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# Fertility Variation and its Effects on Gene Diversity in Forest Tree Populations

Adolfo Dinis Bila



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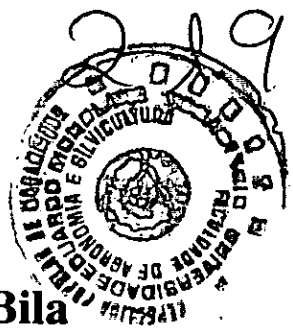

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# Abstract

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Differences in fertility among parents influence progeny relatedness, inbreeding and diversity, they should therefore be evaluated and their impacts mitigated. Flower, pollen, fruit and seed production were used to estimate fertility variation from observations in natural stands, plantations and seed orchards. Fertility variation was also compiled from the literature. Differences in fertility are described by the power function $y = x^a$ $(a \geq 1)$, where $y$ is the accumulative parental contribution to the progeny and $x$ the ranked proportion of parents. Fertility variations were also described by the sibling coefficient $A$, which expresses how parents vary in fertility and the likelihood for sibs to occur compared with the situation when parents contribute equally to the gamete pool. $A$=$a$=1 when all individuals in the population have the same fertility, and both parameters increase with unbalanced parental contributions to the progeny. Tree fertility varied widely with some parents over- and others under- represented in the gamete pool. The power function exponent and the sibling coefficient were higher than 1 in most populations studied. Fertility variation was higher in stands than in seed orchards, and in both cases only about 15% of observations had $A$ values close to 1. Age and flowering abundance appear to have a great impact on fertility variation, higher $A$ values were observed in young populations and during poor flowering years. The increase on group coancestry and the reduction in gene diversity with increasing differences in fertility among parents was quantified. It was also described how relatedness accumulates over generation shifts as a function of differences in fertility. Making parents contribute as uniformly as possible to the progeny, e.g., by collecting the same amount of seed across the population, reduced relatedness and gene diversity was better preserved. The loss of gene diversity at generation shifts is inversely proportional to the number of parents, and using a large number of parents is a way to preserve gene diversity. Knowing the magnitude of fertility variation, the number of parents can be chosen to obtain the desired gene diversity.

*Keywords:* fertility variation, flowering, seed, status number, group coancestry, inbreeding, gene diversity

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# Contents

## Lists of publications included

## Papers I-IV

This thesis is based on the following papers, which are referred to in the text by Roman numerals.

**I.** Bila, A.D, Kang, K.S, Harju, A.M. and D. Lindgren. 2000. Fertility variation in forest tree populations. Manuscript.

**II.** Bila, A.D. and Lindgren, D. 1998. Fertility variation in *Milletia sthuhlmannii*, *Brachystegia spiciformis*, *Brachystegia bohemii* and *Leucaena leucocephala* and its effects on relatedness in seeds. Forest Genetics 5 (2):119-129.

**III.** Bila, A.D., Lindgren, D. and Mullin, T.J. 1999. Fertility variation and its effect on diversity over generations in a teak plantation (*Tectona grandis* L.f.). Silvae Genetica 48(3-4):109-114.

**IV.** Kang, K. S., Bila, A.D., Lindgren, D. and Choi, W-Y. 2000. Predicted drop in gene diversity over generations in the population where the fertility varies among individuals. Manuscript.

# Introduction

## Background

Tree seeds represent the mechanism by which most new forests are established and genetic variation transmitted from one generation to another (Skøppa 1994, Edwards and El-Kassaby 1996). In managed forests, seed trees left in the stand assure natural regeneration after harvesting while the seeds used in sowing and planting are collected from natural forests, plantations or are produced in seed stands and seed orchards.

Natural regeneration by seed trees, supplemented by sowing or planting as necessary, is common in temperate and boreal regions. Seeds collected from good phenotypes or produced in selected seed stands are used worldwide. For the most important commercial species, these are interim seed sources until more permanent seed orchards become available (Zobel and Talbert 1984; Eldridge et al. 1993; Schultz 1999; Sutton 1999).

There is a concern about the effective number of parents in stands and seed orchards. In general, it has been found that only a fraction of individuals in the population contributes to the gamete pool and has its genes transmitted to the progeny generation (Eriksson et al. 1973; Griffin 1982; Rawat et al. 1992; El-Kassaby 1995). This may increase the accumulation of relatedness, inbreeding and loss of gene diversity (Lindgren et al. 1996; Kjær 1996).

The ability to reproduce, that is, to produce pollen and seed, is one of the most important factors in evolution and genetic management of populations. It should be evaluated and taken into consideration when designing and developing tree improvement and genetic conservation programs (Crossa and Vencovsky 1994; Meffe and Carroll 1997; Rodrigues 1999; Varghese et al. 2000).

Fertility is broadly defined as the individual's relative number of successful gametes (Gregorius 1989). For monoecious and hermaphroditic species, like the majority of forest trees, fertility can be regarded as the number of progeny fathered or mothered by an individual relative to all population (Devlin and Ellstrand 1990). Plant fertility is seldom observed directly; most studies estimate fertility from observations of the amount of reproductive structures such as cones, flowers, pollen, fruits and seeds, and from paternity analysis (Schoen and Cheliak 1987; Nakamura and Wheeler 1992; Savolainen et al. 1993; Stoehr et al. 1998).

Large differences in fertility have been reported among individuals within populations of forest tree species (Xie and Knowles 1992; Chaisurisri and El-Kassaby 1993; Were 1998). For example, in seed orchards, maternal and paternal imbalance among families and clones is common and a small number of

reported for various southern US species of *Pinus* (Sprague et al. 1979), *Pinus sylvestris* (Eriksson et al. 1998), *Picea mariana* (Ho 1991), *Picea glauca* (Ross 1992), *Picea abies* (Eriksson 1996), *Tsuga heterophylla* (Harrison and Owens 1992), and *Larix* spp. (Bonnet-Masimbert et al. 1998).

The environment appears to affect female and male fertility differently. For example, in monoecious species pollen production dominates on dry sites, while seed and fruit production are expressed more on wetter sites (Freeman et al. 1981; Lloyd and Bawa 1984). In general, it seems that environments favouring growth also enhance production of female flowers, whereas less favourable conditions are associated with male flowers. These observations corroborate findings that female sexuality is more costly than male sexuality, due to the additional cost of seed and fruit production (Meagher 1988). A similar effect has been reported for tree age. Female flowers dominate in young individuals, while male flowers appear some years later (Matthews 1963; Caron and Powell 1988). The contribution of young individuals to the pollen pool is limited and increases with age. Tree size also influences individual fertility. As indicated by Weiner (1988) and Crawley (1997), if pollination is not a limiting factor, reproductive output is roughly a linear function of tree size in most tree species. Correlations between descriptors of plant size, particularly stem diameter and crown size, and pollen and seed production have been found in many forest tree species (Clausen 1979; Nikkanen and Velling 1987; Dow and Ashley 1998). Pollen production increased with ramet size in *Pinus sylvestris* seed orchards in Finland (Pakkanen and Pulkkinen 1991). In stands of *Tectona grandis*, flowering and fruit production are higher in dominant and co-dominant trees (Hedegart 1976). The best competitors are also successful parents.

Most temperate forest species are wind pollinated. Temperature, wind speed, rain during pollen dispersal, and the physical distribution of inter-pollinating trees are considered important factors for successful pollination (Owens and Black 1985; Sedgley and Griffin 1989). Dominant winds in one direction and the spatial arrangement of parents may isolate some individuals from pollen, and thus affect the expression of their fertility (Erickson and Adams 1989; Di-Giovanni and Kevan 1991). Density dependence reproductive success has been reported in anemophilous species (Allison 1990; Sorensen and Webber 1997; Worrell et al. 1999). In general, the production of viable seeds increases with diminution in neighbour distance (Arista and Talavera 1996).

Animals, mostly insects, pollinate the majority of tropical tree species (Bawa 1992). Pollination is a complex process that results from interaction between animal and plant, and is conditioned by the environment prior to and during anthesis. Rain, temperature and wind influence foraging and behaviour of many pollinators and affect pollination, fruit and seed production. For example, there is little insect activity during the flowering period when temperature is below 10°C or exceeds 36°C (Sedgely and Griffin 1989), or during heavy rain. Limited

genotypes contribute most of the offspring from the orchard (Rawat 1992; El-Kassaby 1995; Adams and Kunze 1996). Differences in male and female fertility have been also reported in plantations (Caron and Powell 1988), and stands (Shea 1987). The genotype of the individual (Matziris 1998), its environment (Freeman et al. 1981; Sidhu and Staniforth 1986) and the management practices (Sweet 1995; Ericksson 1996) have been recognised as factors affecting plant fertility.

Most reproductive traits are considered under moderate genetic control (Bryam et al. 1986; Fries 1994), so variation in fertility should be expected within and among forest tree populations. Consistently good and poor pollen- and seed-producing genotypes have been described in several seed orchards (Eriksson et al. 1973; Burczyk and Chalupka 1997; Kang and Lindgren 1998), plantations (Healy et al. 1999) and natural stands (Linhart et al. 1979).

A successful reproductive cycle is preceded by floral initiation, development of ovules and stamens, adequate pollination, successful fertilization and complete development of seeds and fruits (Owens 1995). Each of these episodes affects plant fertility, is influenced by the environment and ought to be possible to manipulate. The longer is the reproductive cycle, the greater are the opportunities for climate and other factors to affect plant fertility. The duration of the reproductive cycle is correlated with growth habit, which, in turn, is governed by climate (Sedgley and Griffin 1989). Tropical and subtropical species have long growing seasons, are not subjected to subzero winter conditions that kill leaves and buds, and have a short period between floral initiation and anthesis. In contrast, temperate species have a short growing period due to the long, cold winter. Bud initiation occurs during the summer and autumn preceding the year in which anthesis occurs. Growth and development resume the following spring, resulting in anthesis, as early as possible, so that fruit development and seed dispersal occur before the next winter. The result is a long reproductive cycle in temperate conifers and hardwoods, which may last 2 to 3 years from floral initiation to seed dispersal (Owens and Black 1985; Philipson 1997).

Several environmental factors, e.g., temperature, light, water supply and nutrition, are known to play an important role in floral initiation and development, but the mechanism involved is not well understood (Matthews 1963; Owens and Black 1985; Kinnaird 1992). The effects of these factors might be through changes in water status, mineral availability, rate and amount of assimilate, and/or changes in production of, and reaction to, endogenous growth substances (Lyndon 1992). The influence of light, water and nutrient supply on fertility has been demonstrated in seed stands and seed orchards, where flowering, pollen and seed production increase following irrigation, nutrient application, and thinning (Powell and White 1994; Setiawati and Sweet 1995; Sweet 1995; Healy et al. 1999). Other commonly used management practices with similar objectives include hormone application, stem girdling, crown and root pruning. The increase in flowering by hormone application, root pruning and stem girdling has been

activity of pollinators significantly reduces fruit and seed production in *T. grandis* (Hedergart 1976). In general, pollinator activity is maximised on sheltered sites, where weather is mild and sunny during the flowering period. Plants and flowers in the same place may vary in their attractiveness and reward, e.g., blossom colour and architecture, flower size, odour, pollen and nectar feeding qualities (Rathcke 1992; Richard 1986). These variations are important in determining which plants will be visited more frequently and will reproduce successfully (Zimmerman 1988; Campbell and Halama 1993).

The abortion of flowers, fruits and seeds during the reproductive cycle is common in forest tree species. Abortions are not random and affect largely individual reproductive success (Willson 1990; O'Donnell and Bawa 1993; Harriss and Whelan 1993; Brunet 1996). Sexual allocation (Savolainen et al. 1993), resource competition (Bawa and Webb 1984; Casper and Niesenbaum 1993; Niesenbaum 1996), inadequate pollination (Schlichting and Devlin 1992; Carthew 1993; Owens 1995; Tangmitcharoen and Owens 1997) and adverse environment conditions (Johnsen et al. 1994; Palupi and Owens 1998) are the most frequently suggested causes of abortions in forest tree species.

Variation in fertility within forest tree populations should be expected and regarded as natural; the assumption that trees contribute similarly to the gamete pool does not hold in most cases (El-Kassaby 1995). Reduction of differences in fertility through management practices, e.g., increasing pollen and seed production on low-fertility individuals by gibberellin injection, stem girdling or supplementary pollination seems doutful. Fertility variation has a negative impact on diversity. It increases relatedness and inbreeding in the population. Therefore, it should be evaluated and the negative effects mitigated when managing forest genetic resources.

## Objectives

The objectives of this study were: (i) to evaluate variation in fertility in forest tree populations based on flower, fruit and seed production; (ii) to assess its impact on gene diversity; and (iii) to discuss implications of fertility variation in the management of forest genetic resources.

# Material and Methods

## Describing variation in fertility

Each individual has a fertility ($p_i$) value, the ability to produce successful gametes. Fertility can be regarded as the progeny mothered or fathered by an individual relative to others in the population (Devlin and Ellstrand 1990).

Fertility can be described by a probability density function $f(x)$ where $x$ is the percentile of trees ranked by fertility and $\int f(x)\,dx=1$. For a large population of trees $p=f(x)/N$ is the predicted fertility of the parent with rank corresponding to $x$ (**II**). An example of such function is the power function $f(x)=x^a$ ($a \geq 1$). For a given population, $p_i$ can be estimated directly, based on observations. Parents are then ranked for fertility and transformed to cumulative contributions adding up to one. Cumulative contributions are plotted against parents' proportions and the $a$ value that gives the best-fit curve to the data is chosen. As shown in study **II**, the power function is a good fit to empirical data and thus differences in fertility among parents can be described by a single parameter, $a$.

The "sibling coefficient" $A$ can be estimated directly from observations (Kang and Lindgren 1999), as the sum of squared parental contributions

$$A = N\sum_{i=1}^{N} p_i^2 \qquad [1]$$

Note that $p_i^2$ is the probability that two genes in the offspring come from same parent $i$ or that two gametes in the gamete pool originate from the same individual $i$.

$A$ has no dimension and expresses how much fertility varies among parents as the increase in the probability that sibs occur compared with the situation where parents are equally fertile (Kang and Lindgren 1998). The sibling coefficient cannot be smaller than 1. If $A=1$, all individuals have the same fertility. If $A=2$, it means that the probability that two individuals share a parent is twice as large as if fertilities were equal across the population.

The differences in fertility can also be described by the coefficient of variation ($CV$) as

$$CV = \sqrt{\frac{N\left(N\sum_{i=1}^{N} p_i^2 - 1\right)}{N-1}} \qquad [2]$$

where $N$ is the sample size, and $p_i$ the individual fertility (**I**). Sibling coefficient $A$ carries the same information as the $CV$, but is based on a probabilistic aspect while $CV$ is based on a variance aspect.

The exponent of the fitted power function, $a$, can be expressed as a function of $A$ (Kang and Lindgren 1998), thus there may not be direct need of the parameter $a$ fitted to data, as knowledge of $A$ is enough to specify a well-fitted power function.

## Measuring changes at generation turnover

Differences in the contribution of successful gametes influence the genetic constitution of the progeny by overrepresenting the most fertile genotypes (Kjær 1996). The effect of fertility variation among parents can be assessed by analysing changes in group coancestry and related diversity measures at generation shifts. In the present study, group coancestry and group inbreeding (Cockerham 1967), status number (Lindgren et al. 1996) and gene diversity (Lacy 1995) were used to assess the impact of fertility variation on the progeny population.

*Coancestry and inbreeding*

Coancestry ($\theta_{ij}$) between individuals $i$ and $j$ is the probability that random homologous genes sampled from both individuals are identical by descent, and group coancestry ($\Theta$) is the average of all pair-wise coancestries across the population, including self coancestry and reciprocals. Inbreeding ($F_i$) is the likelihood that two homologous genes of individual $i$ are identical by descent, while group inbreeding ($F$) is the average inbreeding over the population (Cockerham 1967; Falconer and Mackay 1996). Coancestry between two individuals becomes inbreeding of their progeny after mating and, likewise, group coancestry is the expected group inbreeding following random mating throughout the population.

For baseline comparison, individuals in the founder population are considered to be unrelated and non-inbred. The group coancestry in such a population of $N$ parents is

$$\Theta_{parents} = \frac{0.5}{N_{parents}} \qquad [3]$$

The new generation arising from the preceding one can be viewed in the following way: each parent contributes gametes to the gamete gene pool, proportionally to its fertility, and then a progeny population is formed from a union of successful gametes, drawn randomly from the large gamete pool. There are two ways that two genes can be identical by descent in the offspring: genes can be sampled twice with a probability of $0.5/N_{offspring}$, or genes can be identical

among the gametes by sharing a common ancestor, with a probability equivalent to the group coancestry of the gametes. The group coancestry in the progeny is **(III, IV)**

$$\Theta_{offspring} = \frac{0.5}{N_{offspring}} + \left(1 - \frac{0.5}{N_{offspring}}\right)\Theta_{gametes} \qquad [4]$$

The coancestry of the gamete pool can be described as a function of the parents fertility, their inbreeding, coancestry and number as **(III, IV)**

$$\Theta_{gametes} = \frac{0.5(1+F_{parents})A}{N_{parents}} + \left(1 - \frac{A}{N}\right)\frac{N_{parents}\Theta_{parents} - 0.5(1+F_{parents})}{N_{parents} - 1} \qquad [5]$$

Note that the gamete coancestry will be the expected inbreeding coefficient of the progeny population. Note also that, for the situation where parents are unrelated, non-inbred and are equally fertile, e.g., as the reference population, the gamete coancestry is the same as the coancestry of parents and thus the group inbreeding of the offspring.

*Status number*

The status number ($N_s$), is an effective number defined by Lindgren at al. (1996) as half of the inverse of the group coancestry

$$N_s = \frac{0.5}{\Theta} \qquad [6]$$

where $\Theta$ is the group coancestry (cf. Cockerham 1967). Status number can be regarded as a way of expressing group coancestry as an effective number (Lindgren at al. 1996). It is often practical to relate status number with the census number of individuals in the population, thus $N_r=N_s/N$, being the relative status number.

*Gene diversity*

Gene diversity (*GD*) is equivalent to the expected heterozygosity in a population following random mating (Nei 1973; Lacy 1995). Gene diversity can be formulated as $GD=1-\sum q_i$ where $q_i$ is the frequency of the allele $i$, and the summation is over alleles at that locus. For the situation where all alleles are unique in a large source population ("wild population") of unrelated and non-

inbred individuals, from which the founder population is sampled, gene diversity can be set to one and the gene diversity of the descendants, as a proportion of diversity in the source population, can be estimated as (Lindgren and Kang 1997; Rosvall 1999)

$$GD_{parents} = 1 - \Theta_{parents} = 1 - \frac{0.5}{N_{s\ parents}} \quad [7]$$

Note that group coancestry and status number are closely correlated to the loss of gene diversity relative to the source population. The decrease in heterozygosity compared to the reference population reflects the accumulation of coancestry and inbreeding associated with variation in fertility among parents.

Sexual reproduction is essentially a selective process in which the most fertile parents have their genes transmitted to the progeny (Eriksson et al. 1973; Sedgley and Griffin 1989; El-Kassaby 1995). Since the successful gametes carry a sample of genes in the parental population, genetic drift might occur if the sample is not large (Falconer and Mackay 1996). Apart from changes in allele frequency, an increase in homozygotes and a decrease of heterozygotes in the population are expected when a limited number of parents is involved in mating.

## Fertility assessment

Information on flower, fruit and seed production obtained from natural stands, plantations and seed orchards was used to estimate individual fertility. Adult individuals constituted most of the studied populations.

Female fertility ($p_{if}$) was estimated from female strobili (**I, IV**), fruit (**I, III**) or seed production (**I, II**), while male fertility ($p_{im}$) was calculated from male strobili (**I, IV**), stamens (**III**) and pollen production (**I**). The total fertility, that is the individual fertility ($p_i$), was the mid-parent value. With one gender assumed constant, the corresponding fertility was equal to $1/N$, being $N$ the census number.

The observed numbers of male and female reproductive structures were expressed as proportions of those found over all trees; thus the gender and total fertilities were established. In general, it was assumed that reproductive success is proportional to the number of reproductive structures. Details of the populations, sampling procedures, data collection and estimation of fertility variation parameters, inbreeding, coancestry and related diversity measures are given in the appended papers.

# Summary of the studies

## I

In the first study, information on flower, fruit and seed production were used to estimate fertility variation within populations of forest tree species. The sibling coefficient, *A*, was estimated for 99 stands (74 conifer stands and 25 broadleaf) and for 36 seed orchards (30 conifer and 6 broadleaf). Female fertility variation was observed in both stands and seed orchards, while variation in male fertility was generally assessed only in seed orchards.

As expected, fertility varied within and among populations. Objects with an *A* value close to 1 were few in both stands and seed orchards. For example, only 15% of the observed objects had female *A* values between 1 and 1.25, which correspond to a coefficient of variation in flower, fruit or seed production ranging from 0 to 50%. Populations with *A* value between 1.25 and 3.20, represented about 55% and 75% of stand- and seed-orchard populations, respectively.

Differences in fertility were higher in stands than in seed orchards, but in both cases, age and flowering abundance appear to have great impact on the sibling coefficient. Variation in fertility was higher in young populations and during poor flowering years. Variation in male fertility seems to be higher than that in female fertility.

The distribution of *A* in stands and seed orchards is positively skewed. There is a need to make forecasts of *A* for planning, and as a rough generalisation it is suggested to use $A = 3$ for stands and $A = 2$ for seed orchards. For particular cases, more accurate forecasts of *A* can be made based on information reported in this study and relevant observations relating to the particular objects.

## II

The second study analysed fertility variation in 5 stands in Mozambique and assess their impact on relatedness in the seed crop. The studied population included 3 natural stands and 2 plantations of 4 tropical species, *Millettia sthulmannii*, *Brachystegia speciformis*, *B. bohemii* and *Leucaena leucocephala*.

A power function $y = x^a$, where $y$ is the accumulative seed production and $x$ the ranked proportion of trees, was used to describe the distribution of seed production. A power function was fitted to observations by using $a$ as a parameter. The agreement between the fitted power function and the observed data was rather good, indicating that a power function is a useful way to describe fertility variation, where $a$ describes the magnitude of fertility variation. The expected relatedness or group coancestry of the seed crop, expressed as status

effective number relative to the number of parents, was estimated to be 0.67, 0.65, 0.54, 0.43 and 0.38, respectively for the five populations.

The effect of collecting an equal amount of seeds per parent was quantified. This was shown to reduce relatedness in the seed lot considerably and is therefore an effective way of maintaining diversity in the population. It is recommended to use this effect in germplasm collection and when establishing stands for gene conservation.

## III

The third study expanded on the former to multiple generations. The aim was to develop formulae to predict diversity and the accumulation of group coancestry and inbreeding in future generations, as a function of differences in fertility among parents and population size in each generation. The sibling coefficient was used to quantify fertility differences within the population, while group coancestry, status number and relative status number were used as diversity indicators.

A mature population of 154 teak individuals (*Tectona grandis* L.f) growing in a plantation in southern Mozambique was used as a case study. The trees varied in fertility with the 20% most fertile genotypes contributing 55% of gametes.

Assuming random mating, constant fertility variation and population size, predictions over 10 generations indicated a rapid increase in coancestry and inbreeding during the first generations and a decrease in status number. The loss of diversity was hastened by differences in fertility among parents. Calculations indicated that the observed fertility variation would result in a similar diversity loss over five generations as would be expected over ten generations if parents contributed equally to the gamete pool.

The accumulation of relatedness, inbreeding and the decrease in diversity occurred at a considerably lower rate when the contribution of one gender was kept constant across the population.

## IV

In the fourth study, predictions were performed for the case where population size remained constant, but fertility varied considerably between genders and among generations.

Female and male fertilities were monitored over 5 consecutive years for 180 clones of Korean pine (*Pinus koraiensis* S. et Z.) growing in a clonal archive in Suwon, Korea. In simulations, the years were considered to be the generations.

Female fertility ranged from 1.79 to 3.12 while male fertility varied from 7.22 to 15.18.

