Loss of Genetic Diversity Monitored by Status Number

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(Received 27th December 1995)

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 overs 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 text books (Falconer, 1989), but for clearity 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).

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N_e	Effective population size (effective number is used as a synonym).
N_s	Status number.
N_r	Relative status number, $N_r = N_s/N$.
F_x	Coefficient of inbreeding for individual X.
F	Coefficient of inbreeding (average coefficient of inbreeding).
f_{PQ}	Coancestry between individuals P and Q.
f	Coancestry (average coancestry).
t	Time in number of generations. If t is used as a subscript it gives the generation of the breeding population. Note that entities in the same equation may refer to different generations, in which case we indicate generation as a subscript. t=1 is the base population, the first generation breeding population. Note that in this paper the founders are regarded as generation 1. (Sometimes they are regarded as generation 0.)
m	Number of individuals which form a sib group.

The concept of status number

We suggest using

$$N_s = 0.5/f, \qquad (1)$$

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 abbreviated "status number". 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.*

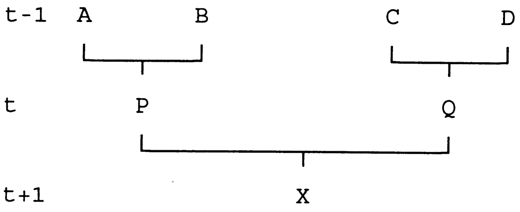

Figure 1. – Pedigree showing the relationships between the individuals P and Q in generation t and their parents and progeny.

Basic relationships

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

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

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

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

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:

$F_1 = F_A = F_B = 0$; $f_{AB} = 0$, $f_{AA} = 0.5$ and $f_1 = 0.5/N$

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 assymmetries 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_t. 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 (CHESSER 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 ($F_1 = 0$) and not related ($f_1 = 0$) 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 neccessary 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:

$$Nf_t = f_{pp} + (m-1) \bullet \text{(coancestry for sibs to P)} + (N-m) \bullet \text{(coancestry for other than sibs to P)}. \quad (2)$$

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 $F_B=F_A=F_{t-1}$, 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*).

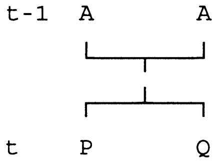

Figure 2. – Pedigree showing the relationships between self sibs.

The coancestry for a pair of self sibs (*Fig. 2*) in a bisexual species will be

$f_{PQ}=f_{AA}=F_x$,

and the inbreeding following mating of self sibs

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

A recursive relationship can be developed,

let $F_A=F_{t-1}$ and $F_p=F_t$

then $F_t=0.5(1+F_{t-1})$.

Consider a breeding population in generation t comprising a family with m self sibs. Average f_t considering the individual P as a member a family of m self sibs will be

$$mf_t = f_{pp} + (m-1)f_{AA} = 0.5(1+0.5(1+F_{t-1})) + 0.5(m-1)(1+F_{t-1}) = 0.25 + 0.5m + F_{t-1}(0.5m-0.25)$$

For the first progeny generation

$t=2$: $mf_t=0.25+0.5m$; $N_s=m/(m+0.5)$;$N_r=m/(m+0.5)$; $f_{PQ}=F_x=0.5$ and $F_p=0.5$.

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

$Nf_t=0.75+0.25F_{t-1}$ and $F_t=0.5(1+F_{t-1})$ 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 $F_t=f_{AB}$ if A and B are mating partners (*Fig. 1*), 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*).

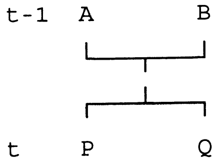

Figure 3. – Pedigree showing the relationships between full sibs.

The coancestry for a pair of full sibs will be

$f_{PQ}=0.25(2f_{AB}+f_{AA}+f_{BB})=F_X$,

if $F_B=F_A=F_{t-1}$ and $F_X=F_{t+1}$ 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

$$mf_t = 0.5(1+f_{AB}) + 0.25(m-1)(2f_{AB}+f_{AA}+f_{BB}) = = 0.5(1+F_t) + 0.25\,(m-1)(2F_t + 2 \bullet 0.5(1+F_{t-1})) \quad (4)$$

If $F_{t-1}=F_t=0$ ($t=2$) then $mf_t=0.25+0.25m$; $N_s=2m/(m+1)$ 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*).

