RECURRENT SELECTION, MATING DESIGN, AND EFFECTIVE POPULATION SIZE

H. Kang[1]

Abstract. -- Many contemporary breeders are building founder breeding populations, and there is a need to learn about the potential long-term consequences of their breeding activities. In this paper impacts of recurrent selection, mating design, and effective population size on dynamics of breeding populations are discussed. A theoretical model of a single-loci population is used to highlight the relevant information on long-term tree breeding.

Keywords: breeding population, mating design, allele fixation, allele frequency

INTRODUCTION

Long before Darwin (1809-1882) and Mendel (1822-1884) provided empirical evidence of the process of evolution and mechanism for inheritance, humans had domesticated animals and crops by practicing artificial selection. These domestication processes demonstrated the human ability to select for modified forms of plants and animals. Likewise, artificial selection remains an important feature of forest tree breeding as contemporary tree breeders domesticate and breed trees. To many tree breeders, however, selection represents only a subset of activities associated with the broader objective of managing genetic resources. Tree breeders are interested not only **in** maximizing immediate genetic gain, but also in learning the potential long-term genetic consequences of various breeding activities. This reflects increasing awareness that whatever tree breeders do today will influence future tree breeding for a long time: what is good for today may not necessarily be good for tomorrow. Decisions made or not made now will limit future options.

Three main questions contemporary tree breeders may ask about long-term breeding are: (1) How large should the overall breeding population size be? (2) How should the breeding population be structured? and (3)What are the long-term consequences of using current breeding techniques? To address these questions, we need to consider dynamics of breeding populations over many generations. Although most forest tree species cannot be used for this purpose, it is possible to learn about population dynamics by means of theory and empirical study of fast generation turn-over plants, including some tree species. These alternative means do not allow us to predict specific conditions of the breeding population at some time in the future, but they do

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[1] Project leader, North Central Forest Experiment Station, USDA-Forest Service and Associate Professor, Department of Forestry, University of Wisconsin-Madison, Madison, Wisconsin, 53706. This work was partially supported by Swedish Council for Forestry and Agricultural Research.

The main objective of this paper is to address some aspects of the above three long-term tree breeding questions. I will: (1) review some basic concepts of artificial selection and effective population size; and (2) discuss recurrent selection, mating design, and population size using a single-loci model.

SELECTION, MATING DESIGN, AND EFFECTIVE POPULATION SIZE

Single cycle of selection:

Quantitative geneticists often consider the change in the population mean ($\Delta\mu$) as the response to a single cycle of selection. This quantity is often equated to the genetic gain -- i.e., $\Delta\mu = \Delta G = ih^2\sigma_p$, where i, h^2, and σ_p represent intensity of selection, heritability, and phenotype standard deviation of the parental population, respectively. In theoretical population genetic models, on the other hand, the change in the frequency of a selectively favored allele (Δq) is often used, where q represents the allele frequency before selection. In a single-loci model, Δq is a function of both allele frequency, selection coefficient(s), and measure of dominance (h). Single loci model means that the character of interest is controlled by many independent loci -- i.e., no linkage and no epistasis. The parameter used in quantitative genetics and the parameter used in population genetics, $\Delta\mu$ and Δq, are related through the expression (Falconer 1981),

$$[1] \qquad s \approx i\alpha\ ,$$

where s, i, and a represent selection coefficient, selection intensity, and the standardized distance between two homozygotes, respectively. This relationship assumes that the environmental effect is normally distributed. For example, Fisher's (1918) infinitesimal model deals with the case where the number of loci influencing the character subjected to selection is effectively infinite, and the environmental effect is assumed to be normally distributed. Even if this normality assumption does not hold, i in [1] could be replaced by the ratio between the ordinate at the truncation point to the proportion selected, as long as truncation selection is made and the gene effects on the character are additive between loci (Kimura and Crow 1978).