In general, with advancing generations, group coancestry, inbreeding and diversity followed the same tendency as in study **III**; but the effect of controlling inbreeding and relatedness and the maintenance of diversity by making female fertility constant was not large. Apparently, the effect seems low due to the weak correlation between female and male fertility and the differences in male fertility, which was very large compared with female fertility for this material.

# Discussion

## Fertility variation in forest tree populations

The ability to produce successful gametes is an important factor from an evolutionary perspective; it determines, to a large extent, an individual's success in contributing genes to its offspring (Devlin and Ellestrand 1990). Studies of flower, fruit and seed production in forest tree species have shown that equal gamete contribution is rarely observed and that relatively few individuals within a given population generally produce most of the progeny (El-Kassaby 1995; Burczyk et al. 1997; Gömöry et al. 2000). The present studies corroborate these findings.

In study **I** (*Figures 1* and *2*), unbalanced parental contributions to the gamete pool were found in most populations. There were few stands and seed orchards with an *A* value close to 1. In studies **III** and **IV**, female, male and total fertility variation measures deviated largely from the situation where parents were equally fertile. Similar results were found in study **II**, in which parameter $a$ was also higher than 1.

Fertility variation can be regarded as a natural phenomenon; panmixis rarely occurs in forest tree populations (Falconer and Mackay 1996; Crawley 1997). For example, trees vary in reproductive investment, flowering phenology (e.g., El-Kassaby and Cook, 1994; Burczyk and Chalupka 1997; Paluti and Owens 1998) and pollination is strongly leptokurtic such that close neighbours are much more likely to mate than more distant individuals (Di-Giovanni and Kevan 1991; Prat 1994; Worrell et al. 1999). There are also incompatibility systems (Sedgley and Griffin 1989), female-male complementarities (El-Kassaby and Ritland 1992; Nakamura and Wheeler 1992) and selective abortion (O'Donnell and Bawa 1993; Harriss and Whelan 1993; Brunet 1996) that might prevent fertilisation and seed maturation. Therefore, gamete contribution to the seed crop, via pollen or ovules, is expected to vary considerably among parents.

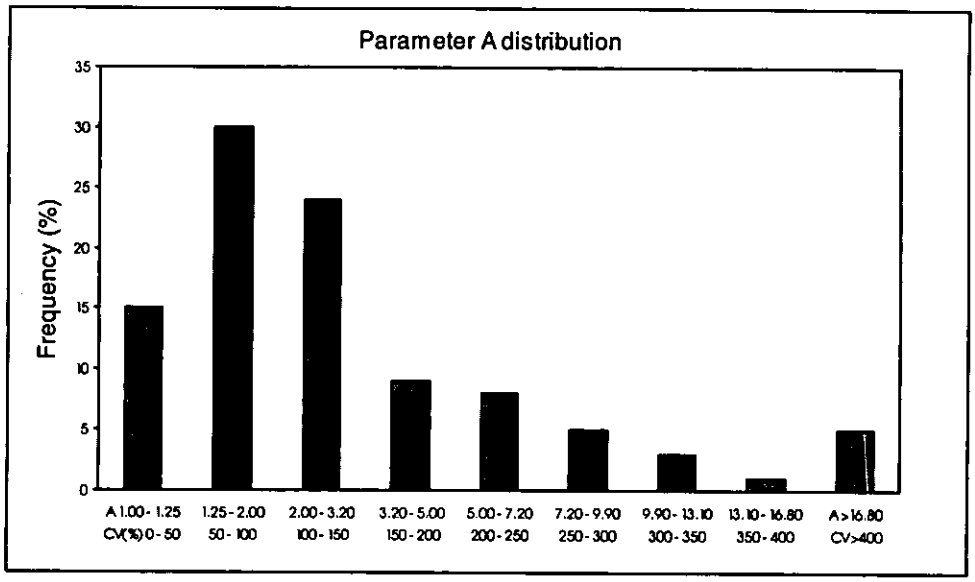


*Figure 1.* Frequency distribution of the *A* values (female fertility variation) of 99 stands. The coefficient of variation (*CV*%) of the reproductive trait used to calculate *A* is also shown on x-axis. (Figure 1 in **I**)

Most of the fertility variation studies used data from stands and seed orchards of conifers in the northern hemisphere. Data from studies of tropical species are limited (**I**). In general, fertility variation was estimated indirectly by counting female and male reproductive structures, assuming that these are good indicators of parental contributions to gamete pool. Fertility variation has also been studied by genetic markers (e.g., Wheeler and Jech 1992; Skrøppa and Lindgren 1994; Siegismund et al. 1996). These techniques are expensive, difficult to get good accuracy on individual gamete contributions, and the available data set is often not large enough for quantification (Lindgren 2000). The method is only adequate if the population is polymorphic for several genetic markers and has few possible parents or has an appropriate combination of markers and male parents (Wheeler and Jech 1992; Stoehr et al. 1998). The counting of female and male reproductive structures is a quick, inexpensive method to estimate fertility differences between parents (Chaissurisri and El-Kassaby 1993; Savolainen et al. 1993; Kang and Lindgren 1999). In most cases, the estimates seem to be sufficiently accurate for use in predictions (Lindgren 2000).

Variation in fertility (*A*) ranged from 1 to 41.67 in stands, averaging 4 with standard deviation (sd) of 6 (**I**). It is lower in seed orchards compared to stands, averaging 2.69 (sd = 2.58). Male fertility variation is also higher in seed orchards (average = 3.44 and sd = 3.54) than is female fertility variation (average = 2.33 and sd = 1.86). In study **IV**, male fertility variation is also higher than female fertility variation in all five observations, while in study **III**, they are about the

same. Generally, higher *A* values were observed during poor flowering years and in younger populations (**I**).

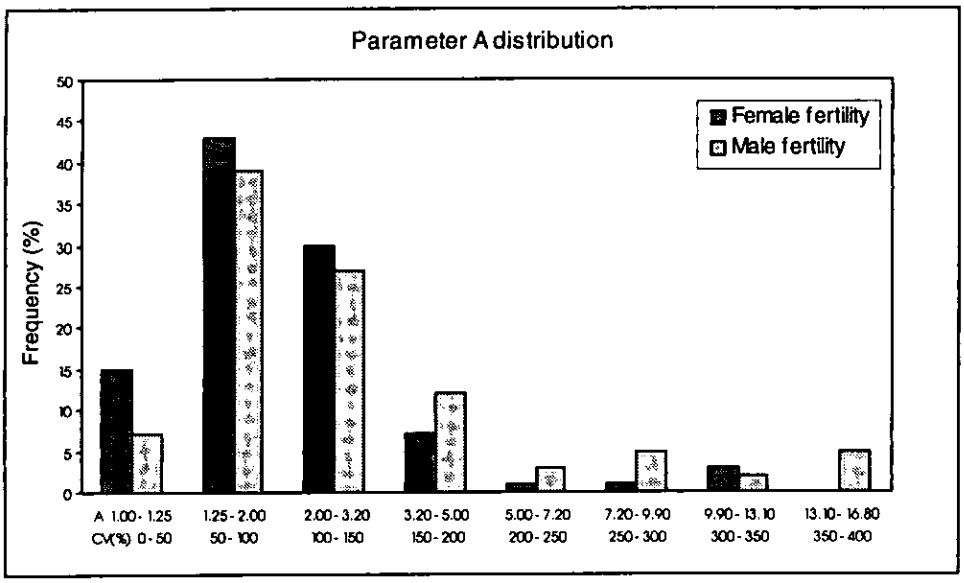


*Figure 2.* Frequency distribution of the *A* values (female and male fertility variation) of 36 seed orchards. The coefficient of variation (*CV%*) of the reproductive trait used to calculate *A* is also shown on x-axis. (Figure 2 in **I**)

Most reproductive traits are under moderate genetic control (Varnell et al. 1966, Fries 1994; Matziris 1998), thus both genotype and the environment affect fertility variation in forest tree populations. The ranking of clones by fertility is fairly constant over time in seed orchards (Jonsson et al. 1976; Griffin 1982; Nikkanen and Velling 1987). Higher and lower fertility genotypes have been described in several seed orchards (Matziris 1993; Adams and Kunze 1996; Gömöry et al. 2000), natural stands (Linhart et al. 1979), and plantations (**II, III**).

Environmental manipulation, e.g., through irrigation, nutrient application and thinning, increase pollen and seed production (Powell and White 1994; Owens 1995). These practices are expected to reduce fertility variation in the population. As mentioned earlier (**I**), parental gamete contribution is more balanced during good flowering years. The age, tree size and site quality are also reported to influence plant fertility (Owens and Black 1985, Crawley 1997; Chalupka and Cecich 1997; Almqvist and Ekbert 1999). The relatively low fertility variation observed in seed orchards might be explained by the uniformity in age, size and tree shape and their better location in terms of adequate climate and edaphic conditions for flowering, fruit and seed production (Zobel et al. 1988; Eldridge et al. 1993; Varghese et al 2000). The comparatively higher male fertility variation may also result from poor pollen production due to the relatively young age of

most seed orchards included in the study (**I, IV**). For example, in most conifers, female flowering dominates on young individuals while male flowering initiates later and increases with age (Matthews 1963; Gömöry et al. 2000).

The distribution of *A* values is positively skewed (*Figure 1* and *2*) with few high values. These values are of little practical significance, as breeding activities are seldom considered in poor flowering years or in very young seed orchards. Fertility variation in stands and seed orchards in good, moderate and average flowering years is expected to be relatively lower. For predictive purposes, and in the absence of relevant data, it is suggested that values for $A=2$ and $A=3$ are generally applicable for both seed orchards and stands.

Making contributions to the seed crop as uniform as possible, by assuring that many trees in the population serve as both male and female parents, diminishes differences in fertility (**II, III**). The control of male contributions is laborious and imprecise. It is difficult to track pollen movements and, besides genetic variation (El-Kassaby and Ritland 1992; Skrøppa and Lindgren 1994) there are differences in pollen size and viability that might influence male reproductive success (Cheliak et al. 1987). Controlling the number of female gametes seems an easier way to limit fertility variation among parents.

The contribution of male and female gametes varies considerably among individuals. Some trees function predominately as males while others produce mainly seeds. There are also individuals that display a more intermediate behaviour (Yasdani et al. 1995; Siegismund et al. 1996) and correlation between male and female fertility might be expected (e.g. Devlin and Ellstrand 1990; Savolainen et al. 1993). The correlation seems to influence the effect of making one gender constant.

In study **II** and **III** correlation is high while in study **IV** are weak and negative (Kand and Lindgren 1999). The effect of making female fertility constant across population is evident in studies **II** and **III,** but less clear in **IV**. It should also be emphasized that female and male fertility in **II** and **III** are of same magnitude while in **IV** male fertility variation is higher compared to female fertility and still has a great impact on total fertility, even after female fertility is made more uniform. This indicates the importance of knowing the magnitude of male and female fertility variation and shows that it is not recommendable to collect seeds during poor flowering years (Kjær 1996; Kang and Lindgren 1999) gamete contribution is so unbalanced that seed quality is compromised.

## Effects and implications of fertility variation

In all these studies, the founders were assumed to be unrelated and non-inbred, and their group coancestry and diversity, relative to that in the source population, is a function of the census number (**III, IV**). Potential changes at generation shifts can be assessed by the increase in group coancestry, e.g., the increase in genetic similarity due to genes being identical by descent (Ballou and Lacy 1995; Falconer and Mackay 1996).

The methodology developed here enables one to evaluate changes in group coancestry, inbreeding and diversity of the descendants, as result of differences in fertility, the number of potential parents and their mating pattern. Developments over generations are described for the case where the number of parents and fertility variation are kept constant (**III**) and for the situation in which the number of parents is constant but fertility differs among generations (**IV**). For one generation, examples are given in **II**.

Parents varied widely in fertility (**II, III, IV**). Some have their gametes over-represented while others are under-represented in the gamete pool (Adams and Kunze 1996; Kang and Lindgren 1998; Gömöry et al. 2000). For example, in study **III**, 20% of most fertile individuals contributed 55% of all gametes, and, in **IV**, 25% of clones provided about 52% and 90% of female and male gametes, respectively. In all studies there were genotypes that did not contribute to the seed crop. This increased the likelihood that gametes sampled randomly came from the same parent and that genes drawn in the progeny population are identical by descent. It also increases the probability of finding sibs in the progeny population (Kang and Lindgren 1999).

As expected, differences in fertility increased relatedness (*Figure 3*) and inbreeding (*Table 4* in **III**), and decreased diversity (*Figure 4*, *Table 2* in **IV**). The decline of status number and gene diversity over generations is evident (*Table 4* in **III**, *Table 2* in **IV**). It reflects the increased coancestry and the accumulation of genetic drift (Lacy 1995; Lindgren and Kang 1997). For example, after five cycles in **IV**, the proportional gene diversity decreased from 1 to about 0.943 and the 180 clones in the seed orchard behaved as if they were 9 non-related, non-inbred and equally fertile clones. Balancing parental contribution to the gamete pool reduces the effects of fertility variation in the population.

Inbreeding and coancestry studies over generations have shown similar results (Wei 1995; Gea et al. 1997; Rodriguez 2000). Controlling individual or family contributions to the next generation, e.g., by limiting the number of crosses or selection within families, delayed the accumulation of inbreeding and coancestry compared to unrestricted mating and unbalanced selection within families. It also reduces the likelihood of gene loss, and diversity is better preserved in the population.

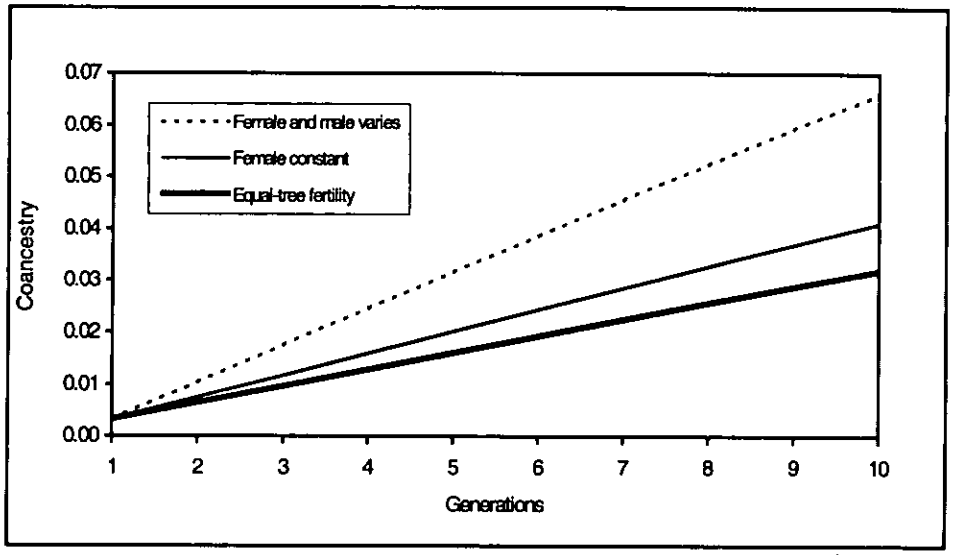


*Figure 3.* Increase of group coancestry over generations. Population size ($N$=154) and fertility variation are kept constant in each generation. The development of coancestry is studied for the case where both female and male fertility varies ($A$=2.22); female fertility is kept constant and male varies ($A$=1.32) and; when all trees in the population have equal fertility ($A$=1)(Figure 2 in **III**).

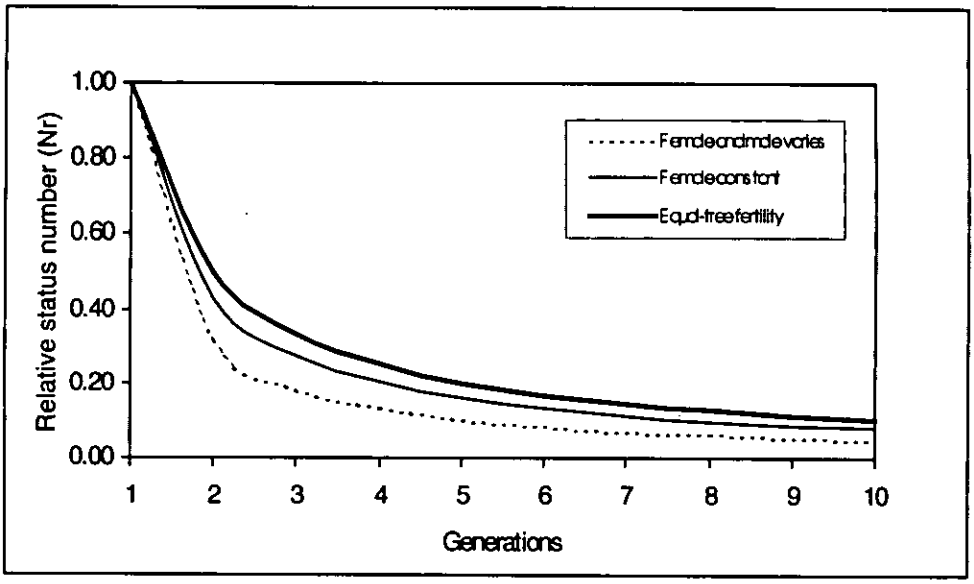


*Figure 4.* Decrease in relative status number over generations at constant population size and fertility variation when female and male fertility varies, female fertility is constant, and when all parents in the population have equal fertility (Figure 3 in **III**)

Collecting the same amount of seed in stands increased diversity of the seed crop, on average, about 40% (*Table 4* in **II**). In **III**, the observed fertility variation would result in loss of diversity after five generations similar to that expected over ten generations if the trees were equally fertile. In **IV**, the effect of equalizing female fertility was not so evident (*Figure 1* in **IV**). As mentioned earlier, differences in pollen production is very much higher than differences in seed production. Sexual asymmetry is higher with few clones producing most pollen in the seed orchard (Kang and Lindgren 1999).

In seed production, it is often assumed that: (1) parents mate randomly, that is, are in reproductive synchrony; and (2) contribute equally to the gamete pool; so the resulting seed reflects both the genetic superiority and diversity present in seed orchards or seed stands (Eriksson et al. 1973; El-Kassaby 1995). In most cases, these assumptions do not hold, due to differences in fertility among parents. Unequal parental contribution to the gamete pool is common, and it is doubtful that balance can be achieved in seed production populations by thinning, pruning or hormone application.

Fertility variation can be balanced and its negative effects mitigated by making parental contributions to the gamete pool as similar as possible. Equalizing female fertility by collecting the same amount of seed across population genotypes (Crossa and Vencovsky 1994; Wei 1995; **II**) seems to be the simplest way to achieve that goal. Another possibility is, knowing the fertility variation magnitude within the population, to compensate for the imbalance in parental contributions by establishing a sufficient number of potential parents, e.g., the number of clones in the seed orchard or the number of selected plus trees in the seed stand, to achieve the desired variability (Kang and Lindgren 1999, **III**).

# Conclusions and recommendations

Fertility variation is a common phenomenon within forest tree population and has a great impact on the genetic diversity of the offspring. Unbalanced contribution of parents to the gamete pool increases genetic similarities among the progeny, inbreeding and the loss of diversity. The method developed here permits evaluation of changes in group coancestry, inbreeding and diversity from the reference population as function of differences in fertility, the number of potential parents and mating system (**III**).

Differences in fertility are described by the power function $y = x^a$ $(a \geq 1)$, where $y$ is the accumulative parental contribution to the progeny and $x$ the ranked proportion of parents and by the sibling coefficient $A$ (Kang and Lindgren 1999), which expresses how much parents vary in fertility and the likelihood for sibs to occur, compared with the situation where parents contribute equally to the gamete

pool. $A=a=1$ when all individuals in the population have the same fertility, and increases with increased variation in parental contributions to the progeny.

Records on flowering ability, pollen, fruit and seed production provided estimates of $A$ values that can be used to predict effects of fertility variation. Populations with a sibling coefficient equal to or approaching unity appears to be rare (**I**). In general, $A$ values tend to be higher during poor flowering years and in young populations. For predictive purposes, $A=2$ and $A=3$ are suggested as typical for mature seed orchards and stands in good or average flowering years, respectively (**I**).

Parents varied widely in fertility with some over-represented, while others were under-represented in the gamete pool. In all studies, there were genotypes that did not contribute at all to the seed crop (**II, III, IV**). Relatedness and inbreeding increased while status number and gene diversity diminished, as expected, with increased differences in fertility and relatedness among parents. In the long term, as generations turn over, besides differences in fertility, the accumulated relatedness also contributes to the increase in inbreeding and the loss of diversity. Making parents contribute to the progeny as equally as possible reduced the negative impact of fertility variation. The effect is high when female and male fertilities are positively correlated and decreases with increasing sexual asymmetry and differences in male fertility.

Collecting the same amount of seed in stands increased on average the seed crop status number by about 40% in **II**, while in **III** the observed fertility variation resulted in similar loss of diversity after five generations as would be expected over ten generation if trees were equally fertile. Compensation for unbalanced contributions to the progeny can be also achieved by using a large number of parents. Knowing the magnitude of fertility variation, a number of parents can be chosen that yields satisfactory diversity in the seed crop.

In these studies population size was kept constant. It was assumed that generations are discrete, and that there is no pollen contamination. It is suggested to study the effects of correlation between female and male fertility on $A$ and to expand the study for the case where population size fluctuates, different generations coexist, and where pollen contamination is an important factor.

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*À Cidália, Kuxa e Hugo*
*À velha e as minhas irmãs*
*Dedico*

I

# Fertility variation in forest tree populations

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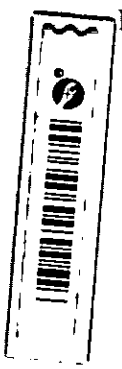

# Abstract

Fertility, the ability to produce successful gametes and viable offspring, determines to a large extend the individual success to contribute genes to the next generation. Flowering abundance, and the production of fruit and seed were used to estimate fertility variation in 99 stands and 36 seed orchards. Fertility variation was higher in stands than in seed orchards. Differences in fertility were often higher during poor flowering years and in young objects. Factors influencing fertility variation and their quantitative magnitude in stands and seed orchards are discussed.



*Key words*: fertility variation, gamete pool, gene diversity, stand, seed orchard.

# Introduction

Sexual reproduction is the most common method through which forests trees species are propagated. In managed forests, seed trees left after harvesting assures natural regeneration to produce new forests. The seeds used in sowing are collected from stand while those utilised for planting come either from seed production areas or from seed orchards (Zobel and Talbert 1984, Skrøppa 1994, Schultz 1999).

Trees vary in reproductive phenology and reproductive output (Bawa and Webb 1984, Moran and Griffin 1985, Matziris 1994). These variations determine, to a large extent, individual success in contributing genes to the progeny. Random mating, reproductive synchrony and similar gamete contribution are rarely observed and a few genotypes in seed orchards and stands produce most of the offspring (Chaisurisi and El-Kassaby 1993, Burczyk and Chalupka 1997, Gömöry et al. 2000).

In this study, tree fertility is broadly defined as the relative number of offspring fathered or mothered by an individual (Roeder et al. 1989). Variation in fertility among forest trees is well documented (e.g., Eriksson et al. 1973, Griffin 1982, Xie and Knowles 1992, Savolainen et al. 1993) and factors influencing productive phenology, pollination, fruit and seed production has been recognized as affecting fertility in plants (Sedgley and Griffin 1986, Owens 1995; El-Kassaby 1995).

Variation in fertility has important implications in tree breeding and gene conservation programs. Unequal gamete contribution among trees influences the genetic composition of the offspring by over representing the most fertile genotypes. This leads to the accumulation of relatedness and inbreeding and reduction in diversity (Gilpin and Soulé 1986, Xie et al. 1994, Kjær 1996). Differences in fertility within a population are an important element to consider when managing forest genetic resources; should be quantified and their impacts in the population evaluated and mitigated.