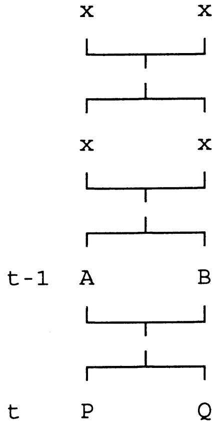

Figure 4. – Pedigree for repeated full sib mating.

Use formula 4 with $m = 2$.

$$mf_t = Nf_t = 0.5(1 + F_t) + 0.25\,(2F_t + (1 + F_{t-1})) = 0.75 + F_t + 0.25F_{t-1} \qquad (5)$$

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 $m = 2$.

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

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

Consider a situation allowing for sibmating 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.

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

Coancestry for half sibs

Consider a pair of half sibs (*Fig. 5*).

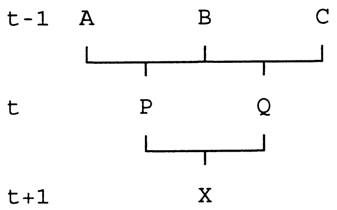

Figure 5. – Pedigree showing the relationships between half sibs.

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

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

If $F_{t-1} = F_t = 0$ $(t = 2)$ then $f_{PQ} = F_X = 0.125$; $mf_t = 0.375 + 0.125m$; $N_s = m/(0.25m + 0.75)$ and $N_r = 1/(0.25m + 0.75)$.

Note that in the present circumstances half-sib families introduce new founders, each member of a half-sib family is associated with an increase of the number of founders.

Double pair mating with random pairing of parents

Consider a breeding system where in each generation N genotypes are arranged so each genotype is mated to 2 different mates. From each full sib family 1 individual is accepted as a member of the next generation of the breeding population, and in that way a new breeding population generation of size N is recruited. The average f_t is calculated using formula 2 for halfsibs noting that $m = 3$ (P with 2 halfsibs).

$$Nf_t = 0.5(1 + f_{AB}) + 2 \bullet 0.25(f_{AC} + f_{AA} + f_{BC} + f_{BA}) + (N-3)0.25(f_{AC} + f_{AD} + f_{BC} + f_{BD}) = 0.5(1 + F_t) + 0.5(3F_t + 0.5(1 + F_{t-1})) + (N-3)F_t =$$
$$= 0.75 + (N-1)\,F_t + 0.25F_{t-1}$$

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

$$F_{t+1}(N-1) = 0.5(3F_t + 0.5(1 + F_{t-1})) + (N-3)F_t =$$
$$= 0.25(1 + F_{t-1}) + (N-1.5)F_t.$$

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

$$N_r = 1/(2fN).$$

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

Table 1. – The status number of a family as a function of family size related to number of families (=1); parents in the first generation (N_1); and offspring in the second generation ($N_2 = m$).

	Self sib, $N_1 = 1$		Full sib, $N_1 = 2$			Half sib, $N_1 = 1 + m$		
Family size	Per family = per parent	Per offspring	Per family	Per parent	Per offspring	Per family	Per parent	Per offspring
m	$N_s = m/(m+.5)$	$N_r = 1/(m+.5)$	$N_s = 2m/(m+1)$	$m/(m+1)$	$N_r = 2/(m+1)$	$N_s = mN_r = m/(.75+.25m)$	$mN_r/(1+m)$	$N_r = 1/(.25m+.75)$
1	0.667	0.667	1	0.5	1	1	.5	1
2	0.800	0.400	1.333	0.667	0.667	1.600	0.533	0.800
3	0.857	0.286	1.500	0.750	0.500	2.000	0.500	0.667
4	0.889	0.222	1.600	0.800	0.400	2.286	0.457	0.571
5	0.909	0.182	1.667	0.833	0.333	2.500	0.417	0.500
10	0.952	0.095	1.818	0.909	0.182	3.077	0.280	0.308
$\to\infty$	$\to 1$	$\to 0$	$\to 2$	$\to 1$	$\to 0$	$\to 4$	$\to 0$	$\to 0$

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 $2N_r$.