We may question the value of [1] because the assumptions used to define the equation are unrealistic. There are many unknowns regarding genetic properties of the population, and [1] cannot be used in a predictive fashion. For example, knowing $\Delta\mu$ will say nothing about Δq. In most quantitative traits, we do not know the number of loci influencing the character and their gene actions. However, [1] is useful because it implies that there is a one-to-one correspondence between s and α for given i, or between s and i for given α. Therefore, when we compare other factors such as mating design with respect to one parameter, say $\Delta\mu$, then we can expect the same trend to hold with respect to Δq.

Multiple cycles of selection and Selection limit

When repeated artificial selection is applied to a population, the population may cease to respond to the selection at some point. The population could reach this selection limit for many different reasons such as (Eisen 1980): (1) fixation of all loci affecting the trait; (2) overdominance for the trait; (3) artificial selection opposed by natural selection; (4) undesirable recessive genes at low frequency; (5) negative genetic correlation between component characters; (6) genotype by environment interaction; and (7) tight linkages. For most of these cases, populations will have genetic variances at the limit and will respond to reverse selection. When all the loci affecting the trait are fixed with one allele, then there will be no genetic variance, and reverse selection will not yield a response.

Many experimental results on recurrent selection are available. Wright (1977) made an extensive review of this subject. Some notable studies of selection limit are: Jones et. al. (1968) for fruit fly, Roberts (1966a,b, 1974) and Eisen (1972, 1974) for mouse, and Enfield (1974, 1977) for flour beetle. These experiments were designed to test the influence of variance effective population size (Nev) and selection intensity (i) (or population structure). Some important conclusions from these studies are: (1) The total response to selection increases when the population size increases. (2) For a fixed population size, the total response increases when the selection intensity increases. (3) The estimates of the time taken to reach the selection limit in general do not agree with the theoretical prediction by Robertson (1960). There are other landmark experiments. Dudley (1977) has shown that the percentage of both oil and protein in maize showed no sign of approaching limits after 76 generations of upward selection. Wright (1977) called the findings of Payne (1918) striking, where a population drawn from a single wild *Drosophila* female responded to selection (scutellar bristle) for more than 35 generations.

Robertson (1960) showed that the "half-life" (number of generations necessary to reach the allele frequency half way to the selection limit) would vary between 1.4Nev and 2Nev. Empirical results showed that this prediction did not work, but we may use these expressions to discuss forest tree breeding. Consider a species with a generation turn over period of 10 years. If 50 individuals are selected every generation, it would take at least 70 generations or 700 years to reach the half-life. It would take a long time before a selection limit is reached. Should tree breeders be concerned about selection limit? It is unrealistic to begin a breeding program with the idea that some day the breeding population will reach its selection limit. Breeders may consider selection limit as a conceptual restriction. It is useful to know that a chosen strategy does not lower the selection limit. Given this restriction breeders may choose the strategy which would allow the maximum short-term genetic gain. The parameters u(q) and t(q) themselves could be used in developing breeding strategies. Understanding these parameters would help in determining necessary breeding population sizes and in designing the structure of breeding populations. It would also offer alternate views on short-term breeding techniques. It is well known that the selection limit is usually smaller than that projected by the gain at the beginning of the breeding program (Bohren 1975). Learning the causes of such discrepancies would greatly help breeders to appreciate the factors that influence population dynamics.

The basic theory of limits to artificial selection was first set forth by Robertson (1960). To develop the theory Robertson used Kimura's (1957) expression for the ultimate probability of allele fixation u(q). This probability is a function of the initial allele frequency (q), variance effective population size (Nev), and selection coefficient (s) such that,

$$[2] \qquad u(q) = \frac{\int_0^q G(x)dx}{\int_0^1 G(x)dx},$$

where $G(x) = \exp[-2N_{ev}s(2h-1)x(1-x) - 2N_{ev}sx]$.
q represents the initial allele frequency,
N_{ev} represents variance effective population size,
h represents the degree of dominance, and
s represents the selection coefficient.

Under an infinite population size model, the selection will not fix the favorable allele when overdominance gene action controls the locus, and u(q)=0. In [2], however, there is always the possibility of chance fixation of alleles ($u(q) \neq 0$), and u(q) is a useful measure regardless of the gene action. The single-loci model also assumes independence among loci (no linkage and no epistasis), discrete generation, and constant Nev and s. Given all these assumptions, the dynamics of the population is completely explained by the three parameters, q, Nev, and s. In artificial breeding where truncation selection is used, we may replace s with i and a (Equation [1]).

