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

By A. D. Bila[1][2], D. Lindgren[2] and T. J. Mullin[3]

(Received 28th October 1998)

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 (θ_{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 Θ, 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:

---

[1] Department of Forestry Engineering, Eduardo Mondlane University, P.O.Box 257, Maputo, Mozambique

[2] Department of Forest Genetics and Plant Physiology, The Swedish University of Agricultural Sciences, S-90183 Umea, Sweden

[3] Genesis Forest Science Canada Inc., C.P. 64 Succursale Haute-Ville Québec (QC) G1R 4M8, Canada

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

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).

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

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 Θ, 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

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

$T2$ 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

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

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:

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

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:

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

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

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

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_{im} and p_{if} were the male and female fertilities of individual i, respectively. The total fertility of individual tree, pi, was calculated as the mid-parent value $pi = (p_{im} + p_{if})/2$. 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_s 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 correlation 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	759	87
No. of buds	272 227	114	322120	100
No. of stamens	1 778 048	113	2102766	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)	0.38 (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≥0.87*). The same was observed with correlations between numbers of buds, stamens, and fruits (*r≥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≥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	2.28	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.

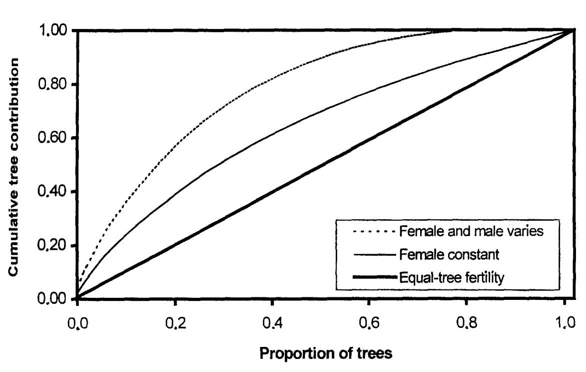

Figure 1. – Cumulative contribution to the next generation when female and male fertilities varies, female constant and male vary and when all trees in the population have equal fertility. Trees are ranked for fertility and cumulative contributions of trees above a certain rank are illustrated.

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 individualís 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.

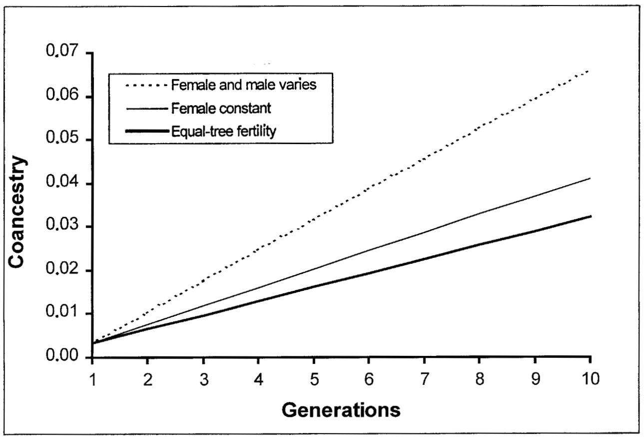

Figure 2. – Increase in group coancestry (the probability that two genes in the gene pool are identical by descent) over generations. Assumptions are that the population size (154) and fertility differences (as observed in a teak stand) are the same in each generation and that the new generation is formed 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.

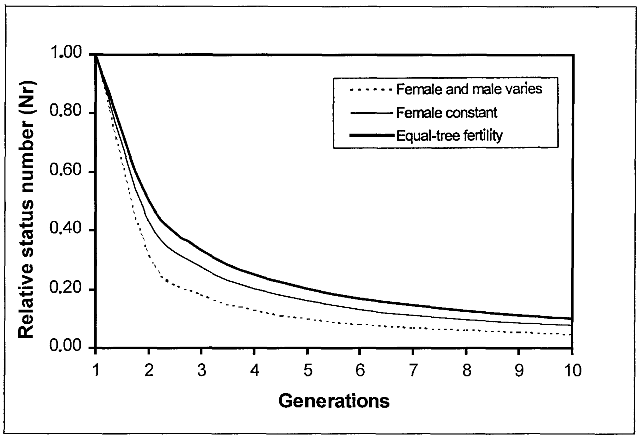

Figure 3. – Decrease in relative status number over generations at constant population size and fertility differences over generations, following random mating, when female and male fertilities varies, female constant and male vary and when all trees in the population have equal fertility.