	Repeated selfing, m=N=1			Repeated full sib mating, m=N=2		
Entity	F_t	f_t	$N_s=N_r$	F_t	f_t	$N_r=N_s/N$
Formula Generation	$0.5(1+F_{t-1})$	$0.75+0.25F_{t-1}$		$0.25(1+2F_{t-1}+F_{t-2})$	$\frac{0.75+F_t+0.25F_{t-1}}{2}$	$\frac{1}{2f_tN}$
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
$\to\infty$	$\to 1$	$\to 1$	$\to 0.5$	$\to 1$	$\to 1$	$\to 0.25$

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: $Nf_t=0.75+(N-1)F_t+0.25F_{t-1}$; $F_{t+1}(N-1)=0.25(1+F_{t-1})+(N-1.5)F_t$ (selfing excluded); $N_r=0.5/(Nf_t)$.

	N=4		N=10		N=50		N=200		$N\to\infty$
Entity	F_t	N_r	F_t	N_r	F_t	N_r	F_t	N_r	$N_r=0.5/(1+(t-3)/4)$
Generation t=1	0	1	0	1	0	1	0	1	1
2	0	0.667	0	0.667	0	0.667	0	0.667	0.667
3	0.083	0.500	0.028	0.500	0.0051	0.500	0.0013	0.500	0.500
4	0.153	0.407	0.054	0.402	0.0102	0.400	0.0025	0.400	$\to 0.400$
5	0.218	0.347	0.080	0.338	0.0152	0.334	0.0038	0.334	$\to 0.333$
10	0.474	0.219	0.197	0.195	0.0399	0.184	0.0100	0.182	$\to 0.182$
$\to\infty$	$\to 1$	$\to .125$	$\to 1$	$\to .05$	$\to 1$	$\to 0.01$	$\to 1$	$\to 0.0025$	$\to 0$

$F_{t+1}=f_t=1-(1-0.5/N)^t$ (FALCONER, 1989, note that FALCONER regards the founders as t = 0).

If t/N is small, then $F_{t+1}=f_t\approx 0.5t/N$ 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.

Results concerned with forced inbreeding is presented in *table 2*. The average inbreeding, average coancestry and relative status number were calculated over a number of generations for repeated selfing and full-sib mating. The status number decreased fast towards the minimum 0.5 in these small sublines, slower for full-sib mating that for selfing. Note that the relative status number is independent of N.

Results for a breeding system where each parent transmits 2 progeny to the next generation breeding population and the

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: $F_{t+1}=f_t=1-(1-0.5/N)^t$; $N_r=0.5/(Nf_t)$.

	N=10		N=50		N=200		$N \to \infty$
Entity	F_t	N_r	F_t	N_r	F_t	N_r	$N_r=1/t$
Generation t=1	0	1	0	1	0	1	1
2	0.050	0.513	0.010	0.503	0.002	0.501	→0.5
3	0.098	0.351	0.020	0.337	0.005	0.334	→0.333
4	0.143	0.270	0.030	0.254	0.007	0.251	→0.250
5	0.185	0.221	0.039	0.204	0.010	0.201	→0.200
10	0.370	0.125	0.086	0.105	0.022	0.101	→0.100
→∞	→1	→.05	→1	→0.01	→1	→0.0025	→0 as 0.5/N

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*).

The status number declines fast by generations in the early generation turn overs. 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 be interpreted as the size of a population of not inbred and unrelated genotypes (see above).
- It can be derived for any population which is linked by pedigree to a known initial population with known coancestry and inbreeding. An algorithm for its calculation in a general situation was presented by Lindgren et al. (1995) based on algorithms for inbreeding presented by Tier (1990).
- It can be calculated or predicted as a function of the mating and selection tactics. For several cases mathematical formulas are appliable (*Table 1* to *3*), while for other situations Monte-Carlo simulation can be used (Mullin and Park, 1995).
- It is the same as the census number for a population with unrelated not inbred genotypes.
- It can never by higher than the census number.
- 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.
- It is based on and follows logically from the well established coancestry concept.

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 0.5 rQ 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 appliability. 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.