Some additional conclusions of Robertson (1960) are: (1) For small populations, the advance due to selection is greatest when 50% of the population is selected. This was also predicted by Dempster (1955), and Cockerham and Burrows (1980). (2) For small additive allele effect (a in Equation [1]), if Nevi is small, then the total response is approximately 2Nev times the response in the first generation. Subsequently, many theories dealing with selection limit have been developed: Conflict between natural and artificial selection (James 1962, Sved 1977, Nicholas and Robertson 1980); Exact probability (Hill 1969a, Carr and Nassar 1970a,b); Finite number of gametes (Schuster and Sigmund 1989); Linkage (Hill and Robertson 1966, Gill 1965a,b, Latter 1965, 1966, Robertson 1970); Mating design (Kang and Namkoong 1979, 1980, Kang 1983); Mutation (Hill and Keightley 1988, Hill and Rasbash 1986, Keightley and Hill 1988); Overlapping generations (Emigh and Pollak 1979); Rate of response (Hill 1969b, Kimura and Ohta 1969); Self-fertilizing population and inbreeding (Bailey 1977, Hill and Robertson 1968, Robertson 1961); Structured population (Baker and Curnow 1969, Madalena and Hill 1972, Hill 1970); and Within-family selection (Dempfle 1975, Young and Skavaril 1976).

The connection between u(q) defined in the theoretical models and observed total advance from selection experiments may be interpreted as follows. The level of the limit, (i.e., the height of the plateau) will be influenced by the number of favorable alleles fixed. Therefore, the greater u(q) for the loci involved, the greater the height of the plateau is likely to be. At fixation, the population will lack genetic variance with respect to the character selected. However, empirical results have shown that when reverse selection was made at selection limit, the population almost always responded, implying that the population had genetic variability at the limit. It was also mentioned before that empirical results did not agree with Robertson's conclusion regarding the half-life. Therefore, selection theories appear to be of limited value as means of predicting total advance from selection. These theories, on the other hand, have been extremely useful in sorting out factors that influence the selection limit. Experimental results, indeed, indicate that Nev and s are two critical factors that influence the limit. Because the factors that influence the population dynamics are completely represented by three parameters, q, Nev, and s, it must be possible to explain any variation in the selection regime by using these parameters. For example, the influence of the mating designs on the selection limit could be explained based on how they influenced the variance effective population size (Kang and Namkoong 1979, 1980, Kang 1983). This will be discussed in a later section.

Mating design, variance effective population size, and allele fixation

Mating design represents "rules" for arranging different control crossings. There are three different standard types of mating designs: nested, factorial, and diallel. Most of these designs allow the estimation of both additive and dominance genetic variance. There are large differences among designs with respect to the number of control matings necessary. To take the most extreme example, full-diallel requires N^2 crossings while pair mating requires N/2 crossings to complete the design, where N represents the census number of parents. Therefore, the full diallel mating requires 2N times more crossings than pair mating, and the ratio will increase as the number of selected parents increases. Using complex designs is often biologically impossible as well as costly and time consuming. Traditional mating designs assume that mating is made randomly after truncation selection. Instead of random mating, assortative mating may be used. These assortative matings could be balanced or unbalanced, where balanced mating means that all the parents have equal probability of passing the same number of alleles to the progeny gene pool. Alternatively, it is possible to assign weights to the ordered breeding values (Kimura and Crow 1978, Crow and Kimura 1979, Lindgren and Matheson 1986, Lindgren et al. 1989, Kang and Namkoong 1988, Kang 1989). These mating systems are necessarily unbalanced.

Mating designs were originally developed as means of estimating genetic parameters such as additive- and/or dominance variance. Mating design has also been used in developing selection strategies in short-term breeding. The designs offer different hierarchical structures, such as half-, full-sib family, and individuals within family, in the progeny population. This hierarchical structure provides the basis for constructing selection indices. In evaluating mating designs with respect to estimation, the sampling variance of the genetic variances are used (Nasoetion et al. 1967, Namkoong and Roberds 1974, Pepper 1983). In general, for a given number of parents, the mating design that includes the larger number of crossings will produce the smaller sampling variance. For example, Klein et al. (1973) indicated that it would take at least 400 families to estimate heritability with a standard error less than 0.1.

