	2.23	3.78
	1.5	1.00	0.97	1.04	1.22	1.65	2.81
	2	1.00	0.91	0.95	1.08	1.41	2.39
	3	1.00	0.85	0.85	0.91	1.13	1.86
	5	1.00	0.79	0.76	0.76	0.86	1.31
	10	1.00	0.77	0.71	0.66	0.64	0.80

[a] See Kang and Lindgren (1999) for the cases of no- and complete-correlation

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