Predictions of conservation and breeding operations e.g. germplasm collection, establishment and utilisation of seed stands and seed orchards require information on fertility variation. In most cases the information does not exist or cannot be collected due to young age of the concerned populations. To predict fertility variation, information based on mature stands and seed orchards can be applied. In present study we compile published data on fertility variation within forest trees populations and estimate their magnitudes. We focused on the differences in fertility, which are important when analysing the consequences of conservation and breeding operations. Factors influencing fertility variation in stands and seed orchards are also discussed.

# Materials and methods

## Theoretical framework for quantifying fertility variations

Each individual has a fertility value, that is, the ability to produce genes transmitted to the offspring. Fertility values can be regarded as samples from a distribution, which can be described by a function with average $\mu$ and variance $\sigma^2$. A random sample of size $N$ from the function has an average $M$. The fertility of an individual $i$ is expressed as $p_i*N*M$, where $p_i$ adds up to 1. Note that $p_i$ can be interpreted as the probability that a gamete originates from individual $i$.

An estimate of the variance of the function can be calculated from a sample as:

$$E(\sigma^2) = s^2 = \frac{(NM)^2\left[\sum_{i=1}^{N} p_i^2 - \frac{\left(\sum_{i=1}^{N} p_i\right)^2}{N}\right]}{(N-1)} \qquad [1]$$

Fertility variation can also be quantitatively described by a coefficient of variation ($CV$) as follows:

$$CV = \frac{s}{M} = \sqrt{\frac{N\left(N\sum_{i=1}^{N} p_i^2 - 1\right)}{N-1}} \qquad [2]$$

Kang and Lindgren (1999) introduced "Sibling coefficient ($A$)" as:

$$A = N\sum_{i=1}^{N} p_i^2 \qquad [3]$$

Where $N$ is the number of parents and $p_i$ the fertility of parent $i$. Note that ($A$) has no dimension and expresses how much fertility varies among parents as it raises the probability that sibs will occur as compared to when there are no differences in fertility. The sibling coefficient ($A$) cannot be smaller than 1. If $A$=1, all individuals have the same fertility. If $A$=2, it means that the probability that two individuals share a parent is double as large as if fertilities were equal.

In a random sample, the relationship between ($A$) and $CV$ from formulae [2] and [3] is (cf. Kang and Lindgren 1998):

$$A = \frac{E(CV)^2(N-1)}{N} + 1 \qquad [4]$$

As formulated here, ($A$) is not a descriptor of a function but is related to a parental population of limited size ($N$) and its relation to the offspring. $CV$ values in this study refer to an imaginary large population (often a large wild forest) and the populations observed in the studies are considered to be a sample from that population. Therefore, ($A$) can be predicted for a sample of size $N$ using formula [4] with the relevant $CV$. The influence of population size ($N$) will be small and of little practical importance for the values presented in this review.

When fertility information from both sexes is available, the data can also be used for calculating the total fertility variation among parents in a sample population. If there is no correlation between female and male fertility, the sibling coefficient is calculated according to Kang and Lindgren (1999) as:

$$A = 0.25(A_f + A_m - 2)\frac{N}{N-1} + 1 \qquad [5]$$

Where ($A_f$) expresses the fertility variation of female parents and ($A_m$) that of male parents. Therefore, $A$ is affected by $N$ but this influence will be smaller as the sample size ($N$) increases. Note that, considering equation [3] sibling coefficient ($A$) can be derived from effective population size measures, such as status number. For example, Kang and Lindgren (1999) gave formulae relating ($A$) with status number and inbreeding effective population size.

## Studied populations

Fertility variation was estimated for 99 stands and 36 seed orchards. The population description, species and reproductive traits for estimation of fertility variation are presented with sources in *Appendices 1* and *2*.

Data on flowering abundance, fruit and seed production were used to estimate tree fertility. It was assumed that individual fertility could be measured by counting reproductive structures, such as female and male strobili, seed cones, flowers, stamens, pollen, fruits and seeds. The number of female and male strobili as well as seed cones was the main traits used in conifers while fruit and seed production was used in hardwoods. The gender fertility was calculated from data

of the respective reproductive traits. In most cases, the number of sampled trees, individual observations or the mean and standard deviation were available, and thus formula [4] was used to calculate both female and male fertility variation. For seed orchards, the average fertility variation was estimated from equation [5].

## Results

### *Stands*

Estimates of fertility variation are presented in *Appendix 1* and a summary is shown in *Table 1*. The number of species and stands of conifers and broadleaf species was unbalanced; conifers accounted for 33% of species and 75% of stands. Female fertility variation was estimated for all stands while male fertility was calculated only for seven stands, being six conifers and one broadleaf specie.

*Table 1.* Coefficient of variation (*CV*) of the reproductive traits used to estimate fertility, sibling coefficient (*A*) in stands.

| | Species | Stands | CV(%) | | *A* | |
|---|---|---|---|---|---|---|
| | | | Average | Median | Average | Median |
| **Female** | | | | | | |
| Conifers | 11 | 74 | 150 | 113 | 4.79 | 2.18 |
| Broadleaf | 20 | 25 | 109 | 92 | 2.38 | 1.80 |
| Conifers and broadleaf (pooled) | 33 | 99 | 144 | 108 | 4.43 | 2.13 |
| **Male** | | | | | | |
| Conifers | 3 | 5 | 75 | 67 | 1.73 | 1.43 |
| Broadleaf | 1 | 1 | 113 | | | |
| Conifers and broadleaf (pooled) | 4 | 6 | 81 | 71 | 1.81 | 1.48 |
| **Female and male (pooled)** | | | | | | |
| Conifers | 11 | 74 | 146 | 109 | 4.66 | 2.18 |
| Broadleaf | 20 | 25 | 109 | 93 | 2.38 | 1.82 |
| Conifers and broadleaf | 33 | 99 | 141 | 108 | 4.33 | 2.13 |

The overall coefficient of variation ranged from 2 to 636% averaged 141% and it was higher in conifers (146%) than in broadleaf (109%). As expected individuals varied widely in fertility. *Appendix 1* shows that there were differences in fertility in most surveyed populations, localities, sites, ages and years. Sibling coefficient (*A*) ranged from 1.00 to 41.67, and the overall average was 4.33. The highest sibling coefficient value was observed in a managed stand of Norway spruce in Sweden (Lindgren and Lindgren 1976) while the lowest value was found in natural stands of *Picea lasiocarpa* (Shea 1987) and managed stands of Scots pine in Canada and Finland (Heikinheimo 1932). Fertility variation was higher in conifers (*A*=4.66) than in broadleaf species (*A*=2.38). The same tendency was observed for female fertility. The overall average reflects mainly female fertility variation since male fertility observations are few.

Flowering abundance had great impact on the *CV* and (*A*). The *CV* and differences in fertility were higher in poor flowering years and lower in good ones. For example, average (*A*) for 31 stands of Norway spruce in Sweden in good, moderate and poor in flowering years (Lindgren and Lindgren 1976) was 2.14, 5.33 and 12.72; the correspondent *CV* was estimated to be 102, 184 and 350%, respectively (*Appendix 1*).

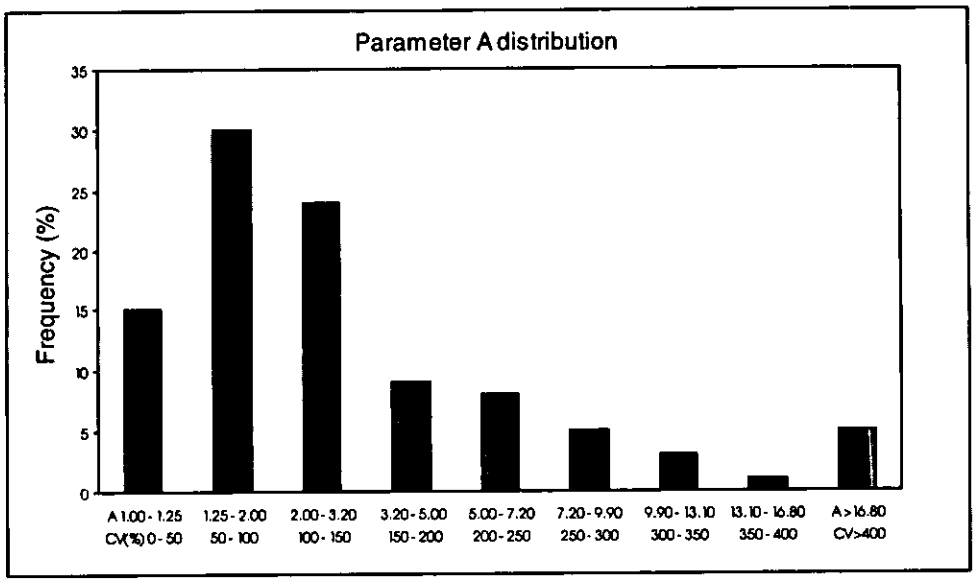


*Figure 1.* Observations of (*A*) value within certain interval in stands. The correspondent coefficient of variation interval is also shown on *x*-axis. Data from both conifers and broadleaf species.

There are few observations with (*A*) value close to 1 (*Figure 1*); only 15% of surveyed stands had $1 \leq A \leq 1.25$, which corresponds to a *CV* of the reproductive trait lower than 50%. Almost half of the stands had $1.25 \leq A \leq 3.20$, that is, a *CV* ranging from 50 to 150%. (*A*) values higher than 3.20 were recorded in approximately 31% of stands. The distribution of the sibling coefficient (*A*) is skewed and a few extreme values had great impact on the arithmetic average. Differences between the arithmetic mean and median are relatively higher where the variation is also higher (*Table 1*). Thus, considering the distribution of (*A*) and the *CV* in stands, it is more reasonable to give an average value of 3 for (*A*) and 140% for *CV*.

### *Seed orchards*

Fertility variation in seed orchards is presented in *Appendix 2* and a summary of the results is shown in *Table 2*. The number of broadleaf seed orchards included in the survey is limited. There are only six seed orchards being three of one specie, *Betula pendula* (Viherä-Aario and Ryynänen 1995).

The majority of seed orchards were relatively young, and the age varied from three to thirty one years, being only two aged over twenty years. Female fertility was estimated in all seed orchards while male fertility variation was estimated in about 70% of seed orchards. In most cases, observations were done in only one or two years. There were three data sets collected in three (Schmidtling 1983, Boes et al. 1991, Kjær 1996) and five successive years (Lindgren and Lindgren 1976, Fries 1994, Kang and Lindgren 1999).

*Table 2.* Coefficient of variation of the reproductive traits used to estimate fertility, sibling coefficient (*A*) in seed orchards.

| | Species | Seed | CV(%) | | *A* | |
|---|---|---|---|---|---|---|
| | | Orchards | Average | Median | Average | Median |
| **Female** | | | | | | |
| Conifers | 14 | 30 | 101 | 89 | 2.36 | 1.79 |
| Broadleaf | 4 | 6 | 100 | 101 | 2.07 | 2.02 |
| Conifers and broadleaf (pooled) | 18 | 36 | 101 | 91 | 2.33 | 1.79 |
| **Male** | | | | | | |
| Conifers | 9 | 21 | 129 | 115 | 3.34 | 2.23 |
| Broadleaf | 1 | 3 | 141 | 123 | 3.45 | 2.51 |
| Conifers and broadleaf (pooled) | 10 | 24 | 130 | 115 | 3.44 | 2.26 |
| **Female and male (pooled)** | | | | | | |
| Conifers | 14 | 30 | 110 | 89 | 2.70 | 1.79 |
| Broadleaf | 4 | 6 | 117 | 106 | 2.62 | 2.12 |
| Conifers and broadleaf | 18 | 36 | 111 | 94 | 2.69 | 1.86 |

In general, *CV* and (*A*) are relatively lower in seed orchards than in stands, except for the male fertility, which is lower in stands (*Tables 1* and *2*). As mentioned, the number of male fertility observations was limited in stands compared to seed orchard records.

Female, male and total fertility varied in most seed orchards, ages and years. The amplitude of variation in the female (*A*) value was 1.04 to 12.02 while the male value ranged from 1.10 to 15.21. Generally, high (*A*) values were found in young seed orchards and in poor flowering years (Lindgren and Lindgren 1976, Kang and Lindgren 1999). The overall average (*A*) was 2.69 and it is 2.70 in conifers and 2.62 in broadleaf. The average of female fertility variation was 2.33 and that of male fertility was 3.44. Male fertility variation is also higher than female fertility variation in both conifers and broadleaf.

The distributions of the sibling coefficient for both male and female genders are shown in *Figure 3*. Similarly to observed in stands, (*A*) distribution are skewed. The number of observations with lower fertility variation is limited. About 15% and 7% of female and male (*A*) estimates varied between 1 and 1.25, respectively. About 75% of female (*A*) value varied from 1.25 and 3.20 while approximately

65% of male (*A*) value in the same interval. *CV* and (*A*) value around 100% and 2, respectively, are suggested as averages for mature seed orchards in good or normal flowering years.

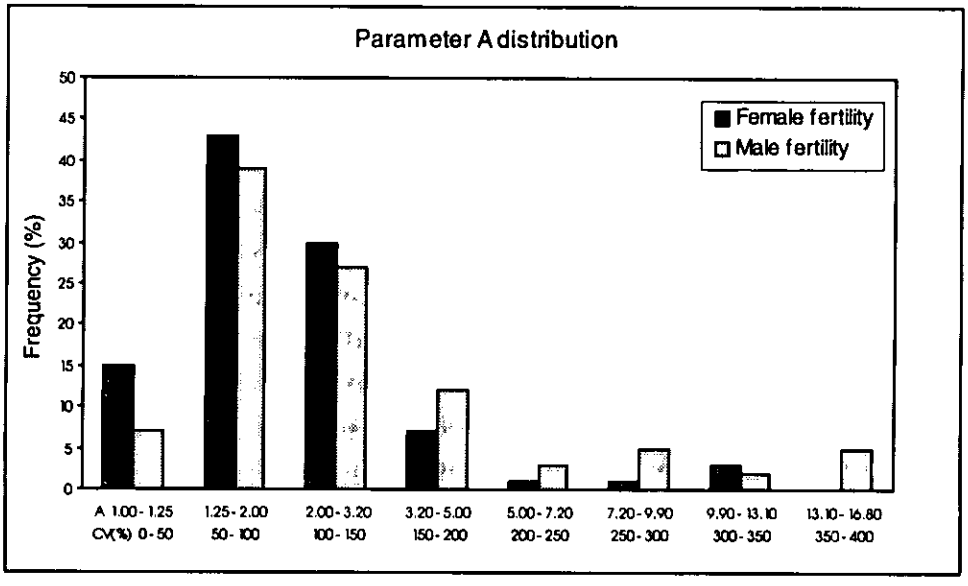


*Figure 3.* Observations of (*A*) value within certain interval in seed orchards. The correspondent coefficient of variation interval is also shown on *x*-axis. Data from both conifers and broadleaf species.

# Discussion

Fertility variation within studied populations was notable. In most stands and seed orchards (*Figure 1* and *2*), sibling coefficient (*A*) was considerably higher than one, indicating that trees contributed differently to the gamete pool. Coefficient of variation, standard deviation or the amplitude of variation could also describe differences in fertility. These parameters give similar information as sibling coefficient (*A*). The advantage of (*A*) value is that it is related to the probability that gametes come from the same parents or that individuals in the progeny are sibs (Kang and Lindgren 1998) while the dispersion parameters are not sensitive to this.

The cumulative contribution curve has also been used to quantify fertility variation in forest populations (Griffin 1982, El-Kassaby and Cook 1994, Adams and Kunze 1996). Trees are ranked by fertility and a proportion of the trees is plotted against accumulative gamete contribution. In most cases, the observed curves deviate largely from the ideal situation in which trees contribute equally to the gamete pool (*A* value=1) and few individuals within the population used to produce most gametes. For example, it has been reported that in most seed

orchards 20% of clones produce 80% of seeds (El-Kassaby 1995). Many other studies have also reported differences in gamete contribution in natural and managed stands (e.g. Linhart et al. 1979, Kärkkäinen 1990, Xie and Knowles 1992, Were et al. 1998) and in several seed orchards (e.g. Askew 1988, Savolainen et al. 1993, Burczyk and Chalupka 1997, Kang and Lindgren 1999).

The reproductive episode may last up to two years in most temperate conifers and hardwoods (Sedgley and Griffin 1989) or some months, as in *Leucaena leucocephala* (Khajuria and Bajwa 1997) and several Eucalypts in tropics (Eldridge et al. 1993). It involves several developmental stages and events, e.g. floral initiation, induction, enhancement and anthesis, in which plant fertility may be affected (Owens and Brake 1985). It has been recognized that genotype of the individual (Schmidtling 1983, Fries 1994, Matziris 1998), its environment (Lloyd and Bawa 1984, Sidhu and Stanifoeth 1986), and management practices influence tree fertility both in stands and seed orchards (Mattews 1963, Owens 1995, Eriksson et al. 1998).

Consistent higher and lower fertile genotypes have been observed in several seed orchards (Griffin 1982, Eriksson et al. 1973, El-Kassaby et al. 1989, Kang and Lindgren 1999, Gömöry et al. 2000), natural stands (Linhart et al. 1979) and plantations (Were et al. 1998). Paternity analysis and pollen mix experiments have shown that genotypes differ in their ability to reproduce. For example, Xie and Knowles (1992) reported that less than 23% of trees in a Norway spruce stand were contributing more than 50% of male gametes to the seed sample. They concluded that floral phenology, pollen production and spatial distribution of male parents were the major factors causing the observed male fertility variation and that the higher pollen producers were also successful fathers. Burczyk et al. (1997) reported similar results in a seed orchard composed of two larch species. One clone of Siberian larch sired almost 93% of sampled ovules while six clones of European larch pollinated only 7%, with some contributing less than 0.2% of all male gametes.

Environmental manipulation is common practice in seed production, either in seed stands or seed orchards (Zobel and Talbert 1984, Owens 1995). In general growth is accelerated, juvenile and the onset of the flowering period is reduced, flowering is made more regular, pollination, fertilization, and fruit and seed maturation are easy to monitor and influence (Bonnet-Masimbert and Webber 1995).

The objects included in the present study varied in terms of species, environment, age, developmental stage and management regime. For example, there are natural stands of tropical species such as *Brachystegia speciformis*, young seed stands of tropical fast growing *Leucaena leucocephala*, mature stands of various temperate conifers such as *Pinus sylvestris*, *Picea abies* and *Pseudodotsuga menziensis* grown for wood production and several seed orchards of the same species. Those

elements are important when analysing fertility variation within and among populations.

In seed orchards, trees are wide spaced with well-developed crowns and limited height. Thinning is done to eliminate families or clones with low genetic value and those with low flowering and fruiting abilities (Zobel and Talbert 1984, Varghese et al. 2000). Topping and pruning are performed to maintain a short wide crown, encourage the growth of lateral branches and thus increase the number of potential flower, fruit and seed production sites (Ho and Schooley 1995). Irrigation, fertilizers and plant growth regulators are used to induce and enhance flowering (Mattews 1963, Setiawati and Sweet 1995). The effects of these practices are likely to make trees more similar, which correspond well with the present results from seed orchards.

The management of a natural forest or wood production stand is far less intensive. In general, the initial density is higher to promote height growth, good form, natural pruning, small and dense crown. Thinning is done mainly to control competition and to concentrate the site growth potential to rather few individuals and the final crop (Zobel et al. 1988). Flowering is generally not a consideration in selecting trees for the main crop. As emphasized by Zobel and Talbert (1984) favourable conditions for vegetative growth may not coincide with the most productive in terms of flowering, fruiting and seed production. Therefore lower fertility variation could be expected in seed orchards compared to seed stands.

The age, size, growth and tree or stand location has been recognized as affecting fertility in plants (Richards 1986, Sedgley and Griffin 1989, Barik et al. 1996). In the northern hemisphere, seed orchards are, in general, located at lower altitudes, where conditions are considered more favourable for flowering and seed production (Zobel et al. 1988). Flower, fruit and seed set in young plants is sparse and sporadic and increases with age and size (Mattews 1963, Barik et al. 1996). Flowering and fruit production, e.g., in *T. grandis* is usually confined to sunny crowns of the dominant and co-dominant trees (Hedegart, 1976) indicating that best competitors are also the most fertile trees in the population (Bila et al. 1999). If pollination is not a limiting factor, seed production is roughly a function of plant size in most tree species (Crawley 1997).

Reproductive success in nature can be assumed to be the results of many components. Flowering ability and ability to set seed are a few, but the ability to survive and grow to a dominant tree are the other important factors. Trees might compensate less flowering with more growth and these factors compensate each other for reproductive success over the life cycle. To discuss evolutionary patterns it is hardly relevant to limit the discussion to fertility, but fertility is an important component. Early flowering and bad flowering years are probably seldom of evolutionary significance, but might be more significant in breeding and seed set operations. This review focuses on fertility variations, which are of

interest for evaluating the "effective size" of seed crops and forest tree breeding operations.

The comparatively low fertility variation observed in seed orchards may also be explained by the better competition control, uniformity in tree size and shape and better location in terms of adequate climate and edaphic conditions for flowering, fruiting and seed production. It should be emphasized that fertility data for many seed orchards are based on clonal averages and thus less variable compared to observations on individual trees in natural and managed stands.

Evaluating the consequences of breeding operations, e.g. seed orchards and seed tree stands, requires predictions of fertility variation. Data cannot be collected for objects that are not established or not yet mature and usually, little information exists for relevant objects. This review may be helpful in these cases. It is suggested that $CV$=100% and $A$ value=2 be used for orchards and $CV$=140% $A$=3 for stands as typical values that can be used in absence of other information. These values seem conservatives and for individual cases they could be modified based on observations in the objects or the most relevant information reported in this review.

