Loss of Genetic Diversity Monitored by Status Number

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Summary

We suggest monitoring genetic diversity (= effective number) in breeding populations with a new concept "status number", which is half the inverse of the average coancestry, including the coancestry of the individual with itself. Formulae and numerical evaluations are presented for status number, average coancestry and inbreeding for different breeding systems. Some properties of status number are discussed.

Our simulation study showed that genetic diversity was best preserved over generations by repeated selfing. Methods that use equal parental representation preserved genetic diversity better than panmixis. Small sublines preserved genetic diversity better than larger sublines, this effect was notable only when subline size was extremely small (like repeated full-sib mating). Rapid declining in status number with the first generation turn over seems unavoidable.

Key words: population size, family size, mating system, status number, inbreeding, coancestry, genetic diversity.

FDC: 165.3; 165.4; 165.5.

Introduction

The possible reduction of genetic diversity is a source of concern for many breeders. A number of problems are associated to loss of genetic diversity. Genetic drift leads to stochastic changes in unpredictable directions, alleles are lost, inbreeding and coancestry increase. A narrow genetic base gives the breeder little flexibility to meet changing demands and may result in forests with low genetic diversity. Genetic diversity is the raw material for breeding, thus sustainable long term breeding is dependent on preservation of genetic diversity. Evidently it is desirable that a breeding program monitors and manages genetic diversity.

To monitor and manage genetic diversity a quantitative measure of it is required. The census number of a breeding population evidently gives insufficient information, additional measures are needed. It is appealing to characterise the state of a population by an "effective number", which is the size an "ideal" population would have to be to get the same property as the considered population for some important aspect. Different alternatives were discussed by Lindgren et al. (1995). However, most conventional concepts like "effective population size" (Falconer, 1989; Caballero, 1994) are not applicable, as they measure a rate of change, or apply only in the first selection cycle.

The objective of this study is to introduce a measure of genetic diversity that we call status number; to develop the mathematics needed for deriving status number; and to investigate how status number is influenced by breeding systems, in particular those that are expected to preserve diversity.

Selection which allows different representation of the progeny of different parents is able to erode genetic diversity drastically even in a single generation (Wei, 1995). Methods to delay loss of genetic diversity are inbreeding (Lindgren and Gregorius, 1976), small sublines (King, 1993) and equal representation for different families (Wei, 1995). Choosing population replacements so families (or rather parents) are equally represented reduces diversity as slowly as possible (Dempfle, 1975). It is therefore of large interest to study how well diversity is preserved over generations in which each parent gives an equal contribution to the following generation, as the most efficient schemes for long term preservation of genetic diversity can be expected to be found among such schemes.

Theory

For definitions, symbols and formula we try to conform to Falconer (1989). We view populations from the forest tree breeder's point of view, but much of our algebra should be applicable to other situations. Many of the results derived concerning inbreeding and coancestry may be found in textbooks (Falconer, 1989), but for clarity we make the derivations rather complete, and inbreeding and coancestry formulations are needed for formulation of status number.

Definitions

The breeding population is the set of genotypes which mate and transmit genes to the next generation. The concept of population is ambiguous, sometimes it refers to certain individuals and sometimes it is regarded as a variable. In this study the term generally refer to certain coexisting individuals in the same generation. In a breeding program membership of the breeding population for existing individuals can be considered as a matter of definition.

Coefficient of inbreeding is the probability that the 2 homologous genes in an individual are identical by descent.

Coancestry (or coefficient of kinship) is the probability that genes sampled from different (or the same) individuals are identical by descent. An equivalent definition is the coefficient of inbreeding that would occur after mating.

Average inbreeding is the average coefficient of inbreeding over a population.

Average coancestry is the average coancestry over all pairs of population members (including individuals with themselves).

Another formulation: Probability that 2 genes sampled with replacement from the breeding population are identical by descent.

Note that the concepts of inbreeding and coancestry require that a reference base population is defined, in which (by definition) no inbreeding or relatives occur. We assume we are dealing with diploid genotypes, thus each individual carries 2 homologous genes at a particular locus.

