

Selection effects on diversity and genetic gain

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TIIVISTELMÄ: VALINNAN VAIKUTUKSET MONIMUOTOISUUTEEN JA JALOSTUSHYÖTYYN

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Four different methods of truncation selection were studied in a population consisting of a large number of large unrelated full sib families of equal size: phenotypic selection, family selection, within-family selection and combined index selection (optimal weighting of individual and family performance to get the best prediction of breeding value). Methods were developed for calculating diversity ("relative effective family number") for the different selection methods. Numerical calculations were made for genetic gain and diversity. Model assumptions are additive gene control and normal distribution. Combined index maximized gain at a given selection intensity. Phenotypic was good at high heritabilities and between family at low heritabilities. Loss of diversity was strongly dependent on selection method and selection strength. Compared at the same diversity, genetic gain was lower for combined index compared to phenotypic. There is a need for methods combining the goals gain and diversity.

Tutkittiin neljää erilaista valintamenetelmää: fenotyypistä, perhevalintaa, perheen sisäistä valintaa ja yhdistettyä indeksivalintaa (jossa yksilön ja perheen menestystä painotetaan optimaalisesti parhaan jalostusarvon ennusteen saamiseksi). Perusjoukkona oli teoreettinen populaatio, joka koostuu suuresta määrästä isoja ja keskenään yhtäsuuria mutta ei-sukulaisia täyysisarjälkeläistöjä. Kehitettiin menetelmä laskea diversiteetti kutakin valintatapaa varten. Jalostushyödyille ja diversiteetille tehtiin numeeriset laskennat. Mallin oletuksia ovat additiiviset geenivaikutukset ja normaalijakautuma. Yhdistetty indeksivalinta maksimoi jalostushyödyn, kun valinnan voimakkuus on vakio. Fenotyypinen valinta on tehokas, kun heritabiliteetti on alhainen, kun taas korkeilla heritabiliteettiarvoilla perhevalinta on tehokas. Valintatavalla ja valinnan voimakkuudella on suuri vaikutus diversiteetin laajuuteen. Jos diversiteetin määrä vakioidaan, yhdistetty valinta tuottaa pienemmän jalostushyödyn kuin fenotyypinen valinta. Tarvitaan menetelmä, joka yhdistää suuren jalostushyödyn ja geneettisen monimuotoisuuden.

Keywords: truncation selection, combined index, phenotypic selection, inbreeding.
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1 Introduction

Selection of genetically superior individuals results in a genetic gain, but also in a loss of genetic diversity. Comparisons for gain have been devoted much more attention than consequences on diversity when designing breeding strategies. The main reason may be that gain is closely associated with economic return, while diversity is a more diffuse concept with less clear definition and significance. Another reason is that the consequences of selection on diversity and their relation to gain have not been well described in a quantitative way allowing optimal decisions to be made, not even for the first generation.

This study focuses on diversity as a result of first generation selection decisions. These circumstances are of particular relevance to forest-

ry. Genetic diversity is of special interest for forestry as the crop is seen as a part of nature, and as management options to counteract diseases and pests by other means than diversity are strictly constrained. First generation decisions are of particular interest simple because the trees have such a long generation time that many breeding programs still operate in the first generations. An understanding of the effects of selection in a single generation is of course a prerequisite for understanding multi-generation changes.

The aim of the paper is a quantitative analyses of the effect of different methods of truncation selections on diversity and to investigate relations between diversity and gain.

2 Model and formulas for predicting selection effects

A population with a family structure is considered. Apart from that there is no coancestry or inbreeding. The population is composed of a number of families, each of equal size. There are values for all members. A member is selected on the basis of its own value (phenotype) and the average value of the family it belongs to. There are only additive gene effects. Family size and number of families will be considered large in numerical calculations, so general conclusions can be made. A continuous normal distribution of breeding values and residuals will be assumed when required for calculation. Numerical calculations will be made for full-sibs (generated from a population in Hardy-Weinberg equilibrium). It is trivial to use the same methods for half-sibs or for other similar types of group structure. The initial diversity is of little importance for the model, as the relative diversity is considered.