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*Appendix 1.* Species, stand description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| Stand Description | Location | Observed trees | Age (yrs) | Trait | *CV* (%)* | (*A*)* | Reference |
|---|---|---|---|---|---|---|---|
| **Conifers** | | | | | | | |
| *Picea engelmannii* | USA: | | | | | | Shea (1987) |
| c, d, g | Niwot Ridge | 13 | 138 | FS[1] | 24 | 1.05 | |
| c, d, g | Niwot Ridge | 13 | 138 | MS[1] | 28 | 1.07 | |
| | | | | Total | | 1.03 | |
| *P. engelmannii* | USA: | | | | | | Shea (1987) |
| c, d, h | Niwot Ridge | 19 | 245 | FS[1] | 18 | 1.03 | |
| c, d, h | Niwot Ridge | 19 | 245 | MS[1] | 27 | 1.07 | |
| | | | | Total | | 1.03 | |
| *Picea lasiocarpa* | USA: | | | | | | Shea (1987) |
| c, d, g | Niwot Ridge | 20 | 127 | FS[1] | 7 | 1.00 | |
| c, d, g | Niwot Ridge | 20 | 127 | MS[1] | 63 | 1.38 | |
| | | | | Total | | 1.10 | |
| *P. lasiocarpa* | USA: | | | | | | Shea (1987) |
| c, d, h | Niwot Ridge | 20 | 154 | FS[1] | 5 | 1.00 | |
| c, d, h | Niwot Ridge | 20 | 154 | MS[1] | 71 | 1.48 | |
| | | | | Total | | 1.13 | |
| *Picea abies* | Finland: | | | | | | Heikinheimo (1932) |
| b, e | Vesijako | 525 | 40 | SC[1] | 54 | 1.29 | |
| c, e | Vesijako | 437 | 80 | SC[1] | 34 | 1.11 | |
| c, e | Ruotsinkylä | 428 | 90 | SC[1] | 59 | 1.35 | |
| c, e | Vesijako | 270 | 100 | SC[1] | 10 | 1.01 | |
| c, e | Vesijako | 109 | 100 | SC[1] | 29 | 1.08 | |
| c, e | Vesijako | 207 | 110 | SC[1] | 71 | 1.49 | |
| c, e | Ruotsinkylä | 113 | 110 | SC[1] | 76 | 1.57 | |
| c, e | Ruotsinkylä | 66 | 110 | SC[1] | 28 | 1.08 | |

*(Continued).* Species, stand description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | |
|---|---|---|---|---|---|---|
| *P. abies* | Sweden: | | | | | Lindgren & Lindgren (1976)[10] |
| c, e | Simlångsdalen | 27 | CC[1] | 214 (46 - 534) | 11.24 (1.21 - 29.41) | |
| c, e | Osby | 39 | CC[1] | 153 (85 - 222) | 3.82 (1.72 - 5.92) | |
| c, e | Rörsbo | 27 | CC[1] | 91 (57 - 137) | 1.94 (1.33 - 2.87) | |
| c, e | Ljungby | 43 | CC[1] | 280 (106 - 510) | 11.72 (2.13 - 27.03) | |
| c, e | Hemse | 28 | CC[1] | 109 (104 - 113) | 2.19 (2.09 - 2.28) | |
| c, e | Sandbäckshult | 37 | CC[1] | 117 (61 - 203) | 2.74 (1.37 - 5.13) | |
| c, e | Buttle | 31 | CC[1] | 220 (104 - 380) | 7.20 (2.09 - 15.38) | |
| c, e | Bollebygd | 24 | CC[1] | 266 (84 - 423) | 10.00 (1.71 - 18.87) | |
| c, e | Målilla | 22 | CC[1] | 150 (130 - 179) | 3.28 (2.68 - 4.18) | |
| c, e | Fagered | 37 | CC[1] | 126 (81 - 171) | 2.79 (1.66 - 3.92) | |
| c, e | Allgunnen | 40 | CC[1] | 123 (108 - 133) | 2.53 (2.17 - 2.76) | |
| c, e | Vimmerby | 23 | CC[1] | 129 (77 - 224) | 3.11 (1.59 - 5.99) | |
| c, e | Segerstad | 32 | CC[1] | 140 (71 - 209) | 3.43 (1.51 - 5.35) | |
| c, e | Nävelsjö | 38 | CC[1] | 103 (85 - 121) | 2.10 (1.73 - 2.46) | |
| c, e | Ulricehamn | 46 | CC[1] | 211 (79 - 322) | 6.47 (1.63 - 11.36) | |
| c, e | Prästkulla | 31 | CC[1] | 308 (116 - 518) | 13.18 (2.34 - 27.78) | |
| c, e | Alvhem | 28 | CC[1] | 199 (103 - 283) | 5.51 (2.06 - 9.01) | |
| c, e | Svarteborg | 36 | CC[1] | 204 (99 - 300) | 5.85 (1.97 - 10.00) | |
| c, e | Åtvidaberg | 39 | CC[1] | 198 (78 - 396) | 6.90 (1.61 - 16.67) | |
| c, e | Remningstorp | 25 | CC[1] | 172 (66 - 266) | 4.64 (1.44 - 8.06) | |
| c, e | Snavlunda | 53 | CC[1] | 187 (121 - 255) | 4.79 (2.47 - 7.52) | |
| c, e | Malexander | 35 | CC[1] | 288 (122 - 568) | 13.28 (2.48 - 33.33) | |
| c, e | Västerås | 19 | CC[1] | 160 (76 - 278) | 4.29 (1.58 - 8.70) | |
| c, e | Röskär | 17 | CC[1] | 129 (42 - 204) | 3.09 (1.18 - 5.15) | |
| c, e | Kårsta | 39 | CC | 208 (80 - 441) | 8.05 (1.64 - 20.41) | |
| c, e | Styckebruk | 32 | CC | 161 (65 - 311) | 4.75 (1.42 - 10.64) | |
| c, e | Åmål | 18 | CC | 146 (82 - 194) | 3.35 (1.67 - 4.76) | |
| c, e | Strängstorp | 32 | CC | 277 (107 - 560) | 12.71 (2.15 - 32.26) | |
| c, e | Arvika | 37 | CC | 211 (125 - 270) | 5.84 (2.55 - 8.26) | |

*(Continued).* Species, stand description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | |
|---|---|---|---|---|---|---|
| *P. abies* | Sweden: | | | | | Lindgren & Lindgren (1976)[10] |
| c, e | Skinnskatteberg | 27 | | CC[1] | 195 (113 - 318) | 5.58 (2.28 - 11.11) |
| c, e | Filipstad | 43 | | CC[1] | 301 (93 - 638) | 15.83 (1.86 - 41.67) |
| J | | | | | 184 (77 - 510) | 5.33 (1.59 - 27.03) |
| L | | | | | 102 (46 - 203) | 2.14 (1.21 - 5.13) |
| I | | | | | 350 (42 - 638) | 12.72 (1.18 - 41.67) |
| *Abies balsam* | Canada: | | | | | Sidhu & Staniforth (1986) |
| c, e | Long Harbour | 80 | | CC[1] | 47 | 1.22 |
| *P. mariana* | | | | | | |
| c, e | Long Harbour | 82 | | CC[1] | 57 | 1.32 |
| *Larix lariciana* | | | | | | |
| c, e | Long Harbour | 28 | | CC[1] | 8 | 1.01 |
| *Pinus sylvestris* | Finland | | | | | Kärkkäinen (1990) |
| E | | 25 | | SC[2] | 148 | 3.10 |
| E | | 25 | | PP[2] | 132 (124 - 140) | 2.68 (2.47 - 2.88) |
| *P. sylvestris* | Finland: | | | | | Harju et al. (1996) |
| c, d, l | Ylläs | 44 | | SC[1] | 16 | 1.02 |
| c, d, I | Ylläs | 40 | | SC[1] | 200 | 4.90 |
| *P. sylvestris* | Finland: | | | | | Heikinheimo (1932) |
| b, e | Ruotsinkylä | 297 | 50 | SC[1] | 47 | 1.22 |
| b, e | Ruotsinkylä | 167 | 55 | SC[1] | 98 | 1.95 |
| b, e | Ruotsinkylä | 76 | 55 | SC[1] | 77 | 1.59 |
| b, e | Punkaharju | 52 | 75 | SC[1] | 4 | 1.00 |
| c, e | Vesijako | 292 | 80 | SC[1] | 94 | 1.88 |
| c, e | Kivalo | 140 | 80 | SC[1] | 41 | 1.17 |
| c, e | Pohjankangas | 104 | 90 | SC[1] | 65 | 1.42 |
| c, e | Ruotsinkylä | 174 | 95 | SC[1] | 58 | 1.58 |
| c, e | Ruotsinkylä | 5 | 95 | SC[1] | 23 | 1.04 |
| c, e | Ruotsinkylä | 394 | 100 | SC[1] | 106 | 2.11 |
| c, e | Vesijako | 95 | 110 | SC[1] | 113 | 2.27 |

*(Continued)*. Species, stand description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *P. sylvestris* | Finland: | | | | | | Heikinheimo (1932) |
| c, e | Vesijako | 66 | 110 | SC[1] | 32 | 1.10 | |
| c, e | Ruotsinkylä | 22 | 110 | SC[1] | 2 | 1.00 | |
| c, e | Punkaharju | 219 | 125 | SC[1] | 53 | 1.28 | |
| c, e | Vesijako | 402 | 130 | SC[1] | 49 | 1.24 | |
| *P. sylvestris* | Finland: | | | | | | Malmivaara (1971) |
| c, e | | 15 | | FS[1] | 38 | 1.13 | |
| c, e | | 99 | | FS[1] | 138 | 2.89 | |
| *Pinus resinosa* | | | | | | | Stiell (1988) |
| E | | 28 | 18 | FS[1] | 74 | 1.53 | |
| E | | 28 | 32 | FS[1] | 60 | 1.35 | |
| *Pinus densiflora* | Korea: | | | | | | Kang (1999) |
| E | Kwanak | 21 | | SC[3] | 99 | 1.94 | |
| E | Dobong | 16 | | SC[3] | 107 | 2.07 | |
| E | Hongneung | 31 | | SC[3] | 61 | 1.36 | |
| *P. caribaea var. hondurensis* | Nigeria: | | | | | | Okoro & Okali (1987) |
| b, f | Ibadan | 11 | 17 | CC[1] | 125 | 2.42 | |
| a, f | Ngow | 11 | 11 | CC[1] | 75 | 1.51 | |
| a, f | Ikom | 12 | 5 | CC[1] | 67 | 1.41 | |
| *Pseudotsuga menziesii* | Canada | | | | | | El-Kassaby et al. (1989) |
| F | British Columbia | 621 | 18-24 | CC[1] | 193 (124 - 237) | 5.12 (2.54 - 10.91) | |
| **Broadleaf** | | | | | | | |
| *Acacia farnesiana* | Costa Rica: | | | | | | Rockwood (1973) |
| c, d | Canas | 10 | | FC[2] | 112 | 2.13 | |
| *Bauhinia ungulata* | | | | | | | |
| c, d | Canas | 10 | | FC[2] | 72 | 1.47 | |
| *Cochlospermum vitifolium* | | | | | | | |
| c, d | Canas | 10 | | FC[2] | 110 | 2.09 | |

*(Continued).* Species, stand description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Grilicidia sepium* | Costa Rica: | | | | | | Rockwood (1973) |
| c, d | Canas | 10 | | FC[2] | 129 | 2.50 | |
| *Spondias purpurea* | | | | | | | |
| c, d | Canas | 9 | | FC[2] | 204 | 4.70 | |
| *Crescentia alata* | | | | | | | |
| c, d | Canas | 8 | | FC[2] | 86 | 1.65 | |
| *Milletia stuhlmannii* | Mozambique | | | | | | Bila & Lindgren (1998) |
| c, d | Inhassoro | 50 | | SC[1] | 71 | 1.49 | |
| *Brachystegia boemii* | | | | | | | |
| c, d | Inhassoro | 50 | | SC[1] | 93 | 1.85 | |
| *Brachystegia spiciformis* | | | | | | | |
| c, d | Inhassoro | 50 | | SC[1] | 117 | 2.34 | |
| *Gliricidia sepium* | Nigeria: | | | | | | Sumberg (1983) |
| a, f | Ibadan | 20 | 2 | SC[2] | 93 | 1.82 | |
| *Leucaena diversifolia* | Kenia: | | | | | | Were et al. (1998) |
| a, f | Machako | 20 | 2 | SC[2] | 91 | 1.79 | |
| *Leucaena pallida* | | | | | | | |
| a, f | Machako | 20 | 2 | SC[2] | 207 | 5.07 | |
| *Leucaena pallida* | | | | | | | |
| a, f | Muguga | 20 | 2 | SC[2] | 286 | 8.77 | |
| *Leucaena trichandra* | | | | | | | |
| a, f | Machako | 20 | 2 | SC[2] | 33 | 1.10 | |
| *Leucaena trichandra* | | | | | | | |
| a, f | Muguga | 20 | 2 | SC[2] | 46 | 1.20 | |
| *Leucaena leucocephala* | Mozambique: | | | | | | Bila & Lindgren (1998) |
| a, f | Maputo | 45 | 0.5 | SC[1] | 129 | 2.63 | |
| *Milletia stuhlmannii* | | | | | | | |
| c, f | Maputo | 100 | 60 | SC[1] | 74 | 1.54 | |

*(Continued).* Species, stand description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *Tectona grandis* | Mocambique: | | | | | | Bila et al. (1998) |
| c, f | Namaacha | 154 | 65 | FC[1] | 113 | 2.27 | |
| | | 154 | 65 | ST[1] | 113 | 2.28 | |
| | | | | Total | | 1.65 | |
| *Hybantus prunifolius* | Panama: | | | | | | Augspurger (1983) |
| c, d | Barro Colorado | 20 | | SC[1] | 91 | 1.78 | |
| *Turnera panamensis* | | | | | | | |
| c, d | Barro Colorado | 20 | | SC[1] | 76 | 1.55 | |
| *Rinorea sylvatica* | | | | | | | |
| c, d | Barro Colorado | 20 | | SC[1] | 85 | 1.69 | |
| *Psychotria horizontalis* | | | | | | | |
| c, d | Barro Colorado | 20 | | SC[1] | 128 | 2.56 | |
| *Erythrina costaricensis* | | | | | | | |
| c, d | Barro Colorado | 20 | | SC[1] | 83 | 1.65 | |
| *Pentagonia macrophylla* | | | | | | | |
| c, d | Barro Colorado | 20 | | SC[1] | 78 | 1.57 | |

a) Juvenile; b) Intermediate; c) Mature; d) Natural stand; e) Managed stand; f) Plantation; g) Wet site; h) Dry site; i) Poor flowering year; j) Moderate flowering year; l) Good flowering year. CC = Cone crop; FC = Fruit crop; FS = Female strobili; MS = Male strobili; SC = Seed crop; PP = Pollen production; ST = Stamens; (nr/tree)[1]; *Nr* = Relative effective population size; (gr/tree)[2]; (nr/cone)[3]; (*A*) estimated from *Nr* (Relative effective population size)[10];* Average and variation amplitude.

*Appendix 2.* Species, seed orchard description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| Seed orchard Description | Location | Observed Genotypes | Age (yrs) | Trait | *CV* (%)* | (*A*)* | Reference |
|---|---|---|---|---|---|---|---|
| **Conifers** | | | | | | | |
| *Picea abies* | Sweden | | | | | | Eriksson et al. (1973) |
| A | Röskär | 20 | 11 | FS[5] | 99 | 1.93 | |
| | Stockolm | | | MS[5] | 115 | 2.26 | |
| | | | | Total | | 1.58 | |
| *P. abies* | Sweden | | | | | | Lindgren & Lindgren (1976)[10] |
| | Jung | 40 | 6 - 13 | FS[5] | 197 (88 - 335) | 5.98 (1.78 - 12.20) | |
| | | | | MS[5] | 156 (73 - 182) | 2.62 (1.44 - 4.31) | |
| | | | | Total | | 2.69 (1.31 - 4.72) | |
| *P. abies* | Denmark | | | | | | Kjær & Wellendorf (1997)[11] |
| A | | 100 | 10 | Total | 65 | 1.42 | |
| *P. abies* | Denmark | | | | | | Kjær (1996)[12] |
| A | | 24 | 28 | Total | 94 | 1.85 | |
| | | 24 | 29 | Total | 85 | 1.69 | |
| | | 24 | 31 | Total | 61 | 1.36[12] | |
| *Picea glauca* | Canada | | | | | | Denti & Schoen (1988) |
| A | Ontario | 12 | 12 | SC[9] | 49 | 1.24 | |
| | | | | MS[9] | 151 | 3.29 | |
| | | | | Total | | 1.69 | |
| *P. glauca* | Canada | | | | | | Schoen et al. (1986) |
| A | Ontario | 33 | 11 - 12 | FS[9] | 125 (83 - 166) | 2.68 (1.67 – 3.68) | |
| | | | | MS[9] | 150 (128 - 173) | 3.24 (2.59 - 390) | |
| | | | | Total | | 2.10 (1.58 – 2.44) | |

*(Continued)*. Species, seed orchard description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *P. glauca* | Canada | | | | | | Ross (1992) |
| | Central Plateau | 15 | 9 | CC[3] | 78 | 1.57 | |
| | | | | PC[3] | 115 | 2.23 | |
| | | | | | | 1.46 | |
| | | 15 | 9 | CC[3] | 156 | 3.27 | |
| | | | | PC[3] | 168 | 3.63 | |
| | | | | | | 2.26 | |
| *P. glauca* | Canada | | | | | | Ross (1992) |
| | Bulkley Valley | 15 | 8 | CC[3] | 92 | 1.79 | |
| | | | | PC[3] | 78 | 1.57 | |
| | | | | | | 1.35 | |
| | | 15 | 8 | CC[3] | 136 | 2.73 | |
| | | | | PC[3] | 117 | 2.28 | |
| | | | | | | 1.77 | |
| *P. glauca* | USA | | | | | | Nienstaedt & Jeffers (1970) |
| Juvenile | Wisconsin | 12 | 6 | CC[9] | 64 | 1.41 | |
| | | | 9 | CC[9] | 45 | 1.20 | |
| *Picea sitchensis* | Canada | | | | | | Chaisurisri & El-kassaby (1993) |
| | British Columbia | 22 | 17 - 19 | CC[1] | 88 (65 - 111) | 1.83 (1.43 – 2.22) | |
| *Picea mariana* | Canada | | | | | | O'Reilly et al. (1982) |
| A | Ontario | 12 | 13 | FS[9] | 57 | 1.30 | |
| | | | | MS[9] | 120 | 2.32 | |
| | | | | Total | | 1.44 | |
| *Pinus contorta* | Sweden | | | | | | Yazdani & Fries (1989) |
| A | Bogrundet | 40 | 13 | FS[3] | 56 | 1.31 | |
| | Sundsvall | | | PP[3] | 89 | 1.79 | |
| | | | | Total | | 1.28 | |

*(Continued).* Species, seed orchard description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *P. contorta* | Sweden | | | | | | Fries (1994) |
| a | Bogrundet | 20 | 12 - 19 | FS[3] | 100 (111 - 177) | 2.15 (1.22 - 3.97) | |
| | Sundsvall | | | MS[3] | 53 (33 - 77) | 1.30 (1.10 - 1.57) | |
| | | | | Total | | 1.54 (1.32 - 1.84) | |
| *Pinus densiflora* | Korea | | | | | | Kang & Lindgren (1998) |
| b | Anmyun | 99 | 20 | FS[1] | 94 | 1.87 | |
| | | | | MS[1] | 64 | 1.41 | |
| | | | | Total | | 1.32 | |
| *Pinus thunbergii* | Korea | | | | | | Kang & Lindgren (1998) |
| b | Anmyun | 60 | 18 | FS[1] | 36 | 1.13 | |
| | | | | MS[1] | 57 | 1.32 | |
| | | | | Total | | 1.11 | |
| *Pinus koraiensis* | Korea | | | | | | Kang & Lindgren (1999) |
| a | Gomae | 180 | 8 - 12 | FS[1] | 118 (89 - 146) | 2.42 (1.79 - 3.13) | |
| | | | | MS[1] | 321 (249 - 377) | 11.54 (7.20 - 15.21) | |
| | | | | Total | | 4.01 (2.76 - 4.92) | |
| *Pinus nigra* | Spain | | | | | | Climent et al (1997) |
| a | Guadalajara | 30 | 3 - 7 | FS[9] | 101 (70 - 132) | 2.05 (1.47 - 2.68) | |
| | Guadalajara | 228 | 3 - 7 | FS[9] | 190 (132 - 255) | 4.78 (2.73 - 7.47) | |
| *Pinus radiata* | Australia | | | | | | Griffin (1982) |
| b | Gippsland | 30 | 8 | SC[2] | 77 | 1.59 | |
| | | | | CPA | 50 | 1.25 | |
| | | | | Total | | 1.22 | |
| *Pinus sylvestris* | USA | | | | | | Boes et al. (1991) |
| | Nebraska | 41 | 13 - 15 | CC[5] | 94 (77 - 123) | 1.90 (1.58 - 2.47) | |
| *P. sylvestris* | Poland | | | | | | Burczyk & Chalupka (1997) |
| b | Gniewkowo | 32 | 18 | CC[1] | 21 | 1.04 | |
| | | | | PP[2] | 56 | 1.32 | |
| | | | | Total | | 1.09 | |

*(Continued)*. Species, seed orchard description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *P. sylvestris* | Sweden | | | | | | Jonsson et al. (1976) |
| a | Långtora | 36 | 12 | FS[1] | 93 | 1.87 | |
| | Enköping | | | MS[1] | 72 | 1.53 | |
| | | | | Total | | 1.36 | |
| *P. sylvestris* | Finland | | | | | | Kärikkäinen & Savolainen (1992) |
| c | Viitaselkä | 24 | 31 | SC | 43 | 1.17 | |
| | | | | PP[2] | 53 | 1.27 | |
| | | | | Total | | 1.11 | |
| *P. sylvestris* | Finland | | | | | | Koski (1981) |
| b | | 25 | 21 - 22 | PP[2] | 64 (61 - 67) | 1.39 (1.36 - 1.43) | |
| | | 25 | 21 - 22 | PP[2] | 116 (115 - 116) | 2.29 (2.27 - 2.30) | |
| *P. sylvestris* | Finland | | | | | | Muona & Harju (1989), |
| c | Viitaselkä | 25 | 31 | CC[7] | 76 | 1.58 | Savolainen et al. (1993) |
| | | | | PP[6] | 57 | 1.32 | |
| | | | | Total | | 1.24 | |
| *P. sylvestris* | Finland | | | | | | Muona & Harju (1989), |
| c | Vihelminmäki | 28 | 27 | CC[7] | 103 | 2.06 | Savolainen et al. (1993) |
| | | | | PP[6] | 136 | 2.85 | |
| | | | | Total | | 1.75 | |
| *Pinus taeda* | | | | | | | Bergman (1968) |
| | | 14 | 7 | CC[5] | 106 | 2.12 | |
| *P. taeda* | USA | | | | | | Schmidtling (1983) |
| | South Mississippi | 18 | 10 - 12 | FS[9] | 114 (70 - 147) | 2.33 (1.47 - 3.01) | |
| *Pinus nigra* | Greece | | | | | | Matziris (1993) |
| b | Peloponnesos | 52 | 11 - 13 | CC[1] | 65 (53 - 80) | 1.44 (1.29 - 1.64) | |
| *Pinus halepensis* | Greece | | | | | | Matziris (1997) |
| a | Amphilochia | 55 | 4 - 10 | FS[1] | 52 (42 - 65) | 1.28 (1.17 - 1.42) | |

*(Continued).* Species, seed orchard description, reproductive trait used to estimate fertility and respective coefficient of variation and sibling coefficient (*A*)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| *P. halepensis* | Greece | | | | | | |
| a | Amphilochia | 60 | 8 - 9 | FSE[1] | 34 (26 - 41) | 1.12 (1.07 - 1.17) | Matziris (1998) |
| *Pseudotsuga menziesii* | USA | | | | | | |
| a | Washington | 21 | 13 | SC[1] | 27 | 1.07 | Erickson & Adams (1989) |
| *Pseudotsuga menziesii* | Canada | | | | | | |
| | Saanichton | 19 | | FSE[1] | 55 | 1.29 | El-Kassaby & Thomson (1996) |
| *Pseudotsuga menziesii* | Canada | | | | | | |
| | Pacific Forest | 35 | 19 | FSE[1] | 104 | 2.05 | El-Kassaby & Cook (1994) |
| **Broadleaf** | | | | | | | |
| *Acacia mangium* | Indonesia | | | | | | |
| a | Sabah | 24 | 1 | FC[9] | 80 | 1.61 | Griffin at al. (1992) |
| *Acacia auriculiformis* | | | | | | | |
| a | Sabah | 25 | 1 | FC[9] | 131 | 2.65 | |
| *Betula pendula* | Finland | | | | | | |
| | Punkaharju | 10 | 3 - 4 | SCK[5] | 114 (101 - 128) | 2.32 (2.02 - 2.63) | Viherä-Aarnio & Ryynänen (1995) |
| | | | | MCK[5] | 207 (125 - 288) | 5.94 (2.56 - 9.32) | |
| | | | | Total | | 2.74 (1.72 - 3.76)) | |
| *Betula pendula* | | | | | | | |
| | Punkaharju | 10 | 3 - 4 | SCK[5] | 108 (75 - 142) | 2.29 (1.56 - 3.01) | |
| | | | | MCK[5] | 107 (85 - 129) | 2.19 (1.72 - 2.66) | |
| | | | | Total | | 1.69 (1.62 - 1.76) | |
| *Betula pendula* | | | | | | | |
| | Punkaharju | 10 | 3 - 4 | SCK[5] | 90 (74 - 106) | 1.84 (1.55 - 2.12) | |
| | | | | MCK[5] | 110 (98 - 121) | 2.22 (1.97 - 2.46) | |
| | | | | Total | | 1.57 (1.56 - 1.58) | |
| *Tectona grandis* | India | | | | | | |
| *b* | Dehra Dun | 20 | 9 | FC[2] | 68 | 1.44 | Rawat et al. (1992) |

a) Juvenile; b) Intermediate; c) Mature; d) Indoor seed orchard; e) Seedling; f) Micropropagated plant.; g) Homoplastic graft ; h) Heteroplastic graft ; i) Poor flowering year; j) Moderate flowering year; l) Good flowering year. CC = Cone crop; CPA = Clone pollen abundance; FC = Fruit crop; FS = Female strobili ; MS = Male strobili; SC = Seed crop; FSE = Filled seed; PC = Pollen cone; PP = Pollen production; SCK = Seed caktins; MCK = Male caktins; (nr/clone)[1]; (gr/clone)[2]; (nr/graft)[3]; (gr/graft)[4]; (nr/tree)[5]; (gr/tree)[6]; (l/tree)[7]; (nr/family)[8]; (nr/ramet)[9]; (*A*) estimated from *Nr* (Relative effective population size) [10]; *Ns* (Staus number) [11]; $N^{(i)}e$ ( Inbreeding effective population size) [12]; * Average and variation amplitude.