The predicted genetic gain under different selections has received great attention. For example, it is well known that family selection is more desirable than within-family selection when the heritability (or intraclass correlation) is low (Falconer 1981). This kind of idea has been generalized into the form of index of family and within-family values. Because family structures can be created by the mating systems, it is possible to evaluate selection-mating design combinations (Cockerham and Matzinger 1966, Namkoong et al. 1966, van Buijtenen 1972, Lindgren 1977, Pepper and Namkoong 1978, Cotterill and Jackson 1989). Mating designs seem to have relatively little impact on the index-mating design combinations (Cotterill and Jackson 1989). For both mass selection and family selection, mating designs have relatively little impact on Aq as long the mating designs are balanced (Kang and Namkoong 1979, Kang 1983).

There are some theoretical as well as empirical findings that indirectly indicate that balanced mating designs may not differ with respect to fixation probabilities: (1) Hill and Robertson (1968) examined the effects of inbreeding in monoecious and dioecious populations when heterozygote advantage existed. They found little difference between the two populations with respect to equilibrium allele frequencies. (2) Lande (1977) found that mating system had no influence on the amount of genetic variance maintained in the model population that allowed mutation, linkage, and natural selection on a polygenic character with additive genes. (3) My unpublished results from the single-locus model showed that selfing did not change u(q). (4) MacNeil et al. (1984) studied effects of mating systems in Japanese quail. In this experiment, an inbreeding and a random mating population were compared. They found that once the inbreeding population overcame the initial depression its performance level increased rapidly. (5) Cockerham and Burrows (1980) indicated that to maximize the selection limit in dioecious populations the optimal procedure would be to equal numbers recorded and selected of each sex.

The theoretical explanation for why u(q) do not differ between balanced mating designs, but differ among unbalanced mating designs can be found by observing the impacts of different mating designs on variance effective population size (Nev). The variance effective population size is defined as (Crow and Denniston 1988),

[3] $$N_{ev} = \frac{2N_t}{1-\varepsilon+\frac{(1+\varepsilon)s_k^2}{\mu_k}}$$, for a monoecious population,

where N_t represents the number of progeny individuals after selection,

ε represents deviation of parent genotypes from Hardy-Weinberg equilibrium,

μ_k represents the mean of the number of gametes transmitted by a parent, and

s_k^2 represents the sample variance of the number of gametes transmitted by a parent.

Under balanced mating, Nev = N_{t-1} regardless of the number of crossings involved, because $sk^2 = \mu k$. This holds for assortative mating also as long as they are balanced. With unbalanced mating, however, Nev < N_{t-1} and $s_k^2 > \mu k$. In a recurrent selection, where the census population size (N) is kept constant, $\mu k = 2$, for all mating designs, and the difference between balanced and unbalanced mating design originates from different s_k^2. Because Nev of unbalanced mating design is always smaller than that of balanced mating design, it generates lower probability of allele fixation (u(q)) for given q, s (or i and a), and N_{t-1}. For example, assume that the number of parents selected (N_{t-1}) is 8, then Nev of full-diallel, pair mating, and selfing is 8, but that of factorial mating with 1 tester is 4.06. When the census number (Nt or N) is 16, Nev of a factorial mating design with 1 tester is 4.01. In general, with 1 tester factorial,

$$N_{ev} = \frac{2N}{1-\varepsilon+\frac{(1+\varepsilon)N(N-2)^2}{2(N-1)^2}}, \text{ which implies that as N approaches infinity, } N_{ev} \text{ approaches 4,}$$

assuming that E = 0. When N=8, q = 0.25, i = 1.755 (10% selection), a = 0.2, and additive gene action, u(q) for all the balanced mating is 0.76. For factorial mating with 1 tester u(q) is 0.54, even if the census number (N) is greater than 8. The value of u(q) is found by evaluating Equation [2] after replacing proper values listed above.