Selection will have two important consequences: (1) The genetic average value will change, this is conventionally measured as gain (genetic gain, response to selection) (2) Change in diversity, this will be measured by relative effective number of families.

In the following methods for predicting these

consequences are discussed for four major selection methods.

Four basic methods of truncation selection are studied: between-family selection; within-family selection; phenotypic selection; and combined index selection. The first two methods are trivial special cases. For the symmetric population we consider, combined index will constitute the "best" prediction of breeding value. When the family size is large the family heritability will be close to one.

The formulas for expected response to selection for the different selection methods are shown in Appendix 1. The gain formulas are given as functions of total selection intensity, phenotypic variance and individual heritability.

We used relative effective family number to define genetic diversity of selected individuals. Effective family number is defined as the square of the sum of the contributions from all families divided by the sum of the squares of the contributions from each family (Robertson 1961). Here this reflects both inbreeding and variance considerations (Kimura and Crow 1963). The relative effective family number, N_r , is the effective family number divided by the initial census family number. This measure of diversity is 1

Table 1. Variance components.

Variance component	Total	Between families	Within families
Symbol	σ_p^2	$\sigma_f^2 = \sigma_x^2$	σ_w^2
General	σ_p^2	$K\sigma_p^2$	$V\sigma_p^2$
Current case ^a	1	$0.5h^2$	$(1 - 0.5h^2)$
Combined index			
General ^b	σ_1^2	$(b_1 + b_2)^2\sigma_f^2$	$b_1^2\sigma_w^2$
Current case ^a	$h^2 / (2 - h^2)$	$0.5h^2$	$0.5h^4 / (2 - h^2)$

^a Large full sib families.

^b $b_1 = h^2(1 - k) / (1 - K)$; $b_2 = h^2(k - K) / K(1 - K)$

before selection and $0 < N_r < 1$ after selection. The measure is conveniently scaled for studying selection effects on diversity. Numerical calculation is easy for a specific situation with real data. However, we evaluate the consequences more in general below, and then the mathematics will become more complex.

In the following we consider the continuous case. There is an infinite number of families of infinite size. The family mean is designated x . A family with mean x will get the share $P(x)$ selected, which is a cumulative probability density distribution. The probability density of family means expressed as a function of family mean value is $f(x)$. Then we have:

$$N_r = P^2 / \int_{-\infty}^{\infty} [P(x)]^2 f(x) dx \quad (1)$$

where the average selected proportion is

$$P = \int_{-\infty}^{\infty} P(x) f(x) dx \quad (2)$$

To evaluate these expressions, the share selected from a family must be expressed as a function of family mean x .

For between-family selection the corresponding diversity is exactly equal to the selected proportion. Within-family selection leads to the same contribution for all families to the next generation. The diversity will be 1. More so-

phisticated calculations must be applied for phenotypic and combined index selection.

For numerical evaluations of expectations, it is only justified to deal with normal distributions. The normal probability density function is denoted ϕ and the corresponding distribution function Φ . Family values and within-family residuals are normally distributed with mean 0. The total variance is standardized to unit value. The variances are compiled in Table 1.

Phenotypic truncation selection means selection of individuals with values above the truncation point, x_T . Family means are ignored. The fraction of values above x_T for a family with mean x and standard deviation σ_w will be

$$P(x) = \Phi(-(x - x_T) / \sigma_w) \quad (3)$$

The distribution of family values can be expressed as

$$f(x) = \phi(x / \sigma_x) \quad (4)$$

Using expressions (3) and (4) in formulae (1) and (2) will enable us to calculate diversity and the corresponding average selected proportion at a given truncation point. With proper transformations of x_T , x , σ_x and σ_w , where x is the value of the combined index rather than the phenotypic value, the same type of substitutions can be made for combined index values (cf. Table 1).

3 Numerical results

Numerical calculations were made for the case of selection of individuals from a population consisting of a large number of unrelated full sib families ($r = 0.5$).

The relations between the different methods were independent on selected proportion (selection intensity), but dependent on heritability. Combined index selection gave the highest gain (Table 2), and that is the main advantage of combined index selection.