II

# FERTILITY VARIATION IN *MILLETIA STUHLMANNII, BRACHYSTEGIA SPICIFORMIS, BRACHYSTEGIA BOHEMII* AND *LEUCAENA LEUCOCEPHALA* AND ITS EFFECTS ON RELATEDNESS IN SEEDS

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## ABSTRACT

Variation in seed production was studied in five stands in Mozambique. It was possible to describe the distribution of seed set as a power function $y = x^a$, where $y$ is the accumulative seeds production, $x$ is the ranked proportion of trees contributing and $a$ a parameter that cannot be less than one. For the studied populations, $a$ = 2.36, 2.45, 3.10, 4.12 and 4.72; this range seems to be in general agreement with data reported by other investigations. The parameter $a$ increased with increasing variation in fertility within stands. The degree of relatedness expected in a seed crop could also be expressed with the status (effective) number relative to the number of investigated trees, that was 0.67, 0.65, 0.54, 0.43 and 0.38, respectively. The effect of collecting an equal amount of seeds per tree could be quantified, and it seems likely that this reduces the relatedness among seeds to a considerable degree and therefore is effective in maintaining diversity. It is recommended to utilize this effect when establishing stands for gene conservation purposes. Formulae for a fertility estimate was derived and the required number of fertility observations was discussed.

**Key words:** fertility variation, seed crop, relatedness, status number, relative status number, diversity, conservation

## INTRODUCTION

Variation in fertility is a major factor in evolution and genetic management of populations. Plant fertility is defined broadly as the capability of an individual to produce living offspring (KREBS 1978). Reproductive structures such as cones, flowers, pollen, fruits and seed are the most frequently used organs for estimating female and male fertility in plants (SEDGLEY & GRIFFIN 1989; ROEDER *et al.* 1989; XIE & KNOWLES 1992; SAVOLAINEN *et al.* 1993)

Variation in flowering, fruit and seed production within and among populations, in plantations and the natural forest, are well documented (*e.g.* AUGSPURGER 1983; BAWA & WEBB 1984; CHAISURISRI & EL-KASSABY 1993; BURCZYK & CHALUPKA 1997). The potential reported causes are the genotype of the individual (VARELL *et al.* 1966; EL-KASSABY & COOK 1994; SORENSEN & CREES 1994), effects of environmental factors such as rainfall, temperature, moisture, wind, microorganisms, age, size, soil fertility (FREEMAN *et al.* 1981; OWENS *et al.* 1991; MURALI & SUKUMAR 1994; SMITH-RAMIREZ & ARMESTO 1994) and silviculture practices such as soil fertilization, irrigation, thinning and pruning (HUGHES & ROBBINS 1982; ZOBEL & TALBERT 1984; FRIES 1994).

Variation in plant fertility has important implications in plant breeding (GRIFFIN 1982; XIE & KNOWLES 1992; EL-KASSABY 1995) and conservation programs (SEDGLEY & GRIFFIN 1989). Differences in gamete contribution among trees influences the genetic composition of offspring by over representing the most productive genotypes (KJAER 1996), which might lead to accumulation of coancestry and inbreeding and loss of diversity (LINDGREN *et al.* 1996).

Studies involving fertility variation between trees in stands of non-selected trees are few. The majority of investigations have been done in seed orchards of commercial species, mostly with conifers (EL-KASSABY 1995). Studies of tropical species in their natural environment are less numerous (BAWA & WEEB 1984). Reported results indicates high variation in male and female fertility and significant variability diminution in the seed crop (LINDGREN & LINDGREN 1976; XIE & KNOWLES 1992)

*Brachystegia spiciformis* Benth and *B. bohemii* Taub. and *Milletia stuhlmannii* Taub. are common timber species in Mozambique (GOMES E SOUSA 1967),

while *Leucaena leoucocephala* (Lam.) de Wit. (SKERMAN *et al.* 1988) is an exotic species widely used in agroforestry in the country. Ecology and silviculture studies involving these species in Mozambique are few and knowledge about population biology, reproductive systems, variation among and within populations is limited (MALLEUX 1981; COSTA 1983).

The objectives of the current study are to evaluate fertility variation of *M. stuhlmannii, B. spiciformis, B. bohemii*, and *L. leucocephala* and to assess its effect on relatedness in the seed crop. We present a general model relating fertility variation among parents to relatedness among progeny.

## THEORETICAL DEVELOPMENT

### Change in relatedness at a generation turn-over

We will base the theoretical development on studies by LINDGREN *et al.* (1996), LINDGREN & MULLIN (1997) and LINDGREN & MULLIN (1998). Let us first introduce some symbols and concepts to be used in our discussion. The group coancestry (average kinship and average coancestry are sometimes used with the same meaning) of a population, which constitute the set of members ω, will be denoted $\Theta_\omega$. Group coancestry is defined as the likelihood that two genes picked at random, with replacement, from the gene pool of the population are identical by descent (cf COCKERHAM 1967). Group coancestry is also a measure of the average relatedness within a population, that can be expressed as an average of all coancestries between all pairs of population members, including reciprocals and self-coancestry (cf., LINDGREN *et al.* 1996). Status number, $N_s$, is defined as half of the inverse of the group coancestry, thus $N_s = 0.5 / \Theta_\omega$ (LINDGREN *et al.* 1996). Status number is a convenient way of expressing group coancestry in terms of an effective population size (WEI *et al.* 1997). It is often practical to relate $N_s$ to the census number of individuals in the population as relative status number, $N_r = N_s/N$.

The trees (genotypes), which will serve as parents to the next generation, vary in fecundity. Another way of expressing this is that the genes in the parental generation will be differently represented in the progeny generation (here the diploid zygotes of the harvested seeds). We assume that there is no genetic drift and no overlap between generations. Drift can be neglected if the following generation is large (can be regarded as infinite), and this may be regarded as the case then seeds are considered as here, but there are other situations, like *in situ* conservation, then drift should not be neglected.

Let us pick two genes at random from the considered progeny population. The probability that one of the genes originates from parental genotype $i$ is $p_i$, and the probability that the other gene has genotype $j$ as a parent is $p_j$. The $p_i$ can be interpreted as the fertility of genotype $i$ or as the proportion of all successful gametes originating from $i$. The likelihood that genes picked from $i$ and $j$ are identical by descent is $\theta_{ij}$, where $\theta_{ij}$ is the coancestry (or coefficient of kinship) between the parental genotypes $i$ and $j$. The probability that any randomly chosen pair of genes in the gene pool of the studied population are identical by descent is found by adding over all possible $N$ contributors to the gene pool of the seeds. If we study the genes from the gene pool of ω, then we must weight the fertility when summing over

$$\sum_{i=1}^{N} p_i \sum_{j=1}^{N} p_j \theta_{ij} = \Theta_\omega \qquad [1]$$

The inbreeding of genotype $i$, thereafter denoted $F_i$, is defined as the probability that two homologous genes in an individual are identical by descent. Self-coancestry is the group coancestry for a population with a single individual; it cannot be lower than one half, nor can it be higher than one. N
ote that the coancestry between the parent $i$ and $j$ becomes the inbreeding of their progeny after mating and the self-coancestry is the inbreeding following selfing and that group coancestry becomes the expected inbreeding following random mating. Specifically considering inbreeding, expression [1] is developed into expression [2] to separate group coancestry into an

$$\begin{aligned}\Theta_\omega &= \sum_{i=1}^{N} p_i \sum_{j=1}^{N} p_j \Theta_{ij} \\ &= \sum_{i=1}^{N} p_i^2 0.5(1+F_i) + \sum_{i=1}^{N} p_i \sum_{j\neq i}^{N} p_j \Theta_{ij} \\ &= 0.5/N_s\end{aligned} \qquad [2]$$

inbreeding and an coancestry term

Let us now formulate the group coancestry of the progeny generation as a function of the fertilities in the previous generation. The group coancestry of the progeny, thus in this case the seeds, is the same as the group coancestry for the parents successful gametes, which for this purpose can be regarded as infinite. There are N genotypes in the parental generation, and $p_i$ is the expected contribution from the individual genotype $i$ to the progeny generation.

Let us say that all individuals in the *parental population* are equally related with coancestry $\theta_1$. Let us

the same for all genotypes, $F_i$. Using formula [2] above we get:

$$\Theta_\omega = \sum_{i=1}^{N} p_i^2 0.5(1+F_i) + (1 - \sum_{i=1}^{N} p_i^2)\Theta_i$$
$$= \Theta_i + (0.5 + 0.5F_i - \Theta_i)\sum_{i=1}^{N} p_i^2 \quad [3]$$

For the special case that $\theta_i = F_i = 0$ the expression 3 simplifies to

$$\Theta_\omega = 0.5\sum_{i=1}^{N} p_i^2 \quad [4]$$

## Describing variation in fertility

The $p_i$ for a given set of genotypes may be observed, and thus (4) and other expressions depending on the square sum of the fertilities can be calculated. Here we are developing another approach to describe the fertility variation among trees with a function, which appearance is controlled by a single parameter. The cumulative contribution to the following generation by the cumulative contribution of genotypes ranked according to their fertility can be expected to fit well to a function of type $F(x) = x^a$, where $x$ is the percentile of genotypes, $a$ a parameter, and $F(x)$ ($0 < F(x) < 1$ for $0 \le x \le 1$) the cumulative reproductive output of those contributing from the *x-th* or lower percentiles. This is one of the most elementary functions, known as the "power function", and a primary candidate for fitting data. It is controlled by a single parameter, which can be seen as an advantage when there is a reasonable fit to the data. The power function is demonstrated in Figure 1.

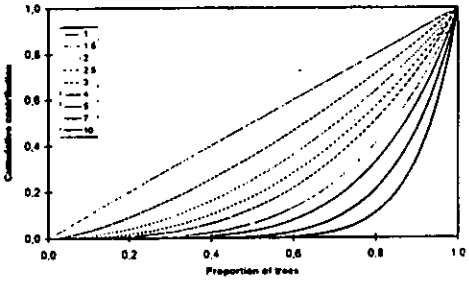


**Figure 1.** Cumulative contribution to the next generation by cumulative proportion of parents ranked for fertility. Graphs for the function $y=x^a$ are shown for different values of $a$.

The power function $F(x)$ has a simple derivative, $f(x) = \frac{dF(x)}{d(x)} = ax^{a-1}$. This derivative corresponds to the fertility of individual genotypes if there is a continuum of genotypes. If there are $N$ genotypes, $f(x)/N$ can be said to be the predicted fertility of the genotype with a rank corresponding to $x$. Actually, a more accurate approximation is $f(x–0.5/N) / N$, which takes into consideration that $N$ number are better approximated by the values of a continuous function at 0.5, 1.5...., $N$–0.5 than by the values at 1, 2, ...$N$.

## Parameter *a* for a continuum of trees

A parent tree, which has a higher fertility than $x$ among all $N$ parents, is expected to give the following contribution to the gene pool of the progeny:

$$p(x) = ax^{(a-1)}/N \quad [5]$$

If parents are unrelated and not inbred, and their population coancestry calculated according to expression [4], the relative status number can be expressed as follows:

$$1/N_r = 2N\Theta_\omega = N\sum_{i=1}^{N} p_i^2$$

For a continuum of genotypes this can be expressed

$$N\sum_{i=1}^{N} p_i^2 = a^2\int_0^1 x^{2a-2}dx = \left[\frac{a^2x^{2a-1}}{2a-1}\right] = \frac{a^2}{2a-1} \quad [6]$$

Thus

$$N_r = \frac{2a-1}{a^2}$$

Now let us study what happens if the contribution of one gender is constant for all N genotypes. The contribution from individual $i$ is

$$p_i = \frac{A_i + 1/N}{2}$$

where $A_i$ is the contribution from the gender with variation as described above, while the contribution from the other gender is constant at $1/N$.

$$1/N_r = N\sum_{i=1}^{N}\left(\frac{A_i+1/N}{2}\right)^2 = \frac{N}{4}\left[\sum_{i=1}^{N} A_i^2 + \frac{3}{N}\right] \quad [7]$$
$$= \frac{a^2+6a-3}{8a-4}$$

**Table 1. Relative status number ($N_r$) as function of $a$ and gender fertility**

| Gender fertility | Parameter $a$ for the variable gender | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1.00 | 1.50 | 2.00 | 2.50 | 3.00 | 4.00 | 5.00 | 7.00 | 10.00 |
| Vary in the same way | 1.0000 | 0.8889 | 0.7500 | 0.6400 | 0.5556 | 0.4375 | 0.3600 | 0.2653 | 0.1900 |
| Constant in one gender | 1.0000 | 0.9697 | 0.9231 | 0.8767 | 0.8333 | 0.7568 | 0.6923 | 0.5909 | 0.4841 |

thus

$$N_r = \frac{8a - 4}{a^2 + 6a - 3}$$

Table 1 shows the $N_r$ as a function of $a$ when genders vary in same way [6] and when one gender makes a constant contribution in the next generation [7].

### Variances

Variances depend on the way proportions are measured. For this discussion, we use a scale where the expected contribution is 1 and thus the summed contributions is expected to be $N$. If the measured fertility of a tree is $f_i$ and the proportion $p_i$, we use the measure $z$ ($z_i$) which is standardized with a mean value of 1.

$$z_i = Np_i = Nf_i / \sum f_i$$

The variance of tree fertilities (the fertility of a tree in relation to the predicted average = 1) is

$$I_z = \int_0^1 (az^{a-1} - 1)^2 dz = \int_0^1 a^2 z^{2(a-1)} dz - 2\int_0^1 az^{a-1} dz + \int_0^1 d.$$

$$= \frac{a^2}{2a - 1} - 1 = \frac{(a-1)^2}{2a - 1} \qquad [8]$$

The fertility of each tree can be considered a sample, so that the variance of the fertility of the average of $N$ trees ($z_\mu$ with expected value 1) around the sample average will be

$$V_{z\mu}(N,a) = \frac{(a-1)^2}{(2a-1)(N-1)} \qquad [9]$$

The number of trees required to get a standard error of the average fertility (note that the average is set to 1) below $e$ (where $e$ indicates how small we want the error to be) will be

$$\sigma_{z\mu} = (a-1)/\sqrt{(2a-1)N} \le e \rightarrow N \ge \frac{(a-1)^2}{(2a-1)e^3} \qquad [10]$$

Note that coefficients of variation (CV) can derived as a function of a or $N_r$

$$CV = \sqrt{\frac{1}{N_r} - 1} = \sqrt{\frac{a^2}{2a-1} - 1}$$

## MATERIAL AND METHODS

### Species studied

*M. stuhlmannii* is a large, fine, spreading tree up to 20 m in height and 50 to 80 cm DBH. It occurs along the cost, at low and medium altitudes, north of the Save river between latitudes 22 and 15° S. It has hermaphroditic flowers that produce a wooden pod, 25 to 35 cm long and up to 6 cm wide. *B. spiciformis* is a medium to large tree, 8 to 15 m in height and 40 to 60 cm DBH. It also has hermaphroditic flowers that develop in a large wooden pod, up to 16 cm long and 5 cm wide. *B. bohemii* is small tree, 6 to 10 m in height and 30 to 50 cm DBH. Its pod grows up to 12 cm long and 3.5 to 4.5 cm wide. Both species occurs over all the country, particularly north of Limpopo river from latitute 25° to latitude 10° S (GOMES E SOUSA 1967). *Leucaena leucocephala* is a small tree native of Mexico which has been spread throughout the tropics and become naturalized in most tropical countries, with latitudinal limits about 30° S and N. It has hermaphroditic flowers that develop into thin and flat pods, up to 20 cm long and 2 cm wide (SKERMAN *et al.* 1988).

### Seed collection areas

Fruits of *B. spiciformis*, *B. bohemii* and one sample of *M. stuhlmannii* were collected in a thicket forest at Inhassoro District, Inhambane Province, in southern Mozambique, approximately 21° 32' S latitude and 35°10' E longitude. The forest extends over 5 500 ha and is located in a plain area at elevations of 0 to 70 m above sea level. The climate of the region is tropical sub-humid; the mean annual temperature varies from 20 to 24 °C and rainfall from 800 to 1 000 mm, distributed in 4 months, from December to March (REDDY 1984). Soils vary from heavy clays to sandy dunes (INIA 1995). The forest is characterized by a dominant

**Table 2. Variance of relative tree fertility (average 1) and number of trees needed to get an accurate estimate of the mean fertility**

| Gender fertility | Parameter *a* | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 1.00 | 1.50 | 2.00 | 2.50 | 3.00 | 4.00 | 5.00 | 7.00 | 10.00 |
| Var. of tree fertility | 0.00 | 0.125 | 0.333 | 0.563 | 0.800 | 1.286 | 1.778 | 2.769 | 4.263 |
| Number of trees* | 0 | 2 | 5 | 9 | 13 | 21 | 28 | 44 | 68 |

*) Required number of trees to get standard deviation of the mean within 25% of true fertility value equal to one (formula 10)

stratum 8 to 12 m above ground with a crown cover up to 40%, and a sub-stratum composed of brushes with a height of 5 to 7 m (SAKET 1994). This forest results from a degradation process following burning, over exploitation and shifting cultivation of the typical miombo forest of the region.

A second sample of fruits of *M. stuhlmannii* was collected in a plantation, in Maputo, at approximately 25°44' S, 34°41' E. The terrain is flat with an elevation of 25 m. The climate is tropical semi-arid, with mean annual temperature of 24°C and precipitation of 800 mm concentrated in four months, from December to March (WILLAN 1981). Soils are sandy with low organic matter and nutrient content. The plantation was established during 1930's with the objective of producing timber and building materials. The initial density was 400 plants per ha and the density at registration was 300 plants per ha.

Fruits of *Leucaena leucocephala* were obtained from an alley cropping experiment in Maputo. The ecological data of the trial location are the same as the plantation of *Milletia stuhlmannii*. Initial spacing among plants was 9 x 0.30 m, which corresponds to a density of 3 700 plants·ha$^{-1}$. The mortality rate is estimated at 20 % and thus the present density is about 3 000 plants·ha$^{-1}$.

### Fruit collection and seed assessment

Trees were selected randomly. Fruits of *Brachystegia* and *Milletia* were collected by climbing; the few remaining high in crown were counted from the ground. In the case of *Leucaena*, all fruits were collected from the ground. In all species, fruits were collected before dehiscence and counted. The number of trees considered in each species was: 50 *B. spiciformis*, 50 *B. bohemii*, 50 *M. stuhlmannii* at Inhassoro, 100 *M. stuhlmannii* at Maputo and 45 *L. leucocephala*.

A random sample of 10 fruits per tree was used to estimate the number of seeds per fruit. The fruits were dried at air temperature and filled seed counted after release from the pods. The calculation of total seed production for each tree was based on the average number of seeds per fruit and the total number of fruits.

Flowering and fruiting of the studied species in Mozambique seems a common phenomenon; it is frequent and abundant in plantations of *Leucaena* and *Milletia* in Maputo. There are no records on fruits and seeds production in natural stands.

### Cumulative curves and estimation of $a$, $N_s$ and $N_r$

Seed production per tree was transformed to proportion of all trees ($p_i$). Group coancestry ($\Theta$), $N_s$ and $N_r$ were calculated as described earlier. To estimate parameter $a$.$\Sigma p_i^2$, was used. The $a$ value which gave the same sum of squared of tree contributions as observed and thus the same $N_s$ was chosen. Note that, as understood from expression 4, $1/\Sigma p_i^2 = NN_r$. $N_s$ and $N_r$ from the model were calculated when genders varies in same way and when one of them is considered constant in all trees, using formulas 6 and 7, respectively.

Fertility data were ranked from low to high yield and transformed to cumulative contributions, summing up to one. Observed cumulative curves (according to GRIFFIN 1982) were produced from the proportion of trees against cumulative contributions percentages, while the expected curves were obtained through the power function $y = x^a$ with a calculated as described above.

## RESULTS

### Fruits and seed production

The average numbers of fruits and seeds produced in each species and the corresponding coefficients of variation (CV) are shown in Table 3.

The results show variation among trees in fruiting and seed set in all stands. Seed production of ranked individual trees is shown in Figure 2. In *L. leoucocephala*, seed production per tree varied from 0 to 19 519. The top producer accounted for about 11 % of the total seed production and 5.2 times that of the average tree. Twenty trees did not produce any seed in this species. Seed production in *B. spiciformis* ranged

**Table 3. Observations of number of fruits and seeds per tree and their variation within stands**

| Stand | Provenance | No of trees | Fruits | | Seeds | | Average seed/fruits |
|---|---|---|---|---|---|---|---|
| | | | Average | CV (%) | Average | CV (%) | |
| *M. stuhlamnii* | Inhassoro | 50 | 147 | 86 | 490 | 71 | 3.73 |
| *M. stuhlamnii* | Maputo | 100 | 119 | 71 | 637 | 74 | 5.32 |
| *B. bohemii* | Inhassoro | 50 | 301 | 80 | 741 | 93 | 2.87 |
| *B. spiciformis* | Inhassoro | 50 | 380 | 124 | 1113 | 117 | 2.45 |
| *L. leucocephala* | Maputo | 45 | 148 | 130 | 3683 | 129 | 24.87 |

**Table 4. Ns and Nr in surveyed stands assuming the male fertility is equal to the female or that it is constant**

| Stand | Parameter *a* | Gender fertility vary equally | | Constant fertility in one gender | | $\frac{(1-N_r^*)}{(1-N_r^{**})}$ |
|---|---|---|---|---|---|---|
| | | $N_s$ | $N_r$ | $N_s$ | $N_r$ | |
| *M. stuhlamnii* | 2.36 | 33.4 | 0.67 | 44.5 | 0.89 | 0.33 |
| *M. stuhlamnii* | 2.45 | 65.0 | 0.65 | 88.1 | 0.88 | 0.34 |
| *B. bohemii* | 3.10 | 27.1 | 0.54 | 41.3 | 0.83 | 0.38 |
| *B. spiciformis* | 4.12 | 21.3 | 0.43 | 37.4 | 0.75 | 0.44 |
| *L. leucocephala* | 4.72 | 17.1 | 0.38 | 31.9 | 0.71 | 0.47 |

$N_r^*$ – expected $N_r$ when fertility varies for one gender and is constant for the other; $N_r^{**}$ – expected $N_r$ when gender fertility vary equally

from 29 to 7 800, with the top producer contributing approximately 14 % of total production and with 7 times that of the average tree. Seed set in *M. stuhlmannii* from Inhassoro, varied between 44 and 1 273, with the top producer contributing about 5 %. Seed and fruit production per tree is closely related, and the patterns of variation in fruit set are similar.

### Fit to power function

Cumulative seed yield curves of observed data as well as the corresponding curves from the model ($y = x^a$) are shown in Figure 2. The estimated parameters *a* were 2.36, 2.45, 3.10, 4.12 and 4.72 for *M. stuhlmannii* from Inhassoro, *M. stuhlmannii* from Maputo, *B. bohemii*, *B. spiciformis* and *L. leucocephala*, respectively.