Equation [2] is not an exact solution, but has been proven to be a good approximation (Hill 1969a, Carr and Nassar 1970a,b). Balanced mating designs of u(q) calculated by using a numerical analysis (Kang and Namkoong 1979, 1980) also resulted in the same values as those obtained from Equation [2]. However, the numerical analysis of factorial mating design resulted in lower u(q) than the solutions from [2] (Figure 1). It is possible that there other than Nev might influence u(q). For example, in the calculation of Nev, ⊂ (deviation from Hardy-Weinberg proportion) is assumed to be zero, which is rarely true. In any case, the discrepancy

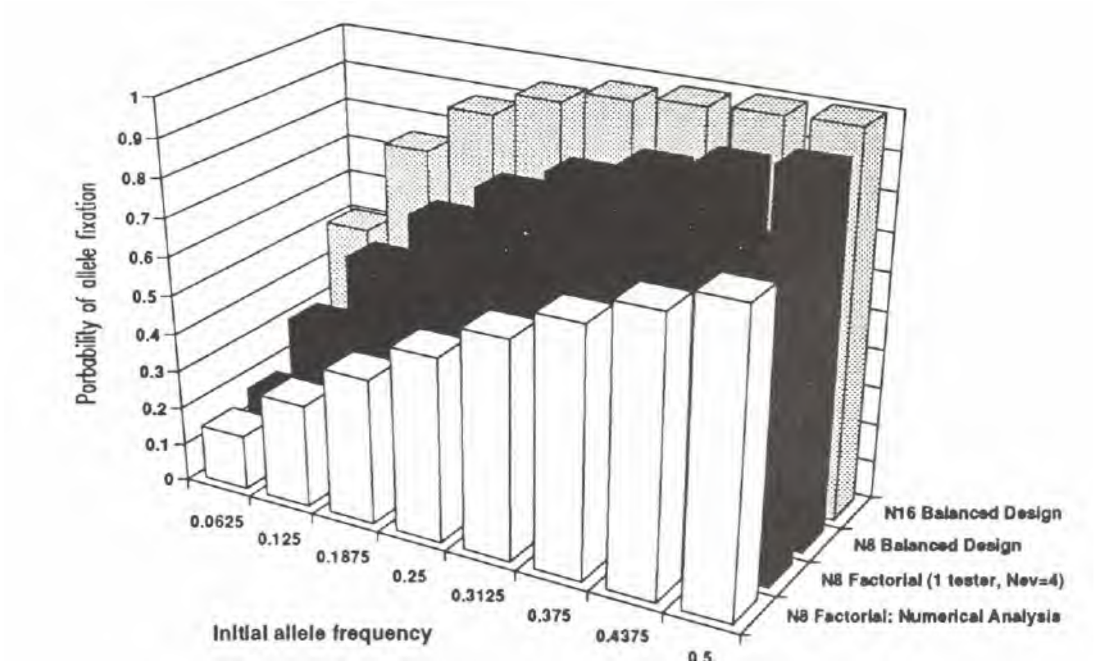

Figure 1. Ultimate probability of allele fixation (u(q)) under different initial allele frequency and population size. N# represents the census number. Initial conditions used are: a=0.2, *i=1.755* (10% selection), additive gene action. The u(q) for balanced designs (N16, N8) and N8 Factorial (1 tester, Nev=4) were obtained by using Equation [2].

appears to be fairly consistent over different initial allele frequencies. Figure 1 also shows that for a moderate initial allele frequency, say q > 0.3, and Nev = 16 the probability of allele fixation, u(q), is close to 1 with balanced mating. Therefore, if the allele fixation under selection is the only concern in long-term tree breeding, then the breeding population size does not need to be very large, unless the breeder wishes to save favorable alleles of very small initial frequency.

COMPARISON OF MATING DESIGNS UNDER A SINGLE-LOCI MODEL: A COMPUTER SIMULATION

In this section, I will discuss findings from a simple computer simulation experiment that compared response to selection to different mating designs. The analytic expression for u(q) in [2], or numerical analysis used in Kang and Namkoong (1979, 1980) provides information on populations at the selection limit, but does not show intermediate progress of the population. Computer simulation was made to observe the pattern of approach to selection limit when different mating designs were used.