For within-family selection $N_r = 1$ for all P ($0 < P$) and h^2 . For between-family selection $N_r = P$ for all h^2 . The diversity for phenotypic and combined index selection is shown as a function of the selected proportion in Fig. 1. When $h^2 = 1$, phenotypic and combined index selection gave the same result as the phenotype was identical to the breeding value. When heritability was small, phenotypic selection tended to be similar to within-family selection while combined index selection tends to be more similar to family selection, particularly as $h^2 \rightarrow 0$, $N_r = 1$ for phenotypic selection and $N_r \rightarrow P$ for combined index selection. The ranking of methods

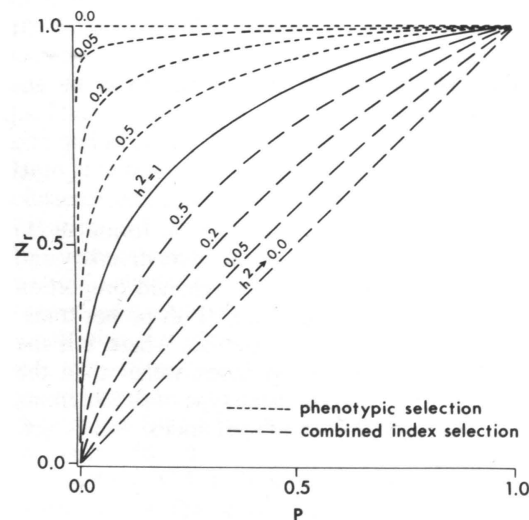


Fig. 1. The diversity (relative effective family number) as a function of the selected proportion for phenotypic and combined index selection. Relationships are given for different individual heritabilities (h^2).

Table 2. Ranking of the merits of different truncation selection methods when compared at the same selected proportion; 1 is best and 4 is worst.

Method	Genetic gain				Diversity		
	$\rightarrow 0$	0-0.5	0.5-1	h^2 1	$\rightarrow 0$	0-1	1
Phenotypic	4	3	2	1	1	2	2
Between-family	1	2	3	4	4	4	4
Within-family	4	4	4	4	1	1	1
Combined index	1	1	1	1	4	3	2

for their ability to preserve diversity is shown in Table 2. Phenotypic selection did not reduce diversity much, unless an intensive selection was combined with a high heritability. Combined index selection had a strong negative impact on diversity, especially when heritability was low and selection was intense. Phenotypic selection was far superior to combined index

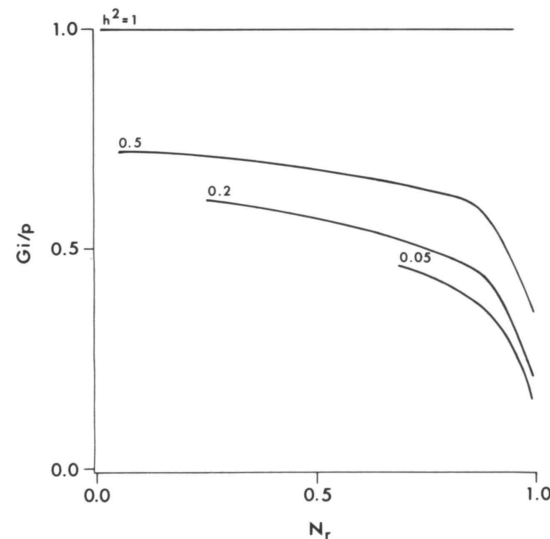


Fig. 2. The ratio of gain between combined index selection and phenotypic selection as a function of diversity for some values of h^2 .

selection at low heritabilities and high selection pressure.

The most interesting alternatives for comparison are phenotypic and combined index selection, as the other two can be regarded as trivial border cases. The ratio between their gain when compared at the same change of diversity is demonstrated in Fig. 2. Compared at the same

4 Discussion and conclusions

Loss of diversity is strongly dependent on selection method and selection intensity. Selection methods which are efficient for gain are not efficient for preserving diversity if comparisons are made at the same selection pressure.