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_r 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 (Meffe and Carroll, 1997). Therefore, the distribution of progenies among parents should be controlled to limit relatedness and maintain genetic variability in the population.

Acknowledgements

We thank the Eduardo Mondlane University for funding support, and the Department of Forest Genetics and Plant Physiology at the Swedish University of Agricultural Sciences; the Swedish Council for Forestry and Agricultural Research; and Föreningen Skogsträdsförädling for additional support.

Literature

Askew, G. R.: Estimation of gamete pool compositions in seed orchards. Silvae Genetica **37**: 227–232 (1988). — Bawa, K. S. and Webb, C. J.: Flower, fruit and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal reproductive patterns. Amer. J. Bot. **71**: 736–751 (1984). — Bila, A. D. and Lindgren, D.: Fertility variation in *Milletia sthlmannii, Brachystegia speciformis, Brachystegia bohemii* and *Leucaena leucocephala* and its effects on relatedness in seeds. For. Gen. **5**: 119–129 (1998). — Bor, N. L.: Manual of Indian forest botany. Oxford University Press, Indian Branch, Bombay. 441 pp. (1953). — Burczyk, J. and Chalupka, W.: Flowering and cone production variation and its effect on parental balance in a Scots pine clonal seed orchard. Ann. Sci. For. **54**: 129–144 (1997). — Chaisurisri, K. and El-Kassaby, Y. A.: Estimation of clonal contribution to cone and seed crops in a Sitka spruce seed orchard. Ann. Sci. For. **50**: 461–467 (1993). — Cockerham, C. C.: Group inbreeding and coancestry. Genetics **56**: 89–104 (1967). — Costa, F.: Plantations and research: news from the past. pp. 403–415. *In:* Reforestation seminar, Namaacha, 22 to 23 November 1983. Ministry of Agriculture and Fisheries, Maputo (1983). — Crawler, M. J.: Plant ecology. Second edition. Blackwell, Oxford. 717 pp. (1997). — DASAPPA.: Geographical distribution and problems of regeneration (natural and artificial) in teak (*Tectona gransis* Linn.f.). Myforest **25**: 337–355 (1989). — Dryndum, K. and Hedegart, T.: Pollination of teak *(Tectona gransis)*. Silvae Genetica **18**: 77–80 (1969). — Dupuy, B. and Verhaegen, D.: Plantation-grown teak *(Tectona gransis)* in Cote-D'Ivoire. Bois et Forêts des Tropiques **235**: 10–24 (1993). — El-Kassaby, Y. A.: Evaluation of the tree-improvement delivery system: factors affecting genetic potential. Tree Physiol. **15**: 545–550 (1995). — El-Kassaby, Y. A. and Askew, G. R.: The relation between reproductive phenology and reproductive output in determining the gametic pool profile in a Douglas-fir seed orchard. For. Sci. **37**: 827–835 (1991). — Fries, A.: Development of flowering and effect of pruning in a clonal seed orchard of lodgepole pine. Can. J. For. Res. **24**: 71–76 (1994). — Gilpin, M. E. and Soulé, M. E.: Minimum viable populations: processes of species extinction. pp. 19–34. *In:* Soulé, M. E. (ed). Conservation biology: the science of scarcity and diversity. Sinauer Assoc., Sunderland, Mass. (1986). — Goudie, A.: The human impact on the natural environment. Fourth edition. Backwell, Oxford. 454 pp. (1993). — Gram, K. and Larsen, C. S.: The flowering of teak *(Tectona gransis)* in aspects of tree breeding. Nat. His. Bol. Sia. Soc. **19**: 1–7 (1958). — Gregorius, H.: Characterization and analysis of mating systems. Ekopan Verlag, Germany, 158 pp. (1989). — Griffin, A. R.: Clonal variation in Radiata Pine seed orchards. I. Some flowering, cone and seed production traits. Aust. For. Res. **12**: 295–302 (1982). — Hauser, T. P., Damgaarg, C. and Loeschcke, V.: Effects of inbreeding in small plant populations: expectations and implications for conservation. pp. 115–129. *In:* Loeschcke, V., Tomiuk, J. and Jain, S. K. (eds). Conservation genetics. Birkhäuser Verlag, Basel, Switzerland (1994). — Hedegart, T.: Breeding systems, variation and genetic improvement of teak (*Tectona grandis* L.f.). pp. 109–122. *In:* Burley, J. and