FOREST GENETICS 5(2):119–129, 1998

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

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Received October 1, 1997, revised June 2, 1998, accepted June 4, 1998

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 & CHAŁUPKA 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 Θ_ω. 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 θ_{ij}, where θ_{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. Note 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

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

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 θ_t. Let us the same for all genotypes, F_t. Using formula [2] above we get:

$$\Theta_\omega = \sum_{i=1}^{N} p_i^2 0.5(1+F_t) + (1 - \sum_{i=1}^{N} p_i^2)\Theta_t$$
$$= \Theta_t + (0.5 + 0.5F_t - \Theta_t)\sum_{i=1}^{N} p_i^2 \qquad [3]$$

For the special case that $\theta_t = F_t = 0$ the expression 3 simplifies to

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

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 $0 \leq x \leq 1)$ 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.

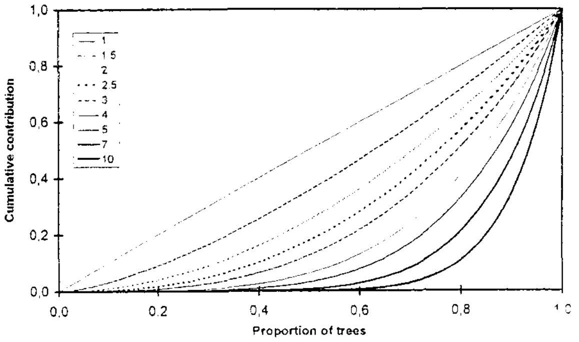

Figure 1. Cumulative contribution to the next generation by cumulative proportion of parents ranked for fertility. Graphs for the function $y=x^a$ are shown for different values of a.

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:

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

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

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

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 $1/N$.

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

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

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

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

The fertility of each tree can be considered a sample, so that the variance of the fertility of the average of *N* trees (z_μ 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 (Θ), 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