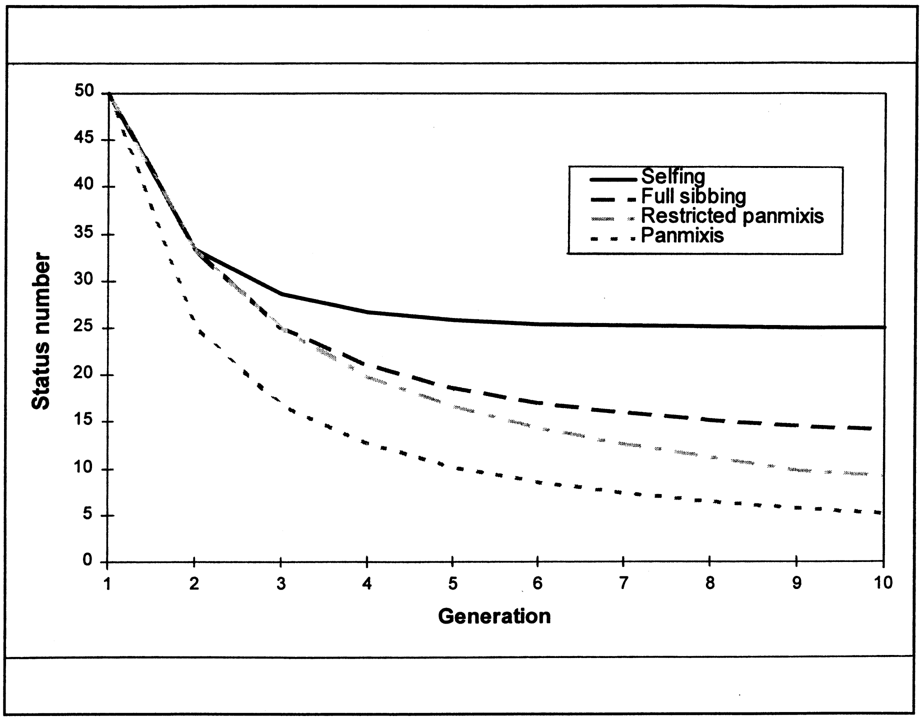

Figure 6. – Decline in status number over generations for a population of size 50 cycled by different breeding systems. "Selfing" refers to repeated selfing (50 sublines of size 1). "Full sibbing" refers to repeated mating of full sibs (25 sublines of size 2). "Restricted panmixes" refers to a system where each parent give raise to 2 progenies, which mate at random (no selfing, subline size 50). "Panmixis" refers to random mating, where the number of progenies per parent is binominal distributed (selfing allowed, subline size 50).

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 cencus 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 there 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 ($N \geq 10$) 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 selfing 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 (DEMPFLE, 1975) is the most conservative strategy, it is really not powerful enough to prevent a fast erosion. Two third of the status number will be lost in most programs within a few breeding generations. This emphasises 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 fullfilled.

The introduction of molecular markers makes it possible to actually measure coancestry and compare the predictions and measurements (Bernardo, 1993). 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.

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Buchbesprechungen

Springer Umwelt Lexikon. Herausgegeben von M. Bahadir, H. Parlar und M. Spiteller. 1995. Springer Verlag, Berlin, Heidelberg, New York. ISBN 3-540-54003-2. 1176 Seiten mit 423 Abbildungen, 724 Formeln und 283 Tabellen. Gebunden DM 290,–.

Für das Verständnis der Vorgänge um die Umwelt gehört die Beschreibung ungestörter Systeme und deren Veränderungen. Der Schwerpunkt des vorliegenden Umweltlexikons weist eine enge Verknüpfung der Begriffe Chemikalien und Umweltbelastungen aus. Chemikalien sind in Abhängigkeit ihrer Konzentration und ihrer synergistischen Wirkungen als potentielle Schadstoffe in den Umweltmedien (Boden, Wasser, Luft) und mit Blick auf die menschliche Gesundheit (u. a. Nahrungskette, Körperkontakt, Abfall) von grundlegender Bedeutung. Die Herausgeber beschreiben das Verhalten von chemischen Verbindungen in der Umwelt sowie die vielfältigen Wechselwirkungen zwischen den chemischen Verbindungen und der belebten und unbelebten Natur. Ebenso werden Methoden vorgestellt, die der Erforschung des Verhaltens von Chemikalien in der Umwelt dienen, und es werden Konzepte zur Bewertung der potentiellen Gefährlichkeit von Chemikalien für die Umwelt besprochen. 64 Wissenschaftler definieren und beschreiben ca. 9000 Stichworte aus etwa 100 Sachgebieten der Umweltwissenschaften. Die Auswahl der Stichworte erfolgte einerseits wegen ihres direkten Bezugs zur Umwelt. Andererseits wurden zentrale Begriffe einer ansonsten für die Umwelt wichtigen Disziplin miterläutert, selbst wenn diese den direkten Bezug zur Umwelt nicht erkennen lassen. Hierdurch wird vermieden, daß das Nachschlagewerk nur gemeinsam mit Fachlexika, z. B. der Naturwissenschaften oder der Technik, benutzt werden kann. Im Anschluß an die Beschreibung der Stichworte wird bei vielen zusätzlich noch auf weiterführende Literatur verwiesen. Dem Springer-Umweltlexikon ist ein Geleitwort von Prof. Dr. Klaus Töpfer, ehemaliger Bundesminister für Umwelt, Naturschutz und Reaktorsicherheit, vorangestellt.