In this experiment, the trait of interest of a population was assumed to be composed of a single locus (or many independent loci). As before, the initial conditions used were q = 0.25, i = 1.755 (10% selection), a = 0.2, and additive gene action. The genotype frequency of the initial population was set to be in Hardy-Weinberg equilibrium. From this founder population N parents were randomly sampled, and crossed according to a mating design. From the progeny population produced, N individuals were selected based on their phenotypic score. These selected individuals were used as parents for the next generation. Before control crossing, these individuals were sorted according to their phenotypic values. Therefore, pair mating in this experiment represents an assortative mating. Selfing, of course, is the most extreme form of assortative mating, regardless of the order of selected individuals. The recurrent selection was continued for 50 generations. This computer trial of 50 generations of selection was repeated 1,000 times. At each generation, the number of subpopulations with allele fixation and allele loss was determined, and average allele frequency was calculated.

As expected, all balanced mating designs approached the same selection limit near 0.75. (Figure 2a). The factorial mating design with 1 tester (Nees = 4) approached a lower selection limit near 0.65. This level is actually higher than u(q) obtained from Equation [2] (0.54) and numerical analysis (0.49). Although all the balanced matings approached the same selection limit, the progress from selection was fastest with selfing, which was distantly followed by pair mating. For all practical purposes, pair mating, half-diallel, and partial-diallel may be considered the same in this experiment. The initial rates of progress from selection by both half-diallel and partial diallel were similar and slow. When compared to balanced mating designs other than selfing, the factorial mating had relatively rapid initial progress from selection, but produced lower plateau.

Numbers of populations with allele fixation or loss at different generations also show consistent results (Figure 2b). To simplify the picture, half-diallel and partial-diallel were not