By visual inspection, the observed and fitted curves are in excellent agreement for *M. stuhlmannii* from Inhassoro, *B. bohemii* and *L. leucocephala*. For *M. stuhlmannii* from Maputo and *B. spiciformis*, the agreement between curves is less good, but still acceptable; the expected values are a bit higher and lower than those observed in high and low percentiles, respectively. An analyses if there was a significant lack of fit between the cumulative seed yields observed and those predicted by the power function was performed using the Kolmogorov-Smirnov test (MASSEY 1951), which investigates the greatest absolute difference between expected and observed cumulative percentages. No indication of any significant lack of fit was observed for any of the five data sets ($P > 0.05$).

### Estimates of $N_s$ and $N_r$

Estimates of *a*, $N_s$ and $N_r$ (Table 4) vary among species reflecting different variation in fertility in each population.

In all stands, $N_r$ is high if one gender fertility is constant. If both genders were equal, an $N_r$ of 1 would be expected. Forming the quotient ($1-N_r$(constant fertility in one gender))/($1-N_r$(gender fertility varies equally)), one obtains values in the range 0.33 to 0.47 (Table 4), thus the effect of one constant gender is considerably greater than half way between two constant genders and two equally variable genders.

At the generation shift between trees and seeds, $N_s$ declines as result of accumulation of coancestry, which will lead to inbreeding at a later stage. The diminution of $N_s$ is related to parameter *a*; it is high in stands with high *a* as a consequence of large fertility variation.

## DISCUSSION

### Describing fertility variations with a model

This study has demonstrated that it is possible to

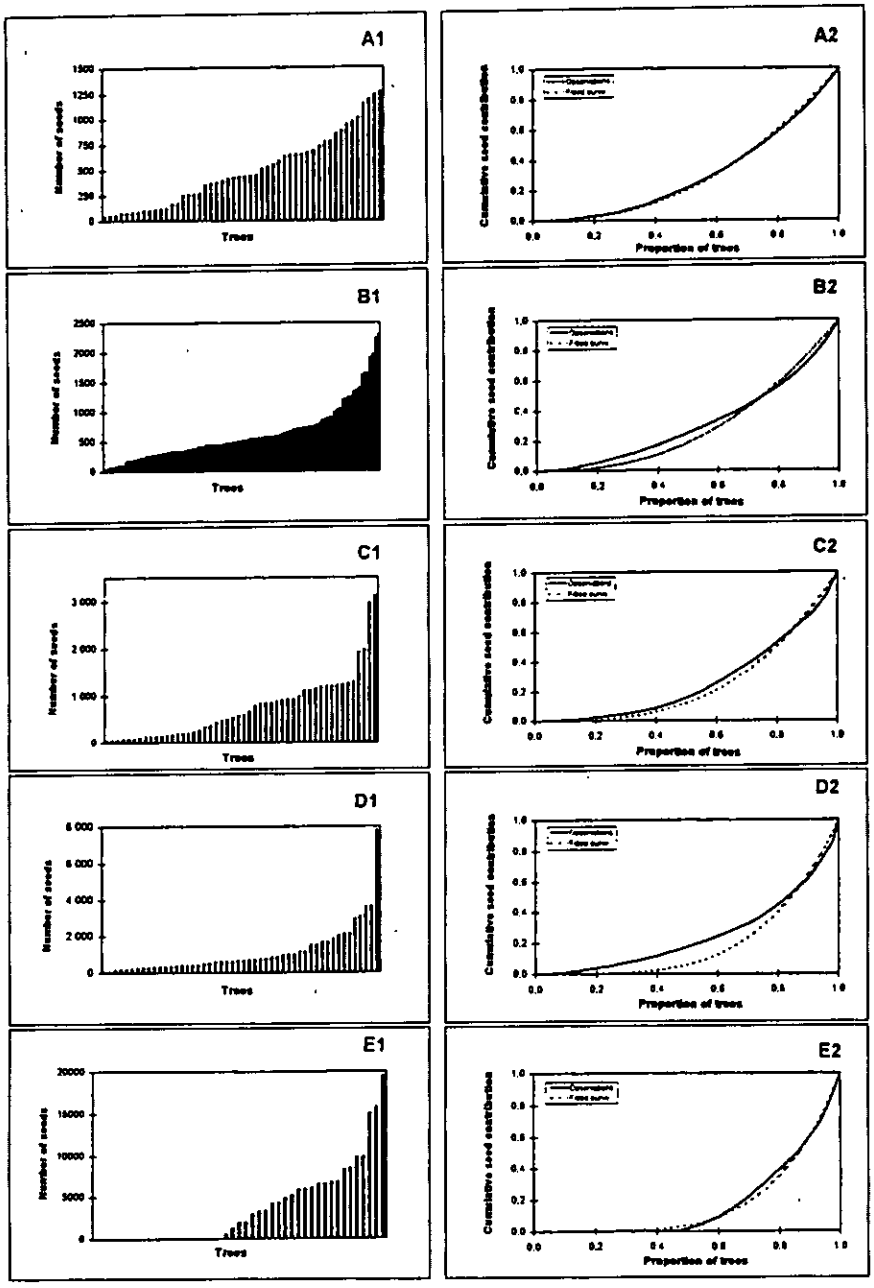


**Figure 2.** Individual seed production (A1, B1, C1, D1, E1) and cumulative contribution to seed set (A2, B2, C2, D2, E2) in surveyed stands. Trees are ranked from low to high yield and transformed to cumulative contributions, summing up to one. Observed curve were produced from the proportion of trees against cumulative contribution percentages and fitted curve were obtained through the power function $y = x^a$. A) *Milletia stuhlmannii*, Inhassorro provenance; B) *M. stuhlmannii*, Maputo provenance; C) *Brachystegia bohemii*; D) *B. spiciformis* and E) *Leucaena leucocephala*.

describe within-population fertility variation rather well with a power function whose shape is controlled by a single parameter. This can be useful for comparative studies, to develop general analytical solutions to problems involving fertility variation, and to generalize and extrapolate experimental information. The variables $N_r$, $CV$ and $a$ actually carries similar information, and it would be sufficient for the calculations presented here to use one of the parameters. However, they highlight different characteristics, and $a$ requires that the general form of the distribution function is known. If the distribution function of fertilities is known, it is logic to use this function when evaluating the mathematics, an analyses in terms of descriptive statistics . Deeper analyses are likely to require the form of the distribution function.

The sample size required (formula 10 and Table 2) to obtain accurate estimates average fertility increases with $a$. The numbers of trees sampled was probably sufficient for the stands included in this study, and 50 trees generally seems more than enough if $a$ is not higher than usually observed when flowering is normal. Still, it seems likely that the fit to the theoretical curve is likely to be worse at higher values of $a$. The worst fit (Figure 2, D2) is observed for a stand with a high $a$ value. It can be noted that for this stand the top-ranking tree has more than double the seed number as that of the second-ranking; this contributes to the bad fit. Monte Carlo simulations (not shown) indicates that variations of that magnitude are possible. We conclude that the method to describe the observed variance by the power function works reasonably well and the relationship between the rank percentile of a genotype and its reproductive output, as well as other derived relationships, can be described by the model.

Fertility variation occur not only among seed parents, but also among pollen parents. This can be studied like the seed parent by counting reproductive structures. Here fruit and seeds were counted, but as ome of the studied species have bisexual flowers, such counts can actually be said to relate also to male contributions in these species. For these cases, there is justification for assuming that seed set is a good indicator of total contributions to gametes. Fertility variation can also be studied by marker genes, but such techniques have not been sufficiently accurate, nor have they produced large enough data sets for quantification. In other studies where both genders were investigated (Table 5), LINDGREN & LINDGREN (1976) found larger variation on the seed parent side while SCHOEN & STEWART (1986) found larger variation on the pollen parent side, so it seems that no general trends can be stated.

### Earlier studies on fertility variation

Fertility variation in forest tree species seems a common phenomenon and indicates that individual genotypes contribute differently to seed production (XIE & KNOWLES 1992; SAVOLAINEN *et al.* 1993; BURCZYK & CHAŁUPKA 1997). In a study of a semi-deciduous lowland tropical forest in Panama involving six species and twenty individuals of each species, AUGSPURGER (1983) found variation among and within species in phenology, number of flower-setting fruits and fruit production. Variation in fruit production within species was high, with CV from 78 % in *Turnera panamensis* to 128 % in *Psychotria horizontalis*. In the case of seed orchards, most seeds use to be produced by a small proportion of genotypes (see review by EL-KASSABY 1995).

Using the model developed here, estimates of parameter $a$ were made from data reported by other studies and presented in Table 5. The results are of same magnitude as those reported in the present study; high $a$ values were found in stands with exhibiting high variation in fertility, and there is considerable parental imbalance in reproductive output.

Variation in fertility within all investigated populations could be attributed to genetic and environment effects since both are confounded in the present study. However, as suggested (RAWAT 1994; KJAER 1996), reproductive traits are rather genetic than environment controlled. The existing reports indicate moderate genetic control of flowering, fruiting and seed production in forest species (VARNELL *et al.* 1966; FRIES 1994; EL-KASSABY & COOK 1994). Thus, in natural forest or plantations, genotypes may consistently produce high or low seeds crop due to their genetic constitution (CHAISURISRI & EL-KASSABY 1993).

Differences in age and environmental variation, mainly in soil proprieties, may have influenced the observed variation in fruiting and seed set within each population in the natural forest at Inhassoro, while competition among trees, particularly in *L. leucocephala*, may explain some of variation found in Maputo plantations.

### Fertility variation, $N_e$ and $N_r$

The present study assumes that parents are drawn from a large population under panmixis with no related genotypes and inbreeding equal to zero. The $N_e$ diminution in all species is quite high (Table 4) and close related with parameter $a$ which describes the fertility variation or the disproportional parent contribution to the next generation. Fertility variation is high in *L. leucocephala* population ($a$ = 4.72) and low in *M.*

**Table 5. Parameter *a* and $N_r$ estimated from literature**

| Reference | Species | Stands | Trait | Parameter *a* | $N_r$ | Remark |
|---|---|---|---|---|---|---|
| BURCZYK & CHALUPKA (1997) | Scots pine | 17-19 yr old seed orchard | Pollen production<br>Seed cone production | 2.00<br>1.40 | 0.7500<br>0.9186 | a-values estimated from field data summary |
| EL-KASSABY & COOK (1994) | Douglas fir | 17-19 yr old seed orchard | Cone crop<br>Seed crop | 2.80<br>3.00 | 0.5867<br>0.5556 | a-values estimated from field data summary |
| CHAISURISRI & EL-KASSABY (1993) | Sitka spruce | seed orchard<br>14 yr old<br>15 yr old<br>16 yr old<br>17 yr old<br>19 yr old | <br>Cone crop<br>Cone crop<br>Cone crop<br>Cone crop<br>Cone crop | <br>7.10<br>4.50<br>2.20<br>2.20<br>1.90 | <br>0.2619<br>0.3951<br>0.7025<br>0.7025<br>0.7756 | <br>20 %, 35 %, 42 %, 42%, and 48 % of clones, respectively, produced 80 % of cone crop |
| XIE & KNOWLES (1992) | Norway spruce | 65 yr old plantation | Male gametes | 2.60 | 0.6213 | Less than 23 % of trees fathered more than 50 % of sampled seeds |
| SCHOEN *et al.* (1986) | White spruce | 111 yr old seed orchard | Male strobili production<br>Female strobili production. | 3.90<br>2.70 | 0.4471<br>0.6036 | 20 % of clones produced 61% of male and 48 % of female strobili |
| SCHOEN *et al.* (1986) | White spruce | 12 yr old seed orchard | Male strobili production<br>Female strobili production. | 6.70<br>6.60 | 0.2762<br>0.2800 | 20% of clones produced 77% of male and 79 % of female strobili |
| GRIFFIN (1982) | Radiata pine | 8 yr old seed orchard | Seed crop<br>Pollen<br>Gametes | 2.60<br>1.70<br>1.50 | 0.6213<br>0.8304<br>0.8889 | 50 % of seeds, pollen and the total gamete contribution was produced by 23 %, 33% and 37 % of clones respectively. |
| LINDGREN & LINDGREN (1976) | Norway spruce | A clonal seed orchard | Female strobili<br>Male strobili<br>Gene contribution | 3.50<br>2.40<br>2.60 | 0.4880<br>0.6480<br>0.6210 | Flowering and correlation between male and female strobili increased with age |
| LINDGREN & LINDGREN (1976) | Norway spruce | 31 adult stands | Female cones followed for three years | 3.30<br>6.00<br>16.00 | 0.5160<br>0.2950<br>0.1140 | High cone set<br>Moderate cone set<br>Low cone set |

*stuhlmanii* from Inhassoro ($a$ = 2.36). Half of the sampled trees produced virtually the entire seed crop in *L. leucocephala* and 75 % in *M. stuhlmannii* from Inhassoro. The reduction in $N_r$ is 62% and 35% respectively. Therefore, diminution of $N_r$ seems higher in populations where fertility variation among plants is very high. As the two plantations had opposite extremes of $a$, no indication of a difference between natural forest and plantation has been found. The plantation with *L. leucocephala* suffers greatly from competition, so it may be unfair to choose that as a representative of a plantation. That the two different stands of *M. stuhlmannii* have very similar $a$ give some support to the idea that species is an important factor for $a$.

The effect of fertility variation on effective population size ($N_e$) of forest species has been investigated in seed orchard and planted stands, and the reported results are similar of those found in this study, *i.e.*, the reduction of the effective size of the breeding population due to different contributions by individuals to the gamete pool (XIE *et al.* 1994; KJÆR (1996)). Female and male $N_e$ estimated by FRIES (1994), from flowers counts, was respectively 80 and 68 % of the total number of genotypes present in a seed orchard of Lodgepole pine in central Sweden. Based on seed-cone

and filled-seed crop, CHAISURISRI & EL-KASSABY (1993) reported that the proportion of female and actual numbers of genotypes in a seed orchard of Sitka spruce were 0.45 and 0.50 of the census number, respectively. In a survey involving a seed orchard and 31 mature stands of Norway spruce in Sweden, LINDGREN & LINDGREN (1976) found that $N_e$ reduction was high in stands and years of poor flowering, but less when flowering and seed set were good. It seems possible that when seed set is poor, it is also less equally distributed. If so, high $a$ values are probably more often found in surveys and experiments (which cover average conditions) than correspond to their ecological importance, as the conditions under which fertility is high contribute most to the next generation.

**Consequences of fertility variation**

Variation in fertility is of great importance in forest populations, although most population genetics models assume equal fertility among plants (SEDGLEY & GRIFFIN 1989). The assumption that trees contribute similarly to the gene pool and have equal reproductive output is, as in this study, not supported by field observations (EL-KASSABY 1995).

As shown in Figure 2, trees contributed differently to the seed production in all studied populations. For example, in *L. leucocephala*, two trees or 5 % of the sampled population produced 21 % of seed, while in *B. spiciformis*, *B. bohemii* and *M. stuhlmannii* from Inhassoro, three trees, also corresponding to 5 %, were responsible for 27, 22, and 15 % of the seed crop respectively. Different contributions in seed production were also found in studies summarized in Table 5.

Fertility variation has a great impact in the genetic structure of the population. It represents fertility selection that changes gene frequencies (EL-KASSABY 1995), and reduces both $N_e$ and variability, thus genetic drift and inbreeding occur more rapidly than would be expected from the actual census number of the population (GILPIN & SOULE 1986; KJAER 1996). Therefore, to avoid rapid genetic erosion in a gene conservation or breeding program, special attention should be given to these effects.

Table 4 illustrates the magnitude of variability diminution in a seed crop due to fertility variation in the parental population. Reductions of up to 60 % of actual variability should be expected when most seeds are produced by a small proportion of the plants. The results suggest also that $N_e$ and diversity could be maintained at higher levels when the contribution of one gender is constant in the population. For example, in *M. stuhlmannii* from Inhassoro, the $N_e$ is increased by 33% when male contribution is simulated to be equal among plants while in *L. leucocephala* the augmentation is 88 %. This effect is likely of greatest importance in stands with high fertility variation.

**Conserving gene resources**

In a random mating population coancestry and inbreeding accumulate at generation shifts and one could minimize the effect of those phenomenon by making all parents contribute equally to the next generation. A similar idea is given by WEI & LINDGREN (1995). They reported that restrictions on the number of selections within families limited genetic loss in breeding population. Since the control of male contribution in a random mating population seems to be difficult and burdensome, limiting the number of seed collected per tree is a more simple and practical way to maintain low coancestry and high $N_e$ in the population. This study evaluates the consequences for seed relatedness, and strengthens the theoretical background for this action. The effect is surprisingly high, as seeds may be considerably less than half as related compared to seed collected in proportion to fertility, rather than close to half as related, as might seem intuitively reasonable (Table 4). Another measure to conserve diversity is to collect seeds from many more parents. The present study does not consider that trees constituting a threatened gene resource usually are related, therefore the effect of this measure may be more limited than this study might indicate.

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III

# Fertility Variation and its Effect on Diversity Over Generations in a Teak Plantation (*Tectona grandis* L.f.)

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**Summary**

Flower and fruit production were used to assess plant fertility in a teak (*Tectona grandis* L.f.) stand in southern Mozambique. The trees varied in fertility, the 20% most fertile trees in the stand producing 55% of the gametes. Formulae to calculate inbreeding, group coancestry and status number over generations were derived. Predictions over ten generations, assuming random mating, showed that inbreeding and group coancestry accumulate rapidly during the first generations while status number decreases. This loss of diversity was hastened by differences in fertility among parents. The calculations showed that the observed fertility variation will result in a similar loss of diversity over five generations as would be expected similar to that expected over ten generations were tif the trees were equally fertile. Inbreeding and relatedness increase, while diversity decreases at a considerably slower rate, when the contributions of one gender are kept constant. An efficient way to reduce the loss of diversity is to collect equal amounts of seeds from each seed parent contributing to the next generation.

*Key words:* fertility variation, inbreeding, coancestry, status number, relative status number, diversity, conservation.

## Introduction

Teak (*Tectona grandis* L.f.) is a native species in Southeast Asia, from the Indian subcontinent throughout Myanmar, Thailand, Laos and Indonesia (BOR, 1953; WHITE, 1962; DASAPA, 1989). It is considered one of the most economically important tropical tree species and has been extensively planted both within and outside its natural range. As an exotic, it is grown in Southeast Asia, East and West Africa and in Caribbean region (HEDERGART, 1976).

Teak was introduced in the south of Mozambique in the early thirties for timber and firewood production (COSTA, 1983). Most old teak plantations have been harvested and the few remaining mature stands are used as seed collection areas from which new plantations are established. Little is known about the origin, diversity and population size of the introduced genetic stock. Neither is there much knowledge regarding flowering or seed production of teak in Mozambique or similar areas.

Studies of flowering, fruit and seed production within teak populations have shown large variation in fertility among trees (GRAM and LARSEN, 1958; WHITE, 1962; NANDA, 1962; HEDERGART, 1976; KUMAR, 1992), and that this variation has a strong genetic component (DUPUY and VERHAEGEN, 1993; RAWAT, 1994). This has important implications for tree improvement and genetic conservation programs (VENCOVSKY, 1987; SEDGLEY and GRIFFIN, 1989) as genes from the most fertile trees will be overrepresented in the progeny population. Fertility variation increases relatedness and inbreeding (GILPIN and SOULÉ, 1986; LINDGREN et al., 1996) and reduces the expected gain and genetic diversity in the breeding population (ASKEW, 1988; EL-KASSABY, 1995).

XIE et al. (1994) showed that variation in flowering, pollen and seed production affects the effective population size of the seed crop and that genetic erosion is higher as variation in these factors increases. One way to reduce genetic losses is to restrict the parental contribution to the next generation (WEI, 1995). By making the contributions as equal as possible among trees, relatedness is minimized and greater diversity maintained in the population (LINDGREN et al., 1996).

The objectives of the present study were: to evaluate fertility variation in a stand of teak by assessing flower and fruit production; to develop a theory for predicting the development over generations of diversity, relatedness and inbreeding as a function of fertility variation; and to demonstrate these predictions for the teak data.

## Theoretical Framework

The theoretical development work presented in this paper extends the work by BILA and LINDGREN (1998) to multiple generations. The aim of the algebra is to predict diversity and inbreeding in future generations as a function of fertility differences and population size in each generation. Group coancestry, status number and relative status number are used as diversity indicators (LINDGREN and KANG, 1997).

Definitions used throughout the paperhere follow LINDGREN et al. (1996) and the literature cited therein. Inbreeding ($F_i$) is the probability that two homologous genes of the individual $i$ are identical by descent, and coancestry ($\theta_{ij}$) is the probability that genes sampled from individuals $i$ and $j$ are identical by descent. Group inbreeding ($F$) is the average inbreeding over the population, while group coancestry, denoted $\Theta$, is the average coancestry over all pairs of population members, including individuals paired with themselves (COCKERHAM, 1967). Note that coancestry becomes inbreeding after mating and that group coancestry is the expected group inbreeding of the offspring following random mating, that is $\Theta_{parents} = F_{offspring}$

Generations are linked by successful gametes, so we envisage that a new generation arises from the preceding in the following way. First, $N_{parents}$ contribute gametes to an infinite gamete gene pool, with contributions from each parent proportional to its fertility. Then, the next generation composed of $N_{offspring}$ offspring arises from the zygotic union of $2N_{offspring}$ successful gametes drawn at random from the gene pool.

There are two ways that two genes in the offspring can be identical by descent. Either one of the $2N_{offspring}$ genes can be sampled twice, the probability of which is $\frac{1}{2N_{offspring}} * \frac{0.5}{N_{offspring}}$, or the genes can be identical among the gamete by common relationship, with a probability equivalent to the group coancestry of the gametes. The group coancestry in the offspring can thus be formulated as:

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$$\Theta_{offspring} = \frac{0.5}{N_{offspring}} + \left(1 - \frac{0.5}{N_{offspring}}\right)\Theta_{gametes} \qquad (1)$$

The group coancestry for the infinite gamete gene pool was developed by the combined work of LINDGREN and MULLIN (1998) and BILA and LINDGREN (1998). The first study considered the seed crop produced by a limited number of distinct genotypes with known fertility, while the second study considered fertility distribution of genotypes as a continuous probability density function.

The group coancestry of the gamete gene pool can be described as a function of fertility of the parents (or rather the relative genetic contributions of the parents, which will be denoted $p_i$), their inbreeding, number, and coancestry (LINDGREN and MULLIN, 1998). Equation (2) to (6) head at getting a relation between the characteristics of the parents and the group coancestry of their gametes. To avoid excessive subscripting, all variables in that section refer to the parents unless stated otherwise:

$$\Theta_{gametes} = \sum_{i=1}^{N} p_i^2 0.5(1+F_i) + \sum_{i=1}^{N} p_i \sum_{j \neq i}^{N} p_j \theta_{ij} \quad (2)$$

Note that $p_i$ can be seen as a probability, the probability that a gamete originates from parent $i$. The formulations in this paper are often written with a probabilistic interpretation in mind. The fertility variation among gametes can be formulated as a standardised probability that two gametes originate from the same parent, which we will denote A, and define as (similar to KANG and LINDGREN, 1998).

$$A = N\sum_{i}^{N} p_i^2 \qquad (3)$$

We can now consider expression (2) as being composed of two terms, $T1$ and $T2$. We will assume that neither inbreeding nor coancestry is correlated with fertility, so that it is adequate to use the group inbreeding and group coancestry for the parental population, $F$ and $\Theta$, respectively. $T1$ is the contribution from cases when a pair of genes (gametes) in the gene pool come from the same parent. As the probability that two genes have the same parent is $\frac{A}{N}$ and the self-coancestry is (on average) $0.5(1+F)$, $T1$ can be rewritten as

$$T1 = \frac{0.5(1+F)A}{N} \qquad (4)$$

$T2$ is the contribution from cases when sampled gametes come from different parents; the chance of this happening is $1 - \frac{A}{N}$. The average of the coancestry values of the parents (not including self-coancestry) is derived as the difference between group coancestry and the contribution from self-coancestry,

$$\frac{N^2\Theta - N0.5(1+F)}{N(N-1)},$$

so that we get

$$T2 = \left(1 - \frac{A}{N}\right)\frac{N\Theta - 0.5(1+F)}{N-1} \qquad (5)$$

Adding $T1$ and $T2$, the group coancestry of the gametes can be expressed as a function of the fertility variation and group coancestry of the parents:

$$\Theta_{gametes} = \frac{0.5(1+F)A}{N} + \left(1 - \frac{A}{N}\right)\frac{N\Theta - 0.5(1+F)}{N-1} \qquad (6)$$

Inserting expression (6) into expression (1), the expected group coancestry among the offspring can now be expressed as a function of that among the parents:

$$\Theta_{offspring} = \frac{0.5}{N_{offspring}} + \left(1 - \frac{0.5}{N_{offspring}}\right)\left(\frac{0.5(1+F_{parents})A}{N_{parents}} + \left(1 - \frac{A}{N_{parents}}\right)\frac{N_{parents}\Theta_{parents} - 0.5(1+F_{parents})}{N_{parents}-1}\right) \qquad (7)$$

It is interesting to compare the group coancestry of the gametes (equation 2) with that of the parents (cf. LINDGREN and KANG, 1998):

$$\Theta_{parents} = \frac{\sum_{i=1}^{N_{parents}} \sum_{j=i}^{N_{parents}} \theta_{ij}}{N_{parents}^2} \qquad (8)$$

Thus, if the parents are non-inbred and equally fertile, the gametes have the same group coancestry as the parents. The group coancestry of the gametes becomes the expected group inbreeding in the offspring, and can be calculated using expression (6).