Symbols

The following designations are used:

N Size of the breeding population (population size, census number).
The concept of status number

We suggest using

$$N_s = 0.5f,$$

where we call $N_s$ "status effective number" and $f$ is the average coancestry of the population (considering the coancestry of individuals with themselves). Burrows (1984) made a similar suggestion, but did not include the self-coancestry in the average coancestry. The status effective number will be regarded as "half the inverse of average coancestry". Status number can be verbally described as "the status number of unrelated and not inbred genotypes that has the same average coancestry as the considered population". Status number can be verbally described as "half the inverse of average coancestry". Status number can be verbally described as "half the inverse of average coancestry". Status number can be verbally described as "half the inverse of average coancestry". Status number can be verbally described as "half the inverse of average coancestry". Status number can be verbally described as "half the inverse of average coancestry".

The relative status number, $N_r$, is defined by

$$N_r = N_s / N.$$

Practical definitions of status number may be formulated: "the status number of unrelated and not inbred genotypes that has the same average coancestry as the considered population" and "the status number of the breeding population is the number of unrelated and not inbred genotypes in an ideal panmictic population, which would produce progeny with the same coefficient of inbreeding as the progeny of the genotypes of the breeding population following random mating." (Note that selfing and mating with relatives is allowed, even if there are no relatives selfing will cause inbreeding.) For tree breeders in particular an analogy with a seed orchard may be of help. "the status number of the breeding population is the number of unrelated and not inbred genotypes in an ideal panmictic seed orchard, which would result in the same coefficient of inbreeding as the crop from a panmictic seed orchard with the genotypes of the breeding population."

Formula for coancestry and inbreeding – general case

Consider the pedigree in figure 1.

$$f_{pq} = \frac{1}{2} (f_{AC} + f_{AD} + f_{BC} + f_{BD})$$

$$F = \frac{1}{2} (f_{AB} + f_{AC} + f_{AD} + f_{BC} + f_{BD} + f_{CA} + f_{CD})$$

Note that coancestry values are commutative, thus $f_{pq} = f_{qp}$. The following basic relationships apply:

$$f_{pq} = 0.25 (f_{AC} + f_{AD} + f_{BC} + f_{BD}) = F_X;$$

$$f_{AA} = 0.5 (1 + F_A);$$

$$f_{AB} = 0.5 (1 + F_P) = 0.5 (1 + f_{AB}).$$

In the founding population (base population, generation 1), we may assume that A and B are not inbred and unrelated founders and then the following values apply:

$$F_A = F_P = 0; f_{AB} = 0.5$$ and

$$f_{pp} = 0.5(1 + F_P) = 0.5(1 + f_{AB}).$$

Structure of coancestry and inbreeding

If the pedigree is known, the coancestry for any pair of members of the breeding population and their average can be calculated. There are no theoretical problems with retrospective calculations of average coancestry (Lindgren et al., 1995, for a method description), and the logistic problems are manageable with modern computers and algorithms. However, it is also desirable to make forecasts and predictions, and it is useful to have specific algorithms for simple situations. In the following we will derive formulas. Sometimes these are dependent on assumptions which will be discussed here.

After some generations predictions usually become complicated, because asymmetries appear between the members of the breeding population. They tend to be differently related to each other and inbred to varying degrees. We will in our calculations, when needed, assume that all pairs of individuals in a generation are equally related to their sibs and to their half-sibs and that they are equally inbred with coefficient of inbreeding $F$. This is correct for the founding first generation (t=1). It is also correct for simple symmetric breeding systems like repeated selfing and repeated full sib mating. There may be some other breeding structures for which it is correct, but generally it is not. There are, however, good reasons to believe that the lack of symmetry in real populations will not cause large errors in our numerical predictions as:

- Many equations are linear, and thus the effects of deviations in one direction will approximately be balanced by deviations in another.
- Variations between individual values will be of a stochastic nature and as the averages concerned will thus be less affected than individual values.
- Our applied calculations in this study will mainly deal with pure within family selection applied in a highly symmetric fashion.
- In a real multi-generation breeding program probably some considerations to avoid large differences in inbreeding would be made when matching breeding mates.
- For predictions in non-symmetric cases, more elaborate algebra than developed in this study would be required (Chessser et al.; 1993). Simulations can always be used instead of formula based predictions to get unbiased estimates. Symmetry requirement sometimes forces $N$ to be a multiple of 2 or 4.