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

Union werden die Begriffe EG und EU nicht immer einheitlich angewendet. So lautet u. a. der Titel der Abbildung auf Seite 357 EU-Organe; in der Abbildung taucht jedoch mehrmals die Abkürzung EG auf. Die unter der Gruppe der Zytostatika angeführten Mitosegifte hemmen nicht allgemein die Zellteilung sondern die Mitose durch Nichtbildung der Spindel. Trotz dieser kleinen Fehler ist das Springer-Umweltlexikon jedem als Nachschlagewerk uneingeschränkt zu empfehlen, der in dem breit gefächerten Feld der Umweltwissenschaften (z. B. Abfallwirtschaft, Arbeitsschutz, Arbeitsmedizin, Biodiversität, Luftreinhaltung, Ökosystemanalyse, Ökotoxologie, Raumplanung, Umweltgesetzgebung) tätig ist.

M. LIESEBACH (Grosshansdorf)

Electrophoresis of Enzymes. Laboratory methods. By G. M. ROTHE. 1994. Springer Press, Berlin, New York. ISBN 3-540-58114-6. ISBN 0-387-58114-6. 307 pages. Hardcover DM 98.–, ÖS 764.40; sFr 98.–.

Electrophoresis of enzymes and isozymes has developed to a standard method of analysing the genetic structure of living organisms. Since 25 years increasingly this method has been applied in tree improvement and there is probably no important tree species in improvement programmes whose genetic structure hasn't been analysed by isozymes. Despite modern PCR and other techniques, isozymes will render good services in characterisation and identification of single or populations of trees. The book introduces in the first chapter the different classes of enzymes and isozymes. The second chapter is devoted to the extraction of enzymes from different types of tissues, going from microorganisms over animal, blood, to plant cells and continuing to the separation of subcellular organelles. The third chapter is a very exhaustive chapter on the separation of enzymes in different media (cellulose acetate, starch gel, polyacrylamide gel, 2-D-electrophoresis). The fourth chapter covers sodium dodecylsulphate electrophoresis (SDS). The fifth chapter explains well the chemistry of enzyme visualization and gives a large number of staining recipies. Chapter 6 is the largest chapter and gives detailed staining protocols for about 100 different enzymes. Chapter 7 deals with data evaluation in terms of population genetics by showing how allozymes are determined in isozyme patterns and goes into the basics of population genetics. At the end of each chapter references are given and a subject index at the back of the book. The book is useful to new as well as experienced workers using isozymes in tree genetic work, however the scope of the book goes above that. The book is highly recommended as a profound up-to-date text for any lab analysing genetic structures by allozymes.

G. VON WUEHLISCH (Grosshansdorf)

Die Weiden von Mittel- und Nordeuropa. Bestimmungsschlüssel und Artbeschreibungen für die Gattungen *Salix* L. 2., überarbeitete Auflage. Von D. und E. LAUTENSCHLAGER-FLEURY, 1994. Birkhäuser Verlag, Basel, Boston und Berlin. ISBN 3-7643-2994-7. 172 Seiten mit über 200 s/w-Abbildungen und zahlreichen Strichzeichnungen. Gebunden DM 58,–.