## Material and Methods

Data were collected from a 1.5 hectare plot of teak at the Namaacha Arboretum in the south of Mozambique. The arboretum is located at latitude 25°59'S, longitude 32°01'W, and elevation of 520 m. The climate of the region is sub-tropical, with average annual temperature and precipitation of 21°C and 910 mm, respectively. The stand was established in 1933, at a spacing of 6 m x 6 m, approximately 275 trees per hectare (NDFW, 1983).

During the first semester of 1998, flower and fruit production were recorded for 154 trees located in the central portion of the plot. For each tree, primary, secondary, tertiary, and fourth-order branches were counted from the ground. Samples of fourth-order branches were cut, and the numbers of inflorescences and developed flower buds were counted at the peak period of flowering in February and March. At the same time, samples of open flowers were taken and the number of stamens per flower recorded. In April and May, when most trees were bearing fruits, samples of inflorescence were taken and the number of fruits counted. All counts were extrapolated to estimate the total number of inflorescences, flower buds, stamens and fruits per tree. Height and DBH were also measured for each individual tree.

The numbers of male and female gametes produced by an individual are male fertility and female fertility, respectively (GREGORIUS, 1989). Cones, flowers, pollen, fruits and seeds have all been used previously to estimate fertility in plants (GRIFFIN, 1982; ROEDER et al., 1989; XIE and KNOWLES, 1992; SAVOLAINEN et al., 1993), and we assume that gender fertilities can be measured by a tally of reproductive structures. In this study, the number of stamens and the number of fruits per tree were used as estimates of male and female fertilities, respectively.

The numbers of stamens and fruit were expressed as a proportion of all trees, so that $p_{i_m}$ and $p_{i_f}$ were the male and female fertilities of individual $i$, respectively. The total fertility of individual tree, $pi$, was calculated as the mid-parent value $pi = (p_{i_m} + p_{i_f})/2$. With one gender assumed to be constant the corresponding fertility was equal to $1/N$. Group coancestry, inbreeding were calculated as described earlier, while $N_a$ and $N_r$ were estimated as described by LINDGREN et al. (1996). Cumulative curves were produced following GRIFFIN (1982).

## Results

The average tree height, DBH, numbers of inflorescences, buds, stamens, and fruit are presented in *table 1*, and correla-

tion coefficients between traits in *table 2*. Height and DBH varied from 7 m to 17 m and 14 cm to 54 cm, respectively. This stand had not been thinned since planting in 1933, so the canopy was closed and some trees were suppressed.

*Table 1.* – Average height, DBH, numbers of inclorescences, buds, stamens and fruits per tree and respective coefficients of variation, for all trees ($n$ = 154) and for those with DBH > 27 cm ($n$ = 109).

| | All trees | | Trees with DBH> 27 cm | |
|---|---|---|---|---|
| Trait | Average | CV (%) | Average | CV (%) |
| Height (m) | 13,1 | 15 | 13,7 | 12 |
| DBH (cm) | 31,7 | 22 | 34,7 | 15 |
| No. of inflorescences | 634 | 101 | 758 | 87 |
| No. of buds | 272 227 | 114 | 322120 | 100 |
| No. of stamens | 1 778 048 | 113 | 2102788 | 99 |
| No. of fruits | 155 284 | 113 | 188479 | 99 |

The numbers of inflorescences, flower buds, stamens and fruits varied among trees, and coefficients of variation were high (i.e., $CV > 100\%$) for all reproductive traits. The average number of stamens per flower was 6.5, and varied from 5 to 8 stamens. The average numbers of buds and fruits per inflorescence were 429 and 245, respectively. The average number of stamens per flower was similar to that reported by HEDEGART (1976) while the number of buds per inflorescence was lower. The bud number per inflorescence might have been underestimated, as sampling was done before development of the inflorescence was complete. In most trees, the inflorescences were bigger at the time of the fruit count compared to when buds were counted. About 20% of the trees did not produce any flowers during 1998. Flowering occurred mostly in the sunny exposed crown of dominant and co-dominant trees. There were no inflorescences on the lower part of these trees, or on suppressed those trees growing under canopy cover.

A thinning was simulated by removing observations for trees with DBH ≤ 27 cm, reducing stand density to about 35% of the initial density. For this sample, the coefficient of variation for growth traits decreased from 15% to 12% and 22% to 15% for height and diameter, respectively. Variation in reproductive traits was also reduced, but remained highly variable. The coefficients of variation for the numbers of inflorescences, buds, stamens, and number of fruits were 87%, 100%, 99% and 99%, respectively. This demonstrates that much of the reproductive variation has causes other than the overall size of the tree or the effects of suppression by neighboring trees.

*Table 2.* – Coefficients of correlation among height, DBH, numbers of inflorescences, buds, stamens and fruits ($n$ = 154), with correlation for the reduced sample ($n$ = 109) shown in parentheses.

| Traits | DBH (cm) | No. of inflorescences | No. of buds | No. of stamens | No. of fruits |
|---|---|---|---|---|---|
| Height (m) | 0,57(0,38) | 0,46 (0,33) | 0,36 (0,24) | 0,36 (0,24) | 0,36 (0,24) |
| DBH (cm) | | 0,40 (0,34) | 0,32 (0,29) | 0,31 (0,28) | 0,37 (0,31) |
| No. of inflorescences | | | 0,88 (0,88) | 0,87 (0,88) | 0,89 (0,87) |
| No. of buds | | | | 0,99 (1,00) | 0,92 (0,91) |
| No. of stamens | | | | | 0,92 (0,91) |

The correlation coefficients *(Table 2)* were all positive and significant ($df$=152 and $P<0.01$). Correlations between height and numbers of inflorescences, flower buds, stamens and fruits, although positive and significant, were weak (0.46, 0.36, 0.36 and 0.38, respectively), while those between DBH and the same reproductive traits were weaker still (0.40, 0.32, 0.31 and 0.37).

The number of inflorescences was – not unexpected – strongly correlated with number of flower buds, stamens and fruits ($r \geq 0.87$). The same was observed with correlations between numbers of buds, stamens, and fruits ($r \geq 0.92$). Most of the variation in flower buds, stamens and fruit production can be explained by variation in the number of inflorescences ($r^2 \geq 0.75$). Thus, vigorous trees tend to produce more inflorescences, and so more flowers, stamens and fruits. Correlations between traits decreased after the simulated thinning, but were still positive and significant ($df$=107 and $P<0.01$). The diminution was highest for correlations between growth and reproductive traits, but small between reproductive traits. The correlations between DBH and the number of inflorescences, buds, stamens and fruits was 0.34, 0.29, 0.28 and 0.31 while the correlation between the number of inflorescence and flower buds, stamens and fruits were 0.88, 0.88 and 0.87, respectively. This indicates strong covariation between reproductive characters even when the variation in tree size is small; thus, it is likely that any reproductive character will function reasonably well as a measure of fertility.

Values of parameter $A$ for different gender contributions are shown in *table 3*. As expected, parameter $A$, which describes fertility variation among trees, is smaller when one gender is constant. Parameter $A$ decreases after simulated thinning, being 1.98, 1.97, 1.93 and 1.25 for male, female, average tree fertility and female constant, respectively. The reduction is approximately 13% for male, female and average tree fertility, and 5% when female is constant.

*Table 3.* – Parameter $A$ for male, female, average-tree fertility and equal-tree fertility.

| | Parameter A | |
|---|---|---|
| Fertility type | All trees | Trees with DBH> 27 cm |
| Male | 2,26 | 1,98 |
| Female | 2,26 | 1,97 |
| Average-tree fertility | 2,22 | 1,93 |
| Female constant | 1,32 | 1,25 |
| Equal-tree fertility | 1,00 | 1,00 |

Cumulative contribution curves are presented in *figure 1*. The straight line illustrates the situation where fertility is the same for all individuals, who contribute equally to the progeny population. The other curves represent cases where female and male fertilities vary (upper curve), and when one gender is constant (intermediate curve). The curves show disproportional parental contributions to the next generation. For example, 20% of trees produced 55% of gametes. When one gender is made constant, by collecting the same number of fruits or seeds per tree, reproductive balance is improved; 55% of gametes are then produced by 34% of tree population. Judging by parameter $A$, thinning also improves reproductive balance among parents, particularly when both gender fertilities vary.

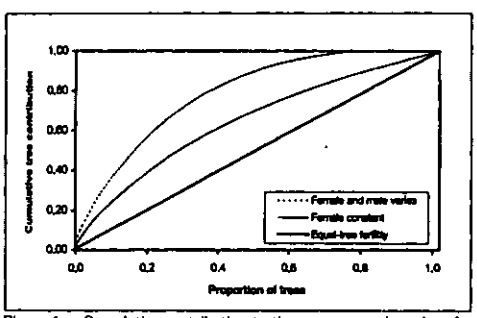


*Figure 1.* – Cumulative contribution to the next generation when female and male fertilities varies, female constant and male vary and when all trees in the population have equal fertility. Trees are ranked for fertility and cumulative contributions of trees above a certain rank are illustrated.

Predicted values of coancestry, inbreeding, status number and relative status number for the teak stand over ten generations are shown in *table 4*, for cases where female and male fertility varies and when female fertility is constant. For all calculations, population size and fertility variation are assumed to be constant over generations. It is also assumed that the observations of the fertility variation observed in a single year areis representative of the variation over a life timelife, and that the population size is that of the trees under study.

Status number and relative status number are reduced in each generation. The diminution is fast in early generation shifts and more severe when fertility variation among trees is greater. As shown in *figure 3*, relative status number is higher when one gender is constant, with the difference decreasing over generations.

## Discussion

### *Fertility variation*

Factors such as stand density, light intensity and site quality are considered to influence flowering in teak (GRAM and LARSEN, 1958; HEDEGART, 1976). The density of the surveyed stand was high; no thinning had been done since planting. Flowering was confined to the upper parts of the crown, exposed to bright sunlight. An individual inflorescence lasts 2 to 4 weeks, producing several thousand buds, although few develop into fruit (DRYNDUM and HEDEGART, 1969). The low fruit and seed set is attributed to insufficient numbers of pollinators, attack by insects, rain damage and premature fruit abortion due to unknown physiological reasons (HEDEGART, 1976; NEELAY et al., 1983; DASAPA, 1989; RAWAT, 1994).

There is little information on phenology of teak in this region, but local observations indicated that flowering begins in middle of the rainy season in January until April. Trees vary in flower receptivity, pollen shedding timing and duration of each activity. An individualis impact on the final gamete pool is dependent on its relative reproductive phenology (EL-KASSABY and ASKEW, 1991). Trees which flower abundantly during the early or late part of flowering period could give similar contributions of successful gametes as trees with a limited amount of flowers at the peak of flowering period. Thus, trees flowering continuously are likely to pollinate a large number of flowers and produce more fruits and seeds, as are trees that are more attractive to pollen vectors.

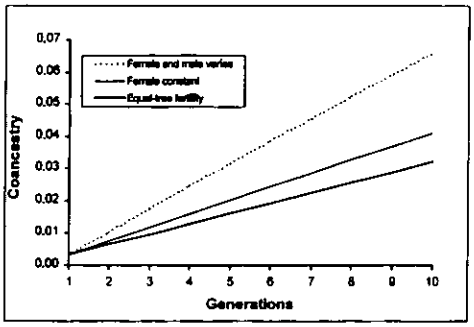


*Figure 2.* – Increase in group coancestry (the probability that two genes in the gene pool are identical by descent) over generations. Assumptions are that the population size (154) and fertility differences (as observed in a teak stand) are the same in each generation and that the new generation is formed by random mating in previous. The development of group coancestry is studied separately for the cases where: both female and male fertilities varies; female fertilities are kept constand (by collecting equal number of seeds from each tree) and male vary; and when all trees in the population have equal fertility.

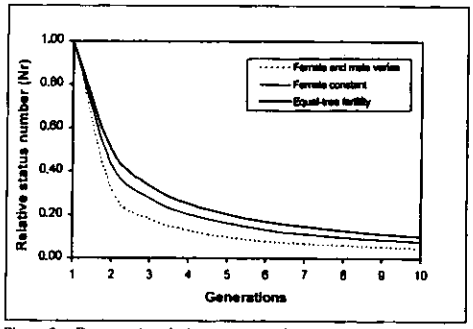


*Figure 3.* – Decrease in relative status number over generations at constant population size and fertility differences over generations, following random mating, when female and male fertilities varies, female constant and male vary and when all trees in the population have equal fertility.

*Table 4.* – Predictions of how group coancestry *(GC)*, inbreeding *(F)*, status number *($N_s$)* and relative status number *($N_r$)* will develop in future generations at constant population size *($N$ = 154)*, following random mating, when female and male fertilities varies, when one gender is constant, and when all trees in the population have equal fertility.

| Generation | Female and male fertility varies *(A=2.22)* | | | | One gender constant *(A=1.32)* | | | | Equal tree contribution *(A=1.00)* | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| t | *GC* | *F* | *Ns* | *Nr* | *GC* | *F* | *Ns* | *Nr* | *GC* | *F* | *Ns* | *Nr* |
| 1 | 0.003 | 0.000 | 154 | 1.00 | 0.003 | 0.000 | 154 | 1.00 | 0.003 | 0.000 | 154 | 1.00 |
| 2 | 0.010 | 0.007 | 48 | 0.31 | 0.008 | 0.004 | 67 | 0.43 | 0.006 | 0.003 | 77 | 0.50 |
| 3 | 0.018 | 0.014 | 28 | 0.18 | 0.012 | 0.009 | 42 | 0.28 | 0.010 | 0.006 | 52 | 0.33 |
| 4 | 0.025 | 0.021 | 20 | 0.13 | 0.016 | 0.013 | 31 | 0.20 | 0.013 | 0.010 | 39 | 0.25 |
| 5 | 0.032 | 0.029 | 16 | 0.10 | 0.020 | 0.017 | 25 | 0.16 | 0.016 | 0.013 | 31 | 0.20 |
| 6 | 0.039 | 0.036 | 13 | 0.08 | 0.024 | 0.021 | 20 | 0.13 | 0.019 | 0.016 | 26 | 0.17 |
| 7 | 0.046 | 0.042 | 11 | 0.07 | 0.029 | 0.025 | 17 | 0.11 | 0.023 | 0.019 | 22 | 0.14 |
| 8 | 0.052 | 0.049 | 10 | 0.06 | 0.033 | 0.030 | 15 | 0.10 | 0.026 | 0.023 | 19 | 0.13 |
| 9 | 0.059 | 0.056 | 8 | 0.05 | 0.037 | 0.034 | 13 | 0.09 | 0.029 | 0.026 | 17 | 0.11 |
| 10 | 0.066 | 0.063 | 8 | 0.05 | 0.041 | 0.038 | 12 | 0.08 | 0.032 | 0.029 | 16 | 0.10 |

Reproductive phenology, fruit and seed production in teak seems to be under strong genetic control (GRAM and LARSEN, 1958; HEDEGART, 1976; DUPUY and VERHAEGEN, 1993; RAWAT, 1994). Therefore, trees may be more or less fertile due to their genetic constitution (CHAISURISRI and EL-KASSABY, 1993).

Trees contributed differently to the gamete pool *(Figure 1)*, with about 20% of trees producing almost 55% of the gametes. Parameter *A* was used to standardize the differences in fertility. We could also have used a function of the coefficient of variance in flowering (KANG and LINDGREN, 1998), but then the relationship would have appeared more abstract, and the link to real distribution functions less apparent. The parameter A is derived from the probability that two seeds have a common parent, while coefficient of variance is based on empirical statistical descriptions.

Reproductive imbalance in the plantation could have been improved by earlier removal of the slower growing trees; these trees will eventually be eliminated by natural thinning. Silvicultural thinning can also be used in a seed stand to rogue out poor phenotypes, and to promote growth, flowering, fruit and seed production for the remaining trees (MATTHEWS, 1963; HUGHES and ROBBINS, 1982; ZOBEL and TALBERT, 1984). Such a treatment might have a positive effect on balancing reproductive output, but will decrease within-stand variability.

The correlation between tree size and reproductive traits indicates that the best vegetative competitors, the dominant and co-dominant trees, are also the most reproductively successful. If there is no limitation in pollination, fruit and seed production is roughly a linear function of plant size in most tree species (CRAWLEY, 1997). For the case of teak, which is an insect-pollinated species, tree size may not be such a good indicator of tree fertility (DRYNDUM and HEDEGART, 1969). The population dynamics of these insects have a great impact on pollination, and influence fruit and seed production (BAWA and WEEB, 1984).

*Coancestry, inbreeding, $N_e$ and $N_s$*

Development over generations was described here for a simple case. Conventional effective population sizes express the average rate of population processes, but do not explicitly describe the situation for each generation. The actual values are strongly dependent on the initial conditions, when the founding trees can be regarded as unrelated and non-inbred. This example assumes a very simple situation, where conventional effective numbers might have been practical. However, the methodology developed here makes it possible to evaluate the consequences of an irregular variation over generations with respect to fertility, census number and mating patterns. Such evaluations would be extremely complicated with conventional effective numbers.

In our example we have used the 154 trees studied. Actually the lot (stand) studied had more than double as many trees, which could have contributed to natural regeneration, so the build-up of relatedness and inbreeding in this object would probably occur only half as fast if the population was left to manage itself. There are also factors like pollen migration and mutation, which may be of importance. The studied object is used to collect teak seed for local planting. Those collections are done from few of the trees, and thus the reduction of diversity in individual forest objects is likely to be much more drastic than indicated by our calculations.

LINDGREN et al. (1996) studied coancestry, inbreeding and diversity over generations for a number of simple situations, and found that regular inbreeding may result in a slower accumulation of group coancestry and a higher status number than random mating. The process was aggravated by variation in fertility among individuals in the population. As in the current study, they reported that by making parental contributions to the next generation as equal as possible, inbreeding and relatedness were delayed and diversity better maintained.

The increase of relatedness and inbreeding, and the reduction in status number and diversity, are likely to be common phenomena in species under domestication (GILPIN and SOULÉ, 1986; GOUDIE, 1993). Seeds used in forest plantations are often collected from a few selected individuals in seed orchards or from rather few stands (ZOBEL and TALBERT, 1984), and there is variation among individuals in fertility (RICHARDS, 1986; SEDGLEY and GRIFFIN, 1989; BURCZYK and CHALUPKA, 1997). Thus, most seeds used for artificial regeneration (over a given planting region) are commonly produced by fewer parents compared to the natural situation (EL-KASSABY, 1995).

KJÆR (1996) studied inbreeding, population size and effective population size in a seed orchard of *Picea abies* in Denmark during three years representing poor, abundant and scattered flowering seasons. He reported that trees contributed differently to the gamete pool in all years and that the accumulation of inbreeding and the loss of variability was high during the poor flowering year when variation in gamete production was high. Similar results were reported by others (CHAISURISRI and EL-KASSABY, 1993; FRIES, 1994; XIE et al., 1994). Loss of genetic diversity is smaller when parental contributions to the next generation are balanced.

Compensation for imbalance in parental contributions can be achieved by using a larger number of parents and, knowing the degree of imbalance, the number of parents (e.g., the number of clones in a seed orchard) can be chosen to achieve satisfactory diversity. Variation in parental contributions to the gamete pool can be regarded as natural and a high degree of balance is doubtful as a goal in the management of a seed production population. For example, improvement in parental balance by thinning in the present study was not so high. When diversity is considered important, it can be better managed by assuring a sufficient number of parents.

Increased relatedness, inbreeding and reductions in genetic variability are expected when a large population experiences a demographic bottleneck (MEFFE and CARROLL, 1997). The chance of mating between relatives is enhanced and the concomitant consequences increased. This may often be the case for exotic species, such as teak in Mozambique, when they are introduced from an unknown or small number of founders. Population number may be expanded in generations to come, but it will be composed of related individuals with limited genetic diversity (HAUSER et al., 1994).

*Implications in breeding and conservation*

Breeders are expected to produce genetic gain through recurrent selection and, simultaneously, are expected to control relatedness so that diversity is conserved in the breeding population (LINDGREN and MULLIN, 1997). In genetic conservation, the avoidance of inbreeding and the maintenance of diversity are considered the main issues (LOESCHCKE et al., 1994). This study shows that keeping the contribution of one gender constant helps to reduce the effect of fertility variation in the population. Whereas, at the current level of fertility variation, 90% of the initial diversity is lost by the fifth generation, the same loss is deferred to the eighth generation if one gender is kept constant, and to the tenth generation if all trees in the population contribute equally in the gamete pool.

It should be noted that the model assumes that a random sample of gametes is successful. Thus, when female fertility is

kept constant, it means that there will be an equal probability of picking a seed from each tree, even though the number of seeds is still assumed to vary at random (following a Poisson distribution). A still better conservation would be obtained if measures were taken so each tree contributes exactly the same number of offspring to the next generation. To achieve this, it could be useful to consider balance among the mothers during the establishment phase and later during thinning operations in a stand of their offspring.

As suggested by VENCOVSKY (1987), when collecting germplasm of panmictic species, one should sample randomly a large number of plants and control the number female gametes per plant, to control relatedness and achieve high variability in the sample. The number of female gametes is controlled by taking an equal number of seeds per plant. WEI (1995) indicated that by limiting the number of selections made within families, gain can be achieved while limiting genetic loss in the breeding population. Diversity is strongly affected by variation in number of selections from different families (MEPPE and CARROLL, 1997). Therefore, the distribution of progenies among parents should be controlled to limit relatedness and maintain genetic variability in the population.


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IV

# Predicted drop in gene diversity over generations in the population where the fertility varies among individuals

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# Abstract

Development of gene diversity and inbreeding of seed crop over generations were derived and predicted as a function of fertility variation and population sizes in forest tree populations. Gene diversity was calculated in terms of group coancestry. Fertility differences were described by sibling coefficient, which is the probability that two genes originate from the same parent, compared to a situation were all parents gave raise to the same number of offspring, thus a measure of the occurrence of half-sibs. Fertility data were collected in a finite population and calculations were made for the case of a constant breeding population size. The change of status number could be associated to the sibling coefficient. Predictions over five generations showed that group coancestry and inbreeding accumulated fast at the first early shifts. Relative status number declined very fast over generations. The increasing of inbreeding and group coancestry was accelerated by fertility variation, and the accumulation was slightly faster and higher when fertility of both genders varied than when maternal fertility was kept constant. Gene diversity decreased faster when fertility variation was large, and maintained higher when the effective population size was reasonably large. Breeding programs that use small status numbers may lead to an accumulation of inbreeding and group coancestry and do not provide a sustainable long-term breeding strategy.