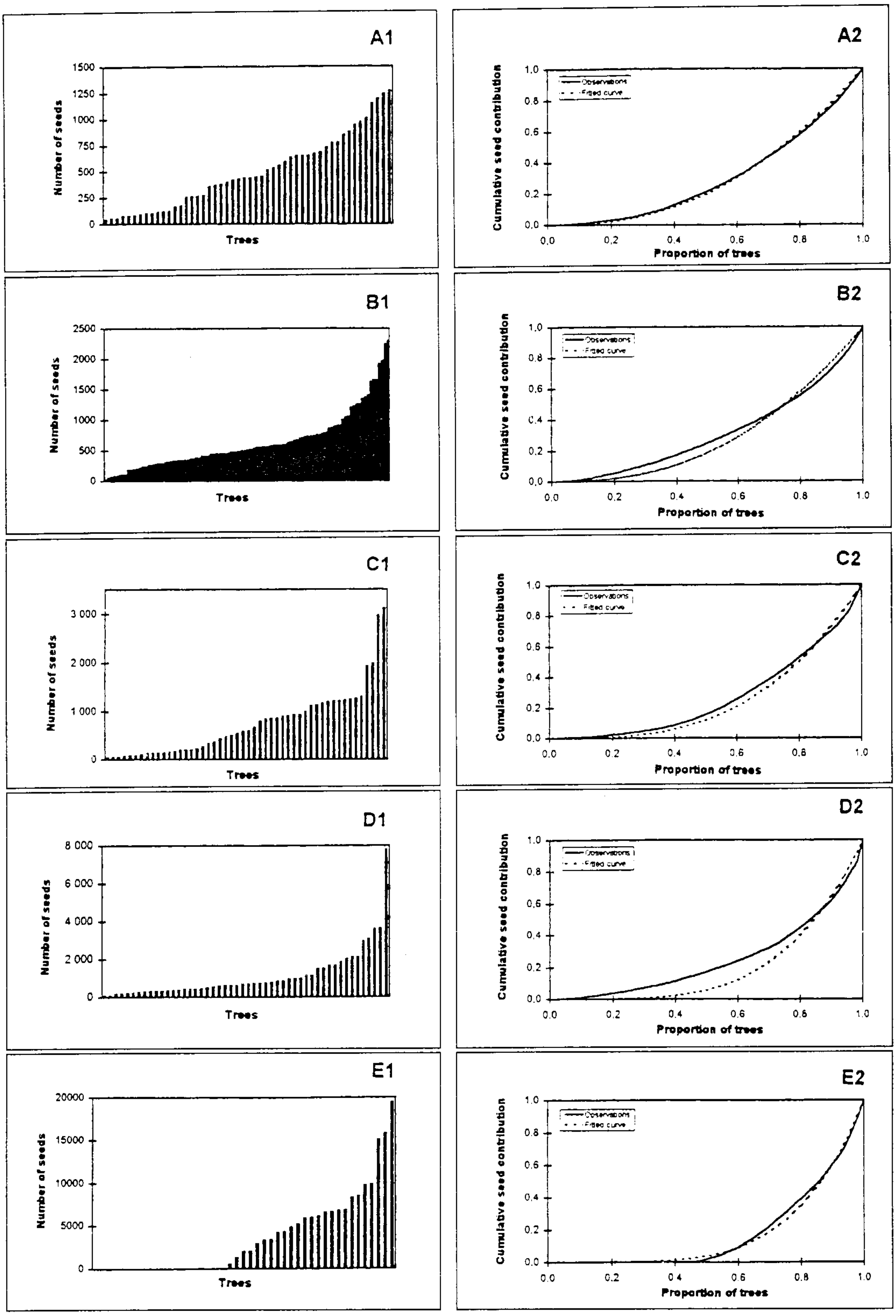

Figure 2. Individual seed production (A1, B1, C1, D1, E1) and cumulative contribution to seed set (A2, B2, C2, D2, E2) in surveyed stands. Trees are ranked from low to high yield and transformed to cumulative contributions, summing up to one. Observed curve were produced from the proportion of trees 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_s 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_s 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	2.00	0.7500	a-values estimated from field data summary
			Seed cone production	1.40	0.9186	
El-Kassaby & Cook (1994)	Douglas fir	17-19 yr old seed orchard	Cone crop	2.80	0.5867	a-values estimated from field data summary
			Seed crop	3.00	0.5556	
Chaisurisri & El-Kassaby (1993)	Sitka spruce	seed orchard 14 yr old	Cone crop	7.10	0.2619	20 % , 35 %, 42 %, 42%, and 48 % of clones, respectively, produced 80 % of cone crop
		15 yr old	Cone crop	4.50	0.3951	
		16 yr old	Cone crop	2.20	0.7025	
		17 yr old	Cone crop	2.20	0.7025	
		19 yr old	Cone crop	1.90	0.7756	
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	3.90	0.4471	20 % of clones produced 61% of male and 48 % of female strobili
			Female strobili production.	2.70	0.6036	
Schoen *et al.* (1986)	White spruce	12 yr old seed orchard	Male strobili production	6.70	0.2762	20% of clones produced 77% of male and 79 % of female strobili
			Female strobili production.	6.60	0.2800	
Griffin (1982)	Radiata pine	8 yr old seed orchard	Seed crop	2.60	0.6213	50 % of seeds, pollen and the total gamete contribution was produced by 23 %, 33% and 37 % of clones respectively.
			Pollen	1.70	0.8304	
			Gametes	1.50	0.8889	
Lindgren & Lindgren (1976)	Norway spruce	A clonal seed orchard	Female strobili	3.50	0.4880	Flowering and correlation between male and female strobili increased with age
			Male strobili	2.40	0.6480	
			Gene contribution	2.60	0.6210	
Lindgren & Lindgren (1976)	Norway spruce	31 adult stands	Female cones followed for three years	3.30	0.5160	High cone set
				6.00	0.2950	Moderate cone set
				16.00	0.1140	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_s 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_r 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_s 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_s 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_s 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.

ACKNOWLEDGEMENTS

This work was done during the first author's Ph.D. studies at The Swedish University of Agricultural Science. We thank the Eduardo Mondlane University for scholarship funding and the Department of Forest Genetics and Plant Physiology and the Swedish Council for Forestry and Agricultural Research for additional support. Dr. T. J. Mullin reviewed and made useful comments as well as checking the language, which helped to improve the manuscript.

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