Styles, B.T. (eds). Tropical trees: variation, breeding and conservation. Academic Press, London (1976). — Hughes, C. E. and Robbins, A. M. J.: Seed stand establishment procedures for *Pinus oocarpa* and *Pinus caribaea* var. *hondurensis* in the natural forest of Central America. Comm. For. Rev. **61**: 107–113 (1982). — Kang, K. S. and Lindgren, D.: Fertility variation and its effect on the relatedness of seeds in *Pinus densiflora, Pinus thunbergii* and *Pinus koraiensis* clonal seed orchards. Silvae Genetica **47**: 196–201 (1998). — Kjær, E. D.: Estimation of effective population number in a *Picea abies* (Karst.) seed orchard based on flower assessment. Scand. J. For. Res. **11**: 111–121 (1996). — Kumar, A.: Teak seed improvement – achievements and problems. Indian Forester **118**: 525–533 (1992). — Lindgren, D., Gea, L. D. and Jefferson, P. A.: Loss of genetic diversity monitored by status number. Silvae Genetica **45**: 52–59 (1996). — Lindgren, D. and Kang, K.: Status number – a useful tool for tree breeding. Res. Rep. For. Res. Inst. Kores **33**: 154–165 (1997). — Lindgren, D. and Mullin, T. J.: Balancing gain and relatedness in selection. Silvae Genetica **46**: 124–129 (1997). — Lindgren, D. and Mullin, T. J.: Relatedness and status number in seed orchard crops. Can. J. For. Res. **28**: 276–283 (1998). — Loeschcke, V., Tomiuk, J. and Jain, S. K .: Introductory remarks: genetics and conservation biology. pp. 3–8. *In:* Loeschcke, V., Tomiuk, J. and Jain, S. K. (eds). Conservation genetics. Birkhäuser Verlag, Basel, Switzerland (1994). — Matthews, J. D.: Factors affecting the production of seed by forest trees. For. Abst. **24**: 1–11 (1963). — Meffe, G. K. and Carroll, C. R.: Principles of conservation biology. Second edition. Sinauer Assoc., Sunderland, Mass. 729 pp. (1997). — Nanda, K. K.: Some observations on growth, branching behaviour and flowering of teak (*Tectona grandis* L.f.) in relation to light. Indian Forester **88**: 207–218 (1962). — NDFW: Namaacha plantation report. Monap Project GE-7, Ministry of Agriculture and Fisheries, Maputo, Mozambique. 8 pp. (1983). — Neelay, V. R., Bhandari, R. S. and Negi, K. S.: Effect of insecticidal and hormonal spray on the production of fruits in teak seed orchards. Indian Forester **109**: 829–837 (1983). — Rawat, M. S.: Fruit/seed setting in teak (*Tectona grandis* L.f.): a point to ponder. Indian Forest **120**: 1076–1078 (1994). — Roeder, K., Devlin, B. and Lindsay, B. G.: Application of maximum likelihood methods to population genetic data for the estimation of individual fertilities. Biometrics **45**: 363–379 (1989). — Richards, A. J.: Plant breeding systems. Allen and Unwin, London, 529 pp. (1986). — Savolainen, O., Kärkkäinen, K., Harju, A., Nikkanen, T. and Rusanen, M.: Fertility variation in *Pinus sylvestris:* a test of sexual allocation theory. Amer. J. Bot. **80**: 1016–1020 (1993). — Sedgley, M. and Griffin, A. R.: Sexual reproduction of tree crops. Academic Press, London. 378 pp. (1989). — Vencovsky, R.: Tamanho efectivo populacional na coleta e preservação de germoplasma de espécies alôgamas [Effective population size in collecting and preserving germplasm of panmictic species]. IPEF, Instituto de Pesquisas e Estudos Florestais **35**: 79–84 (1987). — Wei, R. P.: Predicting genetic diversity and optimizing selection in breeding programmes. Ph. D. thesis. Swedish University of agricultural Sciences, Umea, Sweden (1995). — White, J. K.: Tree breeding with teak *(Tectona grandis)*. Australian Forestry **1**: 90–93 (1962). — Xie, C. Y. and Knowles, P.: Male fertility variation in an open-pollinated plantation of Norway spruce *(Picea abies)*. Can. J. For. Res. **22**: 1463–1468 (1992). — Xie, C. Y., Woods, J. and Stoehr, M.: Effects of seed orchard inputs on estimating effective population size of seedlots – a computer simulation. Silvae Genetica **43**: 145–154 (1994). — Zobel, B. and Talbert, J.: Applied forest tree improvement. John Wiley & Sons, New York. 505 pp. (1984).