Das im Jahre 1989 in 1. Auflage erschienene Werk „Die Weiden der Schweiz und angrenzender Gebiete“ liegt jetzt in einer überarbeiteten und erweiterten Neuauflage vor. Die Gliederung des Stoffes wurde beibehalten. Innerhalb der Kapitel wurden einige redaktionelle Änderungen vorgenommen und neue Ergebnisse der Weiden-Beobachtungen und -Untersuchungen eingearbeitet. Im allgemeinen Teil des Buches wird auf die Standorte, die Morphologie, die Bedeutung und Nutzung der Weiden sowie auf die Systematik eingegangen. Ausführliche Bestimmungstabellen für niedrig wachsende Spalierweiden bzw. für Strauch- und Baumweiden, letztere getrennt für männliche oder weibliche Blüten und für Sommerblätter ermöglichen das Erkennen der Arten. Im speziellen Teil beschreibt die 2. Auflage 34 mitteleuropäische sowie 2 eingeführte Strauch- oder Baumweiden, 4 Spalierweiden und 2 Weidenbastarde auf jeweils 2 Seiten. Damit werden im Gegensatz zur 1. Auflage 3 weitere Weiden beschrieben. Neu aufgenommen wurde auch ein Bestimmungsschlüssel und die Beschreibung von 12 Weiden aus Schwedisch-Lappland. Das Werk ermöglicht damit den Vergleich zwischen alpiner und nordischer Weiden. Die klaren Beschreibungen stellen die wesentlichen Merkmale der jeweiligen Art deutlich heraus und werden durch zahlreiche Zeichnungen ergänzt. Auf der dem Text gegenüberliegenden Seite sind u. a. Blätter, Blüten und Zweige in qualitativ sehr guten Schwarzweißfotografien abgebildet. Eine kurze Literaturübersicht und getrennte Register mit wissenschaftlichen und deutschen Namen der mitteleuropäischen und nordschwedischen Weiden, für letztere sind zusätzlich die schwedischen Namen aufgeführt, runden diese ausgezeichnete Weidenflora ab.

M. LIESEBACH (Grosshansdorf)

Das große Buch der Ziergehölze. Von A. BÄRTELS. 1995. Verlag Eugen Ulmer, Stuttgart. ISBN 3-8001-6593-7. 320 Seiten mit 1520 Farbfotos. DM 68,–.

Mit 1520 Farbfotos werden etwa 930 Gehölzarten und -sorten abgebildet, die für Gärten von Bedeutung sind. Das Buch enthält so gut wie alle in Mitteleuropa heimischen Nadelbaum-, Laubbaum- und Straucharten sowie weitere fremdländische Arten, die an das hiesige Klima angepaßt sind. In alphabetischer Reihenfolge der lateinischen Namen werden in der Regel auf jeder Seite 4 Arten abgebildet. Bei sortenreichen Arten wurden zusätzliche Bildtafeln eingefügt. Zu jeder Abbildung gehört ein knapp gefaßter Text, der über Wuchseigenschaften, Form und Farbe der Blätter, Blüten und Früchte sowie über die Blütezeit informiert. Hinweise findet man auch auf die natürliche Verbreitung und die Standortsansprüche unter Angabe von Kennziffern der Lebensbereiche nach P. KIERMEIER. Die Texte sind informativ und stellen das Wesentliche einer Art oder Sorte heraus. Die Abbildungen sind größtenteils von guter Qualität. Das Typische einer Pflanzenart mit nur einem Foto richtig zu treffen, ist natürlich schwierig. So ist manche Art nur zu identifizieren, wenn man sie kennt. Bedauerlich ist es, daß sich in Publikationen unserer Zeit die Druckfehler immer mehr häufen, was auch vor diesem Buch nicht halt macht. So irritieren vor allem Fehler wie diese: *Berberis vulgaris* mit 10 cm bis 12 cm langen Früchten, *Viburnum farreri* mit 16 m breiten Blüten, usw. Insgesamt kann dieses schöne Buch aber sehr empfohlen werden. Es gibt viele Anregungen, kann die stärkere Verwendung von Gehölzarten in Gärten und Parks fördern und ist nach Umfang, Inhalt und Zahl der Farbabbildungen schon wegen seines relativ niedrigen Preises gegenwärtig konkurrenzlos unter den deutschen Gehölzbüchern.

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Herausgeberin: Bundesforschungsanstalt für Forst- und Holzwirtschaft: Schriftleitung: Institut für Forstgenetik, Siekerlandstrasse 2, D-22927 Grosshansdorf — Verlag: J. D. Sauerländer's Verlag, Finkenhofstrasse 21, D-60322 Frankfurt a. M. — Anzeigenverwaltung: J. D. Sauerländer's Verlag, Frankfurt am Main. — Satz und Druck: Graphische Kunstanstalt Wilhelm Herr, D-35390 Giessen
Printed in Germany.

ISSN 0037-5349