**Key words**: fertility variation, status number, group coancestry, inbreeding, gene diversity

# Introduction

Gene diversity of seed crop is mainly influenced by the level of kinship (Lindgren and Mullin, 1998) and by a difference of gamete production among parental genotypes (Xie *et al.*, 1994; Kjær, 1996; Burczyk and Chalupka, 1997). Variation in fertility is one of the major factors in evolution and genetic management of populations. Here, fertility is defined broadly as the ability of an individual to produce successful gametes; living offspring. Fertility variation among individuals causes the accumulation of relatedness and reduces the status effective number in the seed crop (Kang and Lindgren, 1998; Bila *et al.*, 1999). So, attention should be paid to the fertility variation among parents to maintain gene diversity.

There are further factors that can affect mating among genotypes and thus genetic composition of progeny, such as distance, wind direction, genetic incompatibilities, gene migration and so on. But, their assessment and modelling are difficult and a challenge.

The use of effective population numbers (status number) for monitoring the gene diversity of seed crop from orchard populations was discussed by Lindgren and Mullin (1998). Status effective number expresses the relationship between the orchard and its crop in a single number, so it is neither a characteristic of orchard alone nor its seed crop alone. It also describes what proportion of parents is effectively involved in the production of progeny, and how much is the accumulated genetic drift raised by relatedness and fertility variation (Kang and Lindgren, 1999).

The increasing in inbreeding within the populations during generations of recurrent selection is potentially a major problem in long-term breeding programs (Gea *et al.*, 1997). Breeding and conservation programs that use populations (e.g., seed orchards and seed stands) with a low status effective number may lead to a loss of gene diversity in the plantations (Lindgren *et al.*, 1996). One way to reduce the loss of gene diversity is to restrict the parental contribution, more likely maternal contribution than paternal, to the next generation (Wei, 1995). By keeping the equal contribution among genotypes, genetic relatedness is minimised and gene diversity is maintained high in the population (Lindgren *et al.*, 1996).

The objectives of present study were to derive status number, gene diversity and inbreeding of seed crop and predict their development over generations considering fertility variation and population sizes. The effect of fertility variation on the gene diversity is also discussed.

# Theory

## Fertility variation

Fertility variation can be described by sibling coefficient ($A$) that relates to coefficient of variation ($CV$) in fertility (Kang and Lindgren, 1998). The relative number of maternal and paternal gametes produced by an individual is the maternal and paternal fertility, respectively (Gregorius, 1989). We assume that there is no correlation between maternal and paternal fertility. There was no evident correlation between estimated maternal and paternal fertilities in this study. The sibling coefficient ($A$) can be estimated as (Kang and Lindgren, 1999)

$$A = N \sum_{i=1}^{N} p_i^2$$
$$= 0.25 \left( CV_m^2 + CV_p^2 \right) + 1$$

Where $N$ is the number of genotypes contributing gametes and $p_i$ is the contribution to the gene pool of genotype $i$ and $CV_m$ and $CV_p$ are the coefficients of variation for maternal and paternal fertilities, respectively. When equal amount of seed is collected from each genotype, the maternal fertility is constant. Fertility variation will then be a function of the variation of paternal fertility and the sibling coefficient ($A$) can be described as

$$A = 0.25 \left( CV_p^2 \right) + 1$$

The sibling coefficient is 1 when all individuals are equally fertile and increases with unbalanced parental contribution to the progeny.

## Group coancestry and status number

Group coancestry ($\Theta$) is the probability that two genes in a gene pool are identical by descent (Cockerham, 1967). When we look at the group coancestry over generations ($t$), it can be described as follows (see Bila *et al.*, 1999),

$$\Theta_t = \frac{0.5}{N_t} + \left( 1 - \frac{0.5}{N_t} \right) \Theta_{gametes}$$

The successful gametes of generation $t$-1 are the gene pool of generation $t$. The group coancestry of the gamete gene pool can be described as function of the parents inbreeding ($F$), fertility variation ($A$) and census number ($N$) as

$$\Theta_{gametes} = \frac{0.5(1+F_{t-1})A_{t-1}}{N_{t-1}} + \left(1 - \frac{A_{t-1}}{N_{t-1}}\right)\frac{N_{t-1}\Theta_{t-1} - 0.5(1+F_{t-1})}{N_{t-1}-1}$$

Note that the gamete group coancestry is the same as the parents if they are unrelated, non-inbred and equally fertile.

Status number ($N_s$) is defined as half the inverse of group coancestry ($\Theta$) (Lindgren *et al.*, 1996)

$$N_{s(t)} = \frac{0.5}{\Theta_t}$$

Status number expresses how many ideal genotypes would give rise to the considered offspring, and it can also describe the accumulated genetic drift from the reference population to which the concepts inbreeding and coancestry refer (Lindgren and Mullin, 1998). Group coancestry (status number) and sibling coefficient can be associated to the classical concept, variance effective population size ($N_e^{(v)}$), as follows,

$$N_{e(t)}^{(v)} = \frac{A_t}{2\Theta_t(A_t - 1)}$$

Variance effective population size describes the chance of change in gene frequencies at a generation shift.

## Inbreeding and gene diversity

Group coancestry of present generation becomes the inbreeding of the following random mating (Falconer and Mackay, 1996). Thus, the group coancestry of gametes in the preceding generation becomes the expected inbreeding in the offspring as follows,

$$F_t = \Theta_{gametes}$$

Gene diversity in each generation can be estimated relatively from reference population as (Lindgren and Kang, 1997)

$$GD_t = 1 - \Theta_t = 1 - \frac{0.5}{N_{s(t)}}$$

All concepts which concern identity by decent refer back to a reference population where all genes are unique by definition and individuals are unrelated and non-inbred.

# Materials and Methods

## Clonal archive considered as a hypothetical population

The clonal archive of Korean pine (*Pinus koraiensis* S. et Z.) is located at latitude 36° 30'N, longitude 126° 20'E in Suwon, Republic of Korea, and consisted of 180 genotypes. Trees originated from phenotypically selected plus trees over all the distribution area of Korea. They were propagated by grafting, and planted with the equal number of six ramets. Details of the population and data collection are given by Kang and Lindgren (1999). We assumed that these initial 180 genotypes were unrelated and non-inbred (thus the reference is the forest where the 180 genotypes were drawn from) and pollen contamination was negligible.

Hypothetical situation is that a number of genotypes ($N$=180) are selected from the reference population as parents. They are placed in a seed orchard. Seeds are harvested from the seed orchard. Among the harvested seeds, a number of genotype ($N$=180) are chosen again at random to form a new seed orchard. The fertility of the 180 genotypes can be different from generation to generation. There is random mating in the seed orchard. To illustrate possible variations between generations, observations of fertility differences between years were used.

In this study, three scenarios were analysed; 1) maternal and paternal fertilities were constant over generations, 2) maternal fertility was kept constant by collecting the same number of seeds per genotype, while paternal fertility varied over generations, and 3) maternal and paternal fertilities varied over generations.

## Fertility variation, status number and inbreeding

For each tree in the population, the numbers of female and male strobili were counted for five successive years from 1991 through 1995. In this study, these five years were assumed to represent five consecutive generations. Status number, group coancestry, inbreeding and gene diversity were calculated based on the fertility variation estimated for each of the five years as described earlier in the theory. Calculations were made for the case of a constant breeding population size of generations, where the breeding population was derived at random from the zygotes of the seed crop. For relationship between census ($N$) and status number ($N_s$), relative status number ($N_r$) was calculated as $N_s / N$.

# Results and Discussion

## Fertility variation

There was a large difference in gamete contributions to the seed crop among genotypes. The difference in male strobilus production was much larger than in female (*Table 1*). There was a general lack of flower production over the study period. Some results related with the genetic parameters (e.g., genetic variance and heritability) are reported in Han *et al.* (1997). The difference in male strobilus production among genotypes was very extreme. The differential gamete production may have important impact on gene diversity of seeds, as uneven production will cause a reduction of the $N_s$.

Fertility variation was estimated based on flowering assessment for the five successive years, assuming that pollination success is a saturating positive function of strobilus production (Allison, 1990; Schoen and Stewart, 1987). The sibling coefficient ($A$) varied between genders and among years. In 1994, the sibling coefficient for both genders was the smallest among the studied years, while the production of female strobili was not peak. Maternal fertility was most poor in 1991, and paternal fertility variation was very large in 1995.

Genetic base of seeds produced in good flowering years is much broader compared to that produced in a poor year (Matziris, 1993; El-Kassaby *et al.*, 1989; El-Kassaby and Reynolds, 1990). In the present study, only one reproductive phase has been observed. There are many other phases between flowering and viable offspring, e.g., pollen or ovule development, sexual selection, cone development, embryo development, polyembryo competition, seed maturation, germination, and early seedling survival or competition (Siegismund *et al.*, 1996). Even the timing of anthesis and the receptivity of female flowers may have an effect on the parental contribution to the seed crop (Ruotsalainen and Nikkanen, 1989). However, the quantitative number of flowers is the most important contributing factor to genetic composition of seed crops, especially for the species where most trees have a short flowering period of less than a week, such as *Pinus densiflora* (Jang, 1993) and *Pinus sylvestris* (Kärkkäinen and Savolainen, 1993).

## Status number and group coancestry

Status number ($N_s$) varied over five generations. Status number and relative status number ($N_r$) declined over generation (*Table 2* and *Figure 1*). The decrease was remarkably fast in the first generation shift. For the idealised population having equal fertility and constant population size, $N_r$ were calculated as 0.50, 0.33, 0.25, 0.20 and 0.17 for the five successive generations, respectively (*Figure 1*).

*Table 1.* Average number of strobili per graft, coefficient of variation (*CV*) and sibling coefficient (*A*) for female and male strobilus production

| | 1991 | | 1992 | | 1993 | | 1994 | | 1995 | |
|---|---|---|---|---|---|---|---|---|---|---|
| | female | male | female | male | female | male | female | male | female | male |
| Average | 2.2 | 49.7 | 3.5 | 25.6 | 8.1 | 44.1 | 5.8 | 75.2 | 3.4 | 43.9 |
| *CV* | 1.455 | 3.665 | 1.233 | 3.331 | 1.167 | 2.777 | 0.888 | 2.494 | 1.125 | 3.766 |
| *A** | 3.12 | 14.43 | 2.52 | 12.09 | 2.36 | 8.71 | 1.79 | 7.22 | 2.27 | 15.18 |

* Fertility variation estimated independently for the each gender; $A = (CV)^2 + 1$.

For the studied population, however, $N_r$ was much smaller than for the idealised situation, mainly due to the large fluctuations in male fertility. $N_s$ was slightly higher when maternal fertility was kept constant than when both fertilities were varied. It is clear that the status number decreases as the fertility variation is increases, but the effect of fertility variation on gene diversity is not linear.

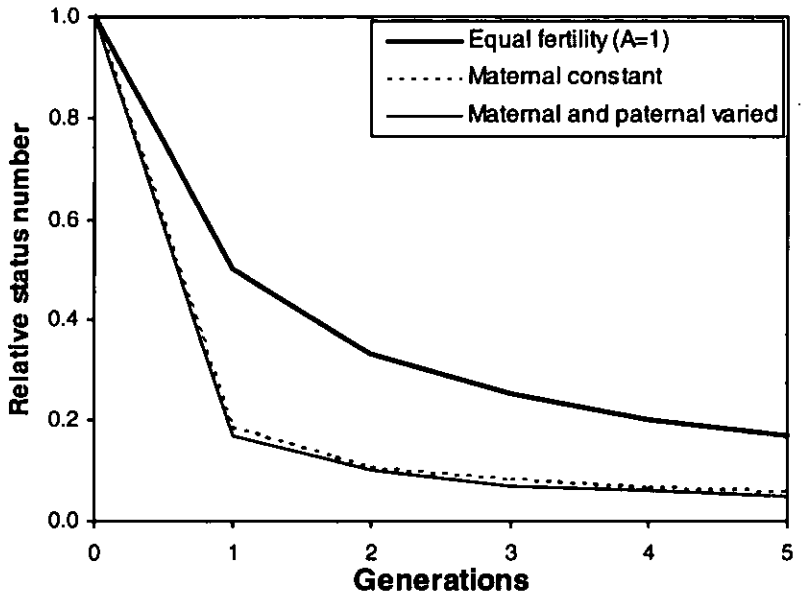


*Figure 1.* Decreasing in relative status number ($N_r$) over five generations at constant population size ($N$=180) and different fertility variations (as observed in a breeding population), following random mating. Generation 0 can be seen as an initial breeding population consisting of unrelated and non-inbred genotypes.

For quantification of gene diversity of seed crops, several concepts of effective population sizes have been used. The concept of effective population size is characterised by two traditional ways; inbreeding and variance effective population size, and by the status effective number. The traditional concepts are developed to describe a process, but the status number expresses a state of a population (Lindgren and Mullin, 1998). Status number describes the population as if it were so many unrelated and non-inbred genotypes (Kang and Lindgren, 1999). Thus, $N_r$ shown that 17%, 10%, 8%, 6% and 5% of the initial numbers of genotypes could be expected to have the same group coancestry and degree of relatedness as the seed crop for the five successive years, respectively.

The variance effective population sizes ($N_e^{(v)}$) as described here becomes infinite in the initial generation where there is equal fertility among genotypes (*Table 2*), reflecting that in a large seed crop from where parents are equally represented, the gene frequencies will be the same in the parents as in the progeny. When the

sibling coefficient equals two ($A$=2), $N_e^{(v)}$ is double as high as status number over generations. Also, $N_e^{(v)}$ decreased as fertility variation increased, and the decreasing had the same trend as status number when the generation shifts.

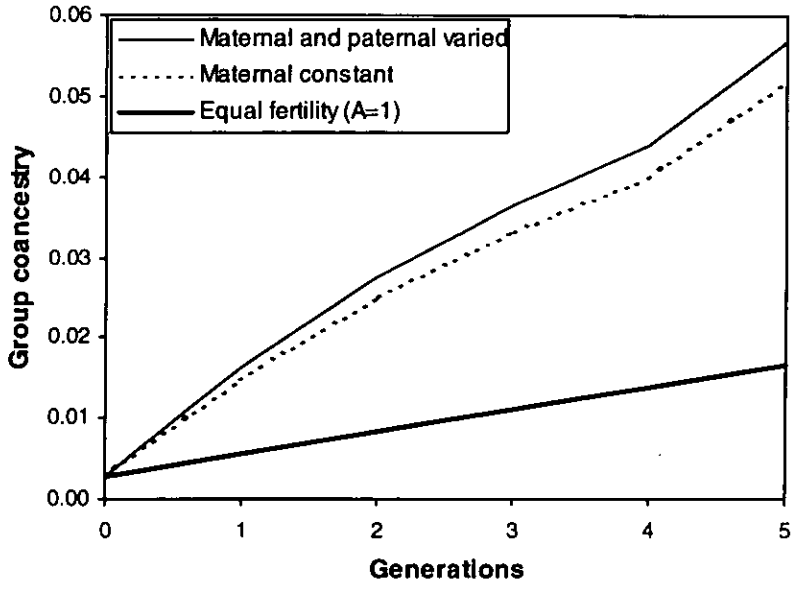


*Figure 2.* Accumulation of group coancestry (Θ) over five generations, assuming that the population size is constant ($N$=180) and the new generation is formed by random mating.

Group coancestry (Θ) and inbreeding ($F$) were increased over generations (*Figure 2*). If there are $N$ equally fertile founders in the generation 0 with $N$ offspring and with equal fertility, the group coancestry of founders, $\Theta_0 = 0.5/N$, and that of next generation, $\Theta_1 = 0.5/N + (1-0.5/N)(0.5/N)$. Therefore, the change of group coancestry ($\Theta_1/\Theta_0$) in the first generation shift is almost double as much as in the founder generation (*Figure 2*). The relatedness of founders and the effect of fertility variation will also accelerate this increment, as it shown that more than 80% of the decreasing in $N_s$ was occurred during the first generation turn over (*Figure 1*).

The accumulation of inbreeding and group coancestry was faster and higher when the fertility variation was larger (*Table 2* and *Figure 2*). By keeping maternal fertility constant, inbreeding and group coancestry of seeds could be improved. However, the improvement was small because the fertility variation among maternal parents was small while paternal fertility variation was large. The improvement would be remarkable if the paternal fertility could be kept equally (data not shown).

*Table 2.* Prediction of group coancestry ($\Theta$), status number ($N_s$), relative status number ($N_r$), variance effective population size ($N_e^{(v)}$), inbreeding ($F$), and gene diversity ($GD$) in the future generations at constant population size ($N$=180) following random mating

| | Maternal and paternal fertility varied | | | | | | Maternal fertility constant | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Generation | 0 * | 1 | 2 | 3 | 4 | 5 | 0 * | 1 | 2 | 3 | 4 | 5 |
| $A$** | 1.00 | 4.89 | 4.15 | 3.27 | 2.75 | 4.86 | 1.00 | 4.36 | 3.77 | 2.93 | 2.55 | 4.55 |
| $\Theta$ | 0.0028 | 0.0163 | 0.0277 | 0.0365 | 0.0439 | 0.0568 | 0.0028 | 0.0149 | 0.0252 | 0.0331 | 0.0400 | 0.0521 |
| $N_s$ | 180 | 31 | 18 | 14 | 11 | 9 | 180 | 34 | 20 | 15 | 13 | 10 |
| $N_r$ | 1.00 | 0.17 | 0.10 | 0.08 | 0.06 | 0.05 | 1.00 | 0.19 | 0.11 | 0.08 | 0.07 | 0.05 |
| $N_e^{(v)}$ | Infinite | 39.8 | 24.4 | 19.3 | 18.0 | 11.3 | Infinite | 43.7 | 27.0 | 22.9 | 20.6 | 12.3 |
| $F$ | 0.000 | 0.014 | 0.025 | 0.034 | 0.041 | 0.054 | 0.000 | 0.012 | 0.022 | 0.030 | 0.037 | 0.049 |
| $GD$ | 0.997 | 0.984 | 0.972 | 0.964 | 0.956 | 0.943 | 0.997 | 0.985 | 0.975 | 0.967 | 0.960 | 0.948 |

* Generation 0 can be seen as the initial population (180 genotypes) that is drawn from the reference population.

** Sibling coefficient ($A$) estimated from individual years was considered successively as the fertility variation over five generations.

There was no correlation between genders in this study. But high correlation will affect strongly to the improvement of gene diversity by the equal seed harvest, depending also on how fertility varies. Bila *et al.* (1999) reported that gene diversity decreased at a considerably slower rate when the contributions of one gender were kept constant, but the maternal and paternal fertility variation was similar and highly correlated in that investigation.

The coancestry of two individuals is the probability that two gametes taken at random, one from each, carry alleles that are identical by descent (Falconer and Mackay, 1996). Thus, the coancestry of any two individuals is identical with the inbreeding coefficient of their progeny if they were mated. Group coancestry is the expected average coefficients of inbreeding among the offspring following random mating, and it increases with number of individuals per genotype. This tendency will also be pronounced with increasing numbers of generations (Muller-Starck, 1982) and with variation in fertility. On the other hand, pollen contamination will increase $N_s$ and *GD* (Harju, 1995; Lindgren and Mullin, 1998).

## Inbreeding and gene diversity

There was very low inbreeding when compared to reference population over generations, indicating that the gene diversity of the seed crop was maintaining high over generations if individuals mate randomly (*Table 2* and *Figure 3*). So, if we establish plantations from the seed crops produced over generations, the increasing of inbreeding in the seeds from the forest would not seem alarming. The accumulation of inbreeding (and also group coancestry) was a bit faster and higher when the fertilities of both genders were varying than when the maternal fertility was constant (*Figure 3*). Kjær (1996) reported that the accumulation of inbreeding was high when the flowering was poor. So, the loss of gene diversity or genetic variability will be mitigated when parental fertility is close to balance or when maternal fertility is kept constant.

Increasing of inbreeding and reduction of gene diversity depend also on the effective population sizes. For all level of fertility variation, the gene diversity (*GD*) was decreasing dramatically when the effective population size was getting smaller than 10 (Kang *et al.*, 2000). Gea *et al.* (1997) reported that population size was an important factor for delaying inbreeding, and $N_s$ was slightly better preserved by small disconnected groups over generations than large population. But, the population should be large enough because a small status number in a population will reduce the gene diversity and adaptive potential of the progeny.

Direct assays of effective parental fertility have only been possible using biochemical markers such as isozymes (Wheeler and Jech, 1992). However, isozyme markers show less genetic variation in most operational populations, and thus are limited in their ability to apply an estimates fertility variation (Joly and Adams, 1985; El-Kassaby *et al.*, 1989). Using isozyme marker, within population

gene diversity estimates in conifers range from 0.0 to 0.35 (Hamrick *et al.*, 1992), while polymorphic cpDNA marker yields a gene diversity estimate of 0.91 (Stoehr *et al.*, 1998).

In the ideal random mating population, the inbreeding due to a given generation of ancestors is found after two generations and thereafter remains almost constant (Robertson, 1961). In breeding populations, however, the loss of gene diversity (*i.e.*, group coancestry) appears in the next generation of the reference population due to the selection and the gene diversity decreases steadily over generations if there is equal contribution among parents (*Figure 3*).

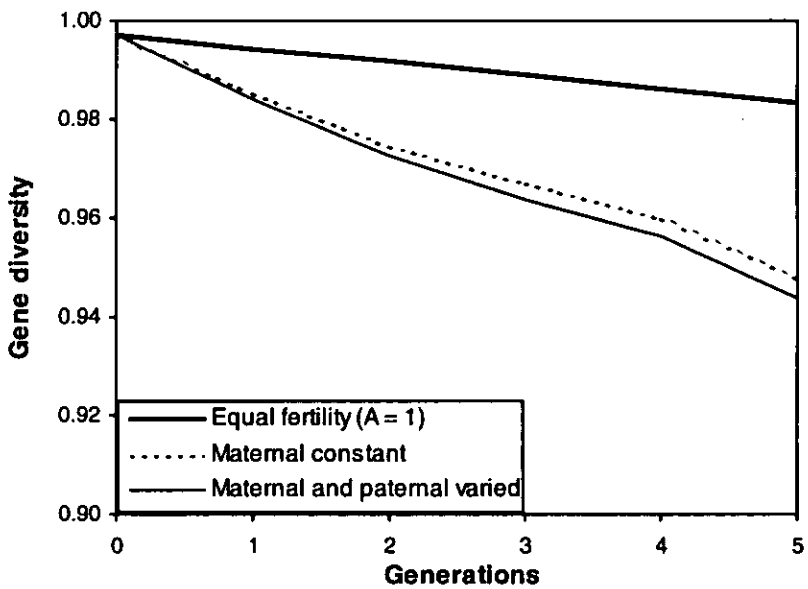


*Figure 3.* Gene diversity ($GD$=1-$\Theta$=1-0.5$A/N$) over five generations at the constant population size ($N$=180) and with fertility variation for each generation.

# Conclusions

This study has demonstrated that group coancestry can accumulate fast and status number can decrease fast over generation shifts. The fast change is partly due to the large paternal fertility variation in the material used for the study. The gene diversity preserved in the breeding and production populations may partly be utilised to boost the genetic response. It is concluded from our results that;

1. The loss of diversity is proportional to fertility variation (measured as $A$) and census number ($N$) in finite populations. For an idealised population, an expected increment of inbreeding in next generation will be $A/(2N)$ that is the probability that uniting gametes carry identical genes.

2. Inbreeding and reduction of diversity in seed crops over generations are greatly influenced by the fertility of individuals as well as relatedness among genotypes.
3. A small status number in the production population will reduce the gene diversity of seeds because $N_s$ expresses the accumulated genetic drift from the reference population to which the concepts inbreeding and coancestry refer.
4. Breeding population size with small effective numbers will not be able to maintain for longer than a few generations without inbreeding, which may become so severe as to cause fertility problems and to hamper selection.
5. The accumulation of group coancestry can not be effectively prevented by keeping the maternal fertility constant (*i.e.*, by equalising the number of seeds collected from each mother genotype) if the variations in paternal fertility are very large, while the variation in maternal fertility are marginal.

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