Both high diversity and high gain are desirable characteristics of a method. If two methods are equal for one characteristic, the method superior for the other is evidently the best. Thus, as phenotypic selection is superior for gain when compared to combined index selection at the same diversity, phenotypic selection is a better method than combined index selection. Thus, for the case studied, it has been proven better to use a rather bad breeding value prediction (phenotype) as criteria for selection than the best breeding value prediction (combined index). We think this observation deserves some thought among breeders. The reason for this paradox is that different uses of pedigrees are confounded. Constraining selection of related individuals in some intelligent way may be more important than accurate breeding value predictions. The paradox may be a reflection of that none of the selection methods is optimal.

Combined index selection is still the best choice if the practically possible selection pressure is more constraining than diversity considerations, in particular if heritability is low and high short time gain is the main objective.

For the numerical calculations we consider infinite populations, while real world populations are finite. In small populations stochastic effects like genetic drift becomes important. The main aim of this paper is to study effects of selection, and from that point of view the effects of limited population is a disturbance which will tend to hide the selection effects. We have made simulations and based on that we think

N_r , the genetic gain was lower for combined index selection than for phenotypic selection. There was no difference between the methods when $h^2 = 1$, but the difference grew larger when h^2 became smaller. Combined index selection could be regarded as inferior to phenotypic selection for gain. The inferiority was considerable if the heritability was not close to 1.

that the infinite approximation is reasonable good for predicting selection effects in populations of the size common in most forest tree breeding programs.

The methods and numerical values presented here may find several applications. E.g. our "diversity" is directly proportional to inbreeding in a seed orchard, thus the inbreeding in a seed orchard with forward selections can be predicted as a function of selection method, P and h^2 .

There are some strategies to counteract the loss of diversity. Dempfle (1975) suggested that within-family selection would be the most beneficial in the long run as a higher selection limit would be achieved. This is supported by the present investigation. However, within-family selection is no compromise but a complete surrender to the diversity aspect, and means a low gain for a large number of initial generations. Constraints can be formulated for a maximum number of selections per family, but if such decisions are made arbitrarily without a theory behind, they may be far from optimum. Another strategy is sublining. There is still a problem what happens within sublines.

A better compromise than any of the methods discussed above, is likely to exist between the desire to achieve high gain and the desire to avoid loss of diversity. "Linear deployment", as suggested by Lindgren (1986, 1991), may be such a compromise.

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Appendix 1. Formulas for expected response to selection.

General formula: $R_j = i\sigma_p h^2 L_j$,

where j (P,B,W or I) symbolizes method of truncation. Formulas for L_j are listed.

Method	j	L_j		
		Small families	Large families ($n \rightarrow \infty$)	
			General	Full sib ($r = 0.5$)
Phenotypic	P	1	1	1
Between-family	B	k / \sqrt{K}	\sqrt{r} / h	.707 / h
Within-family	W	v / \sqrt{V}	$(1-r) / \sqrt{(1-rh^2)}$.5 / $\sqrt{(1-.5h^2)}$
Combined index	I	$\sqrt{\frac{K(1-k) + k(k-K)}{K(1-K)}}$	$\sqrt{\frac{h^2(1-2r) + r}{h^2(1-rh^2)}}$.707 / $\sqrt{h^2(1-.5h^2)}$

Denotations used are developed more in detail in the following:

General	$k = [1 + (n-1)r] / n$	$K = [1 + (n-1)t] / n$	$v = (n-1)(1-r) / n$	$V = (n-1)(1-t) / n$
$n \rightarrow \infty$	r	t	(1-r)	(1-t)
“, full sib	.5	.5h ²	.5	1 - .5h ²

$v\sigma_p^2 h^2$ = the share of all additive variance and $V\sigma_p^2$ = the share of all phenotypic variance, which occurs within family; k and K have corresponding characteristics.

- n = family size
i = intensity of selection (selection differential in standard measure)
 σ_p = standard deviation of phenotypic values of individuals
h² = heritability of individual values
r = correlation of breeding values; with full-sib families r = 0.5; half-sib families r = 0.25
t = correlation of phenotypic values of members of families; t = rh².