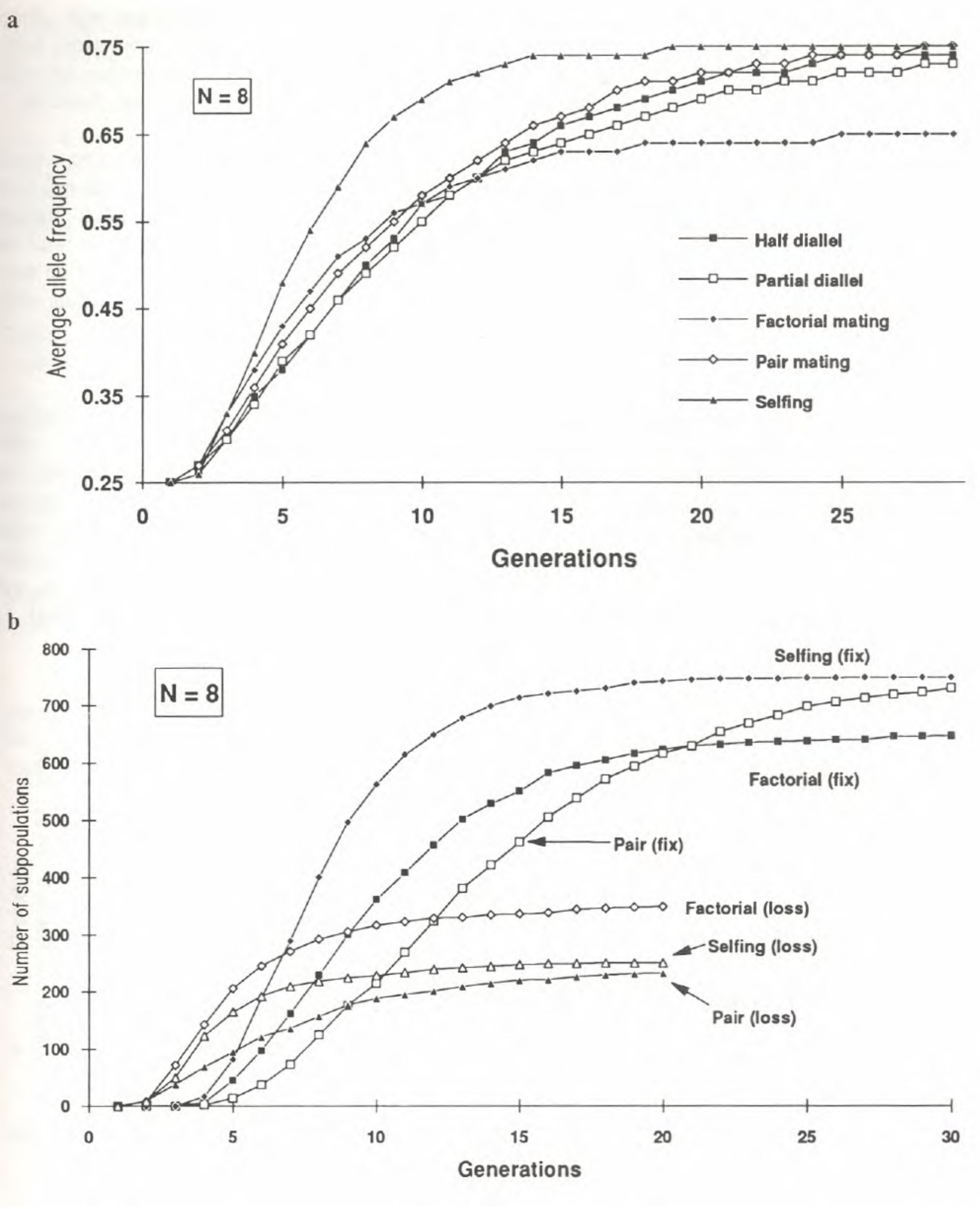

Figure 2. Results from single-loci selection simulation. a. Changes in the average allele frequency of 1,000 trials. b. Number of populations with allele fixation or loss.

included in Figure 2b. Selfing tends to have a larger number of subpopulations with allele fixation at earlier generations than pair mating. Eventually the number of subpopulations with allele fixation merged. Factorial mating also had a fairly large number of subpopulations with fixation during earlier generations, but a lower overall number of subpopulations with fixation.

Selfing also had a larger number of subpopulations with allele loss in early generations, when compared to pair mating (Figure 2b). Both have plateaus at the same level. Factorial had larger number of subpopulations with allele loss in early generations than balanced mating designs, and a higher plateau. This is primarily because of the reduced variance effective population size (Nei = 4). The loss level, however, was lower than that expected based on loss probability (1 - u(q)). The number of subpopulations with allele loss is greater than that with allele fixation, which is a result of using a low initial allele frequency in this simulation (q = 0.25).

The average allele frequency of populations increases faster and reaches a higher plateau as the variance effective population increases (Figure 3). The number of subpopulations with allele fixation increases faster with smaller effective population size. This brings out an intriguing question in tree breeding. Which of the two parameters, average allele frequency and the number of subpopulations with allele fixation, is more important in developing a long-term breeding strategy? If we chose average allele frequency, then we would opt for larger subpopulations. On the other hand, if we maintained a large set of smaller subpopulations, we would be able to obtain populations with fast allele fixation possibility. For a given individual