Cases discussed here are when the breeding population is cycled from one generation to the next in distinct steps, and no distinction is made between males and females. A base population comprising $N$ genotypes is assumed. These genotypes are not inbred ($F=0$) and not related ($f=0$) and in genetic equilibrium (Hardy-Weinberg equilibrium), if not otherwise stated. These assumptions are convenient, but may often be relaxed. The members of the base population may be called founders.

All genes are assumed to be strictly neutral with respect to selection, and not affect the probability that their carrier will
belong to the breeding population. This assumption is frequently used and more or less necessary for quantitative predictions of inbreeding and coancestry.

**Derivations of coancestry and inbreeding for specific mating systems**

There are 7 distinct possible types of relationships applicable to the pedigree in Figure 1. Four of these comprise pedigrees including selfing (B=C=D=A; B=A and D=C; B=C=A; B=A). Of these only the first type (which we will call self sibs) will be considered. The 3 more conventional types of relationships, which do not involve selfing in their pedigrees, are full sibs (C=A and D=B), half sibs (D=A) and non sibs.

Consider a breeding population of size N, where P belongs to a family with m members. The average coancestry for an individual (P) is the sum of the contributions from this individual and all other individuals in the breeding population. The breeding population can for this purpose be seen as composed of 3 parts, the individual itself, its sibs and the rest. The contribution from these components will be:

\[ N_{ft} = f_{pp} + (m-1) \times \text{(coancestry for sibs to } P) + (N-m) \times \text{(coancestry for other than sibs to } P). \]

If all individuals in the breeding population have equivalent pedigrees the average over the whole breeding population will be the same as that for P. Note that one prerequisite for equivalent pedigrees is that families are of equal size. As the population is symmetric all members of a certain generation of the breeding population have equal inbreeding \( F_t = F_{t-1} \), and all pairs which are not sibs have the same coancestry. In general we try to derive average coancestry for one generation as a function of particular coancestry relationships in the previous generation.

**Coancestry for self sibs**

For many plant species, including many commercially important conifers, selfing is possible and usually results in viable plants, which have a potential value in breeding. Such sibs, which we call self sibs, form an uniparental progeny and are closer related than ordinary full sibs (Fig. 2).

For the first progeny generation:

\[ t = 2: \ m_f = 0.25 + 0.5m; \ N_s = m/(m + 0.5); \ N_r = m/(m + 0.5); \ f_{pq} = F_t = 0.5 \text{ and } A_p = 0.5. \]

**Repeated selfing**

Consider N selfing sublines with m = 1 family members. The coancestry between individuals belonging to different sublines is 0. The average coancestry and inbreeding will be

\[ N_{ft} = 0.75 + 0.25F_t \text{ and } F_t = 0.5(1 + F_{t-1}) \text{ for } t > 1. \]

**Constraints on matings**

In the following we assume that selfing does not occur in the breeding population. The members of the breeding population form pairs at random independently of relationship between them. Note that \( F_t = f_{AB} \text{ if } A \text{ and } B \text{ are mating partners} \), thus the average coancestry over all pairs in the previous breeding generation (excluding selfing) may be denoted \( F_t \).

**Coancestry for full sibs**

Consider a pair of full sibs (Fig. 3).

\[ f_{PQ} = 0.25(2f_{AB} + f_{AA} + f_{BB}) = F_x, \]

if \( F_{AA} = F_t \text{ and } F_x = F_{t+1} \text{ then } f_{PQ} = F_{t+1} = 0.25(1 + 2F_t + F_{t-1}). \]

Consider a breeding population comprising of a family with m full sibs

\[ m_f = 0.5(1 + f_{AA}) + 0.25(m-1)(2f_{AB} + f_{AA} + f_{BB}) = 0.5(1 + F_t) + 0.25(m-1)(2F_t + 0.5(1 + F_{t-1})). \]

If \( F_{t-1} = F_t = 0 \) (t = 2) then \( m_f = 0.25 + 0.25m; \ N_s = 2m/(m + 1) \) and \( N_r = 2/(m + 1). \)

**Repeated full sib mating**

Consider a breeding population of size N composed of unrelated sublines with repeated full sib mating (Fig. 4).

\[ f_{PQ} = 0.25(2f_{AB} + f_{AA} + f_{BB}) = F_x, \]

if \( F_{AA} = F_t \text{ and } F_x = F_{t+1} \text{ then } f_{PQ} = F_{t+1} = 0.25(1 + 2F_t + F_{t-1}) \text{ and } \]

Consider a breeding population of size N composed of un-related sublines with repeated full sib mating (Fig. 4).
Use formula 4 with $m = 2$.

$$m_f = N_f + 0.5(1 + F_t) + 0.25(2F_t + (1 + F_{t-1})) = 0.75 + F_t + 0.25F_{t-1} \quad (5)$$

Single pair mating with random pairing of parents

Consider a breeding system where in each generation $N$ genotypes are arranged in pairs. Each pair becomes parents to a full sib family. From each full sib family two individuals form the next generation of the breeding population (Fig. 4). The average $f_t$ is calculated using formula 2 with $m = 2$.

$$N_f = 0.5(1 + f_{AB}) + 0.25(2f_{AB} + f_{AA} + f_{BB}) + (N-2)0.25(f_{AC} + f_{AD} + f_{BC} + f_{BD}) = 0.25 + (N-2)F_t = 0.75 + (N-1)F_t + 0.25F_{t-1} \quad (6)$$

We need a recursive formula for $F_t$ in the offspring of the parent pairs. This is dependent on restrictions. It can be derived using $F_{t+1} = F_t + f_{PQ}$.

Consider a situation allowing for sib-mating but not selfing, when the inbreeding in the next generation can be derived from the average of coancestry considering the terms of formula 6 corresponding to when mating actually may occur.

$$F_{t+1} = 0.25(2F_t + 1 + F_{t-1}) + (N-2)F_t = 0.25 + (N-1.5)F_t \quad (7)$$

We also need a recursive formula for $F_t$ in the offspring of the parent pairs. This is dependent on restrictions. It can be derived using $F_{t+1} = F_t + f_{PQ}$. If the parent pairs are formed at random

$$F_{t+1} = 0.25(1 + Ft) + 0.5(1 + Ft_{t-1}) + (N-3)F_t = 0.25(1 + F_{t-1}) + (N-1.5)F_t \quad (8)$$

There is no difference between single pair mating and double pair mating as far as the accumulation of coancestry and inbreeding is concerned, probably they can often be regarded as equivalent.

The relative status effective number is

$$N_e = 1/(2F_t).$$

An ideal random mating population

An ideal random mating population is useful as a reference. Such a population is different to the populations discussed above, where mating was at random except that selfing was not allowed, but progeny size was kept constant to 2. In an ideal random mating situation, selfing is allowed and the progeny is Poisson-distributed (if the population is large, else binomial) among parents.

In an ideal population the average coancestry in one generation will be the average coefficient of inbreeding in the next, thus

$$F_t = f_{t-1}.$$ 

After $t$ generations of random mating where base population is $t = 1$ the forecasted inbreeding and coancestry is

$$F_{t+1} = F_t$$

The coancestry can be expressed (A is the common parent)

$$f_{PQ} = 0.25(f_{AC} + f_{AA} + f_{BC} + f_{BA}) = F_{X}$$

Consider a breeding population comprising of a family with $m$ half sibs

$$m_f = 0.5(1 + f_{AB}) + 0.25(m-1)(f_{AC} + f_{AA} + f_{BC} + f_{BA}) = 0.5(1 + F_t) + 0.25(m-1)(3F_t + 0.5(1 + F_{t-1}))$$

The coancestry can be expressed as a function of family size related to number of families ($N_f$), parents in the first generation ($N_1$); and offspring in the second generation ($N_2=m$).

<table>
<thead>
<tr>
<th>Family size</th>
<th>Self sib, $N_1=1$</th>
<th>Full sib, $N_1=2$</th>
<th>Half sib, $N_1=1+m$</th>
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<tr>
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<td>$N_1=m/(m+.5)$</td>
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Figure 5. – Pedigree showing the relationships between half sibs.

Table 1. – The status number of a family as a function of family size related to number of families ($N_f$); parents in the first generation ($N_1$); and offspring in the second generation ($N_2=m$).
\[ F_{t+1} = f_t = 1 - (1 - 0.5/N) t \] (FALCONER, 1989, note that FALCONER regards the founders as \( t = 0 \)). If \( t/N \) is small, then \( F_t = f_t \approx 0.5t/N \) and \( N_r \approx 1/t \). In particular after the first generation shift (\( t = 2 \)), \( N_r \approx 0.5 \).