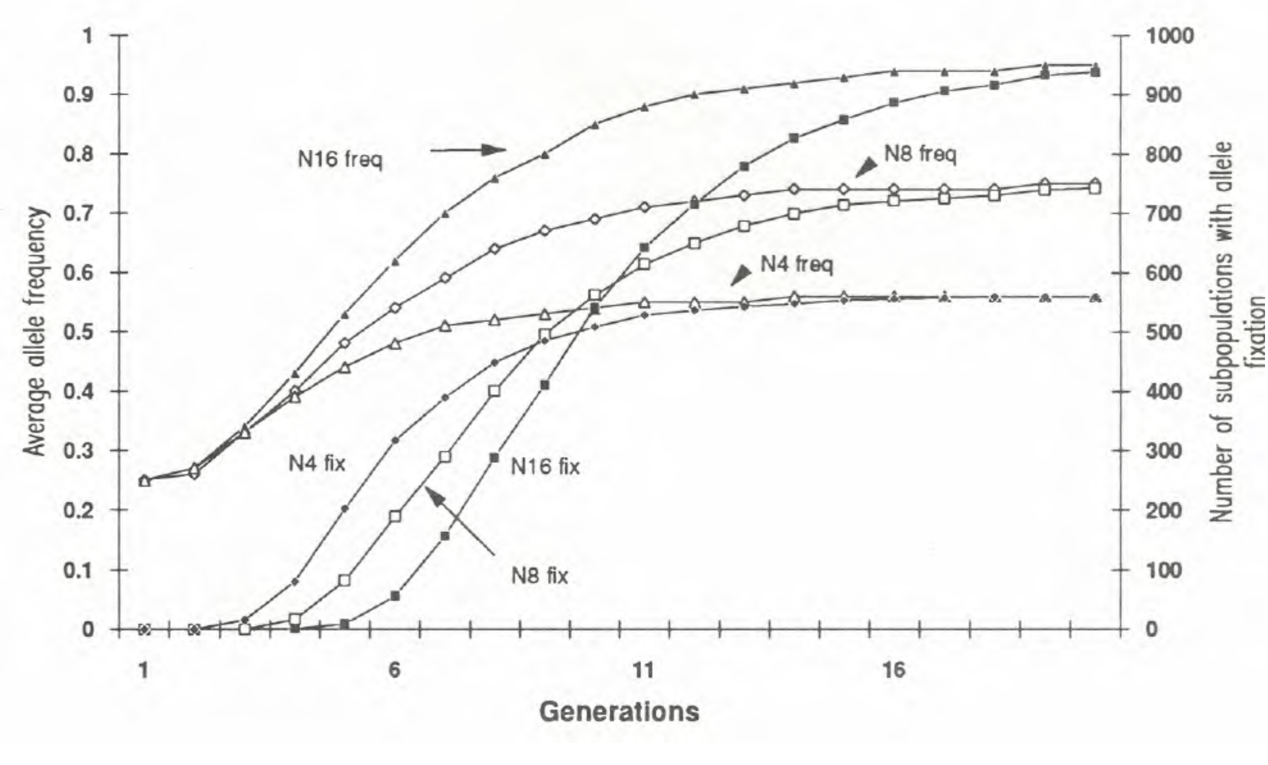

Figure 3. Average allele frequency and number of subpopulations with allele fixation under selfing.

subpopulation, the probability of allele fixation will be lower; but when all the subpopulations are combined, the overall probability of allele fixation can be maintained by hybridizing subpopulations when they reach their selection limits (Baker and Curnow 1969, Madalena and Hill 1972). As discussed before, selection limit may be viewed as a conceptual restriction, and breeders may choose the strategy that will allow the quickest response to selection. It is clear from Figure 3, that if we have a population with $N_{ev} = 1$, then the early rate of increase in the number of subpopulations with fixation will be greatest. However, $N_{ev} = 1$ implies selfing in monoecious species, which is often avoided by tree breeders.

Inbreeding would, no doubt, expose deleterious alleles in the breeding populations, and would be a source of concern for tree breeders. It is, however, desirable to purge deleterious alleles during early generations of tree breeding (Kang 1982, Kang and Nienstaedt 1987). Fisher (1965) emphatically argued for the importance of inbreeding and purging of deleterious alleles from breeding populations: "Practical breeders of farm animals are naturally deterred from a form of mating which is liable to produce animals undersized, unproductive, and prone to disease. Their reluctance is doubtless enhanced by a subconscious abhorrence of incest in their own species. Nevertheless, when an inbred line is formed from elite stock, it can contain no genes, however inferior it may appear, which were not present in its admired progenitors, nor can it hand any others on to its descendants. At the expense of some loss of appearance, and immediate utility, and with the real inconvenience of lower fertility, which may make the maintenance of such stocks difficult, the germ plasm may have been purified of many unnecessary defects, and the great boon of reliability of breeding performance gained."

This simulation shows that values of different breeding techniques vary depending on the perspectives used by tree breeders. There is a clear need to evaluate different breeding techniques with respect to long-term breeding, and then search for ways to combine short- and long-term breeding activities.

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