### Results

Values for inbreeding, average coancestry and status number have been calculated for a number of situations (Table 1 to 4, Figure 6). Formulas given in the tables 1 to 4 are easily derived from the theory section above. Similar inbreeding calculations have been presented frequently, but the authors are not aware of similar calculations for average coancestry and status number is a new concept.

The status number of a single family with parents which are not inbred or related is shown as a function of family size in Table 1. If a single selection is made from each family, the status number will be lower for self sibs than other families. This is because inbred individuals may carry identical copies in both their homologous genomes. The preservation of the parental genes will depend on the size of the progeny, but all parental genes will not be preserved even if the progeny is large. If several selections are made per family, half-sib families are able to provide high status number. This is because each selection from such families introduce new founders into the breeding population, and has relevance only in the presence of a large pool of unrelated potential fresh founders.

In Table 2 to 3 development over a number of generations are derived for systems where the parents give equal contributions to the next breeding generation.

| Table 2. – Average inbreeding, average coancestry and relative status number for some mating systems with close inbreeding. Note that for repeated selfing \( F_t = f_{t-1} \) and for repeated full sib mating, \( F_t = f_{t-2} \). Status number for full sib mating is \( 2N_r \). |
|---|---|---|---|---|---|---|---|---|
| Entity | \( F_t \) | \( f_t \) | \( N_r = N/N \) | \( F_t \) | \( f_t \) | \( N_r = N/N \) |
| Formula Generation | \( 0.5(1 + F_{t+1}) \) | \( 0.75 + 0.25F_{t+1} \) | \( 0.25(1 + 2F_{t+1} + F_{t+2}) \) | \( 0.75 + F_{t+1} + 0.25F_{t+2} \) | \( 2 \) | \( 1 - 2t/N \) |
| \( t = 1 \) | 0 | 0.5 | 1 | 0 | 0.25 | 1 |
| 2 | 0.500 | 0.750 | 0.667 | 0 | 0.375 | 0.667 |
| 3 | 0.750 | 0.875 | 0.571 | 0.250 | 0.500 | 0.500 |
| 4 | 0.875 | 0.938 | 0.533 | 0.375 | 0.594 | 0.421 |
| 5 | 0.938 | 0.969 | 0.516 | 0.500 | 0.672 | 0.372 |
| 10 | 0.998 | 0.999 | 0.500 | 0.826 | 0.886 | 0.282 |
| \( \rightarrow \) | -1 | -1 | -0.5 | -1 | -1 | -0.25 |

| Table 3. – Status number and inbreeding in a population composed of 2 progenies, from each of the members in the previous generation, as a function of generation and population size. Formulas used: \( N_r = 0.75 \times (N-1) F_t + 0.25F_{t-1}; \ F_{t+1} = (N-1)^2 F_t + (N-1.5)F_t \) (selfing excluded); \( N_r = 0.5/(1 + (t-3)/4) \). |
|---|---|---|---|---|---|
| Entity | \( N_r = 0.5/(1 + (t-3)/4) \) |
| Generation \( t = 1 \) | \( N = 4 \) | \( N = 10 \) | \( N = 50 \) | \( N = 200 \) | \( N = \infty \) |
| \( F_t \) | \( N_r \) | \( F_t \) | \( N_r \) | \( F_t \) | \( N_r \) | \( F_t \) | \( N_r \) | \( F_t \) | \( N_r \) |
| 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0.067 | 0 | 0.067 | 0 | 0.067 | 0 | 0.067 | 0 | 0.067 |
| 3 | 0.083 | 0.500 | 0.028 | 0.500 | 0.0051 | 0.500 | 0.0013 | 0.500 | 0.0005 |
| 4 | 0.153 | 0.407 | 0.054 | 0.402 | 0.0102 | 0.400 | 0.0025 | 0.400 | -0.400 |
| 5 | 0.218 | 0.347 | 0.080 | 0.338 | 0.0152 | 0.334 | 0.0038 | 0.334 | -0.333 |
| 10 | 0.474 | 0.219 | 0.197 | 0.195 | 0.0399 | 0.184 | 0.0100 | 0.182 | -0.182 |
| \( \rightarrow \) | -1 | -0.125 | -1 | -0.05 | -1 | -0.01 | -1 | -0.0025 | -0 |

\( F_{t+1} = f_t = 1 - (1 - 0.5/N) \) (FALCONER, 1989, note that FALCONER regards the founders as \( t = 0 \)). If \( t/N \) is small, then \( F_t = f_t = 0.5t/N \) and \( N_r = 1/t \). In particular after the first generation shift (\( t = 2 \)), \( N_r = 0.5 \).
members of the breeding population are mated at random, but selfing is excluded is presented in table 3. This may be called restricted panmixis. The relative status number is almost independent of the population size down to N = 4. It appears that it is only at low population sizes such as N = 2 or N = 1 (Table 2) that the small population size really influences the evolution of status number over generations (compare with Table 3). This difference between small and big sublines increases with time. Thus small sublines is a way of preserving status number. However, the difference between sublines of size 4 and sublines of infinite size does not become important before generation 10. Inbreeding becomes substantial after a few generations. Inbreeding will become large with small sublines even if the increase of inbreeding by time is minimized.

In random mating (panmictic) populations (Table 4) coancestry and inbreeding accumulate faster over generations and the relative status number is lower than for populations where parents contribute equally (Table 3). This is illustrated in figure 6, where 4 different alternatives are compared over generations for a constant population size 50. The 3 top alternatives are theoretically interesting as they represent strategies which minimizes the loss of genetic diversity over generations under different inbreeding management strategies.

Discussion

Properties of status number

Status number has the following characteristics:

- It can never be lower than 0.5, and it is 0.5 for a homozygous line (a gamete).
- It generally declines at generation shifts, but there are exceptions.
- It is only dependent on the current state of a population, not the history or scenarios about the future or its gender. It measures a state but not a rate of change. It measures a position but not a speed.
- The sum of the status number of unconnected sublines of similar size and structure is close to that of the pooled population.

Many other formulations of effective number than the status number focus on average speed of change over a period of time or number of generations, as discussed by Lindgren et al. (1995), and are unsuitable to study how change develop by time, in particular if several generation shifts are involved.

BURROWS’ effective population size concept

The concept status number is similar to a suggestion by Burrows (1984). He defined $N_B = 1/rQ$, where $0.5rQ$ is the average pairwise coancestry of the selected group (excluding self pairings). It is therefore the average inbreeding coefficient of progeny obtained by random mating among selected individuals (excluding self matings). He applied the measure only to single generation turn over. The difference between our and Burrows’ approach is that we consider also the individual itself for calculation of average coancestry. This modification makes an important difference in applicability. If the coancestry with the individual itself is excluded, $N_B$ will be infinite (or undefined) if there are no relatives, and $N_B$ easily exceeds the census number. Calculations by Wei and Lindgren (1994, their Table 1) demonstrate some undesirable features with $N_B$, like that the effective population size sometimes increases by decreasing census number.

We believe status number is well suited for the needs of forest tree breeding, which still operates in the early generations of improvement, pedigrees to the wild founders are still short. Forest tree breeding seldom keep to the same mating designs over time or over the whole breeding population, and the breeding population is usually structured in unconnected sublines or divided into base and elite populations.

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**Table 4.** Inbreeding and status number in a random mating population (selfing occurs and progeny size varies at random) as a function of generation and population size. Formulas used: $F_{t+1} = 1 - (1 - 0.5N^t)^t$; $N_r = 0.5(NN^t)$. 

<table>
<thead>
<tr>
<th>Entity</th>
<th>$N=10$</th>
<th>$N=50$</th>
<th>$N=200$</th>
<th>$N \rightarrow \infty$</th>
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Decline of the status number over generations

Actually, there is a conceptual problem with status number that it declines fast initially. This may be an artifact created by the concept of an initial population with unrelated founders. In a way members of a species are always related. The status effective number drops to approximately half following a single generation of random mating (Fig. 6, Tab. 4), but it takes approximately 5 generations to reduce the status number to half of the value it has at generation 5 instead of just a single generation. This points at the speed of decay is very dependent on the definition of the founding population. Another way of expressing it is that it is not possible (selfing excepted) to keep the status number on more than 40% of the census number, and it requires much effort to keep it above 20% of the census number for some generations (Fig. 6). From this point of view, status number may be particularly suitable for forest tree breeding, where only a few well-pedigreed generations have passed since domestication started by composing breeding populations from the whole range of natural populations, and thus even the fast initial decay of status number is of interest to follow in detail.

A general goal of gene conservation can be formulated as keeping the accumulation of coancestry at a low level, and thus to keep the status number high. Three tools for this purpose are demonstrated in the tables and figure provided. The first one is to make the contributions to the next generation as equal as possible among parents, the second is to keep sublines of the breeding population disconnected and the third is to encourage early inbreeding.

Random contributions to the progeny with an average of 2 progenies per parent (Tab. 4) resulted in considerably lower relative status numbers than if there are 2 progenies per parent (Tab. 3). It does not matter if the progenies are full-sibs or half-sibs. The breeding population needs to be approximately 75% larger if the same status number is to be obtained after 10 generations by a random mating population compared to a population where each parent has 2 offspring. It seems possible to conserve status number considerably better in artificial breeding populations than panmixis may be restricted than in random mating panmictic populations (Fig. 6).

The relative status number is increased by decreasing the size of breeding groups, but it was not very dependent on the size as long as it was rather big (Tab. 3 and 4). Thus, structuring a population in large sublines (N ≥ 10) is not an efficient strategy for preserving status number, at least not if parental contributions are not very variable. The dependence of population size increases by generations and is smaller following equal contributions than random mating.

Extremely small population sizes associated with strong inbreeding (N = 1 or 2) are able to preserve a high relative status number (Tab. 2). Sib mating is more efficient for gene conservation than mating with less related individuals, and by a program of repeated full sib mating less than half the breeding population is required compared to random mating. To avoid high coancestry without expanding the size of the breeding population repeated sibbing is by far the most efficient scheme. However, inbreeding depression often make schemes with close inbreeding unrealistic.

Status number is lost even if there is a perfect balance, so the members of one generation contribute equally to the next. Thus even if within-family selection (Demmple, 1975) is the most conservative strategy, it is really not powerful enough to

Figure 6. – Decline in status number over generations for a population of size 50 cycled by different breeding systems. “Selfing” refers to repeated selfing (50 sublines of size 1). "Full sibbing" refers to repeated mating of full sibs (25 sublines of size 2). "Restricted panmixis" refers to a system where each parent give raise to 2 progeny, which mate at random (no selfing, subline size 50). "Panmixis" refers to random mating, where the number of progeny per parent is binomial distributed (selfing allowed, subline size 50).
prevent a fast erosion. Two third of the status number will be lost in most programs within a few breeding generations. This emphasizes the large "cost" by increased coancestry and lost status number occurring at generation turn over. Forest tree breeders have options to make cycling earlier or later during the life-cycle of the trees, the status number decrease at cycling is a strong argument that there are conservational reasons to keep rather long rotation times in breeding operations rather than maximizing gain per generation.

Use of half sib families can be an efficient instrument to introduce more founders into the breeding population at an early stage (Tab. 1), however, this works only as long as there really are new unrelated founders introduced; it is not applicable on a situation like the forest tree breeders' polycross.

The neutrality assumption

One may ask about the evolutionary significance of the fast drop in status number. Counter-balancing forces must be important, such as mutation, disruptive selection, selection against inbreeding, selection against homozygotes, balanced polymorphism or frequency-dependent selection. In the real world it is likely that the assumption that genes are neutral means that many predictions based on pedigrees will go wrong. This is a disadvantage for traditional effective numbers and inbreeding as well as for status number.

If selection forces are at work some genes may make it more likely that their carriers are selected, and other genes may be linked with those. Chromosome fragments from ancestors carrying such genes may be more common than indicated by the pedigree, and that would increase coancestry. Such effects may be of importance even at within-family selection. It may be noted that natural tree populations seem to have F = 0 as some sort of natural base-line for the breeding population, and the founder concept is thus adequate. The excess of homozygotes formed by selfing and mating between relatives seem to die off between fertilization and maturation. This indicates that the assumption of neutrality may often be badly fulfilled.

The introduction of molecular markers makes it possible to actually measure coancestry and compare the predictions and measurements (BERNAUDO, 1995). Such comparisons will probably help to identify the situations when predictions are unreliable.

Acknowledgements

We appreciate helpful comments from R. BURDON and T. J. MULLIN on the manuscript.

Literature


Buchbesprechungen


Beim einem derartig umfangreichen Werk bleiben Ungenaugkeiten nicht aus. Zum Beispiel ist unter dem Stichwort WWF die Umbenennung in World Wide Fund for Nature nicht berücksichtigt worden. Im Themenkomplex zur Europäischen


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