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On a genetic assessment of the adaptedness of forest reproductive material

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Abstract Assessment of the adaptedness of forest tree populations and the reproductive material derived from them is largely based on historical records and observations on extant distributions of phenotypic traits. Genetic criteria are, if at all, usually considered only in the form of heuristic reasoning. A main reason for this situation lies in the lack of operational concepts that clearly distinguish between viability selection and adaptation. The present paper makes an attempt towards this aim by showing that the adaptational optimization of viability selection processes rests on three constituent features which allow minimization of the implied overall mortality at each relevant selection stage and across all of these stages. Indices are developed that measure the degree of adaptational optimization of viability selection. The concept and its indices are applied to an analysis of isozyme data obtained for an approved beech seed stand and reproductive material derived from this stand. An approved seed stand is required to be adapted, and this property is expected to be preserved in the derived reproductive material. Our observations revealed substantial degrees of overall reductions and suboptimal selection during the production process. Suboptimality is unevenly distributed over the stages of the production process, and stages of strongest suboptimality vary among gene loci. A preliminary explanation is given for a conspicuous effect on selective optimality that is consistently observable at the stage of seedling development across all loci.

Keywords Forest reproductive material · Source population · Viability selection · Assessment of adaptedness · Beech · Isozymes

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Introduction

Basically, the reason for a population to be declared as a source population for obtaining reproductive material (approved seed stand) is to be found in its special phenotypic characteristics (usually of economic, ecological, etc., interest) and in its adaptedness to the local environmental conditions. Reproducibility of the phenotypic characteristics in the progeny of the source population is therefore one of the central demands of the forest practice for afforestation and reforestation. As the expression of phenotypic traits is determined by genotype and environment, the reproductibility of a trait in the reproductive material depends on the degree to which its genetic structure and environmental conditions resemble those of the source population. The problems arising with the specification of the genotype-environment interactions that produce the phenotype (Lundkvist 1982; Namkoong 1988) explain why it is common practice to confine demands for the use of reproductive material to sufficient resemblance of its environmental conditions with those of the source population (see Anonymus 1979; Kleinschmit and Svolba 1996). By this it is hoped that the material holds the adaptedness that is a prerequisite for the development of the desired phenotypes.

On the other hand, it is well-recognized that the genetic component of resemblance between reproductive material and its source population is at least as important as the environmental component (Adams and Campbell 1982). In fact, since the environmental conditions in which the reproductive material is grown are under limited control, an essential part of the phenotypic resemblance with the source populations can be guaranteed by genetic resemblance only. It is therefore important to make sure that the process of production of reproductive material does not essentially alter the genetic composition of the source population. However, simply guarding constancy of genetic structures during the production process may be inappropriate. An obvious reason is that changes in genetic structures may be necessitated by the natural forces of adaptation acting in the source popula-

tion during the same ontogenetic stages that are treated in the production process.

Hence, in order to preserve the degree of adaptedness realized in the source population, genetic structures may indeed be required to change during the production process of reproductive material. Only in very exceptional situations, however, can these changes be observed in the source population so that they could provide a reference of adaptedness. Even if such observations were possible, it would still be difficult to assess the adaptational value of the realized viability selection processes. All viability selection entails population reduction, and there seems to exist no concept which distinguishes between adaptationally superior and inferior forms of viability selection. Methods of analysis, which are solely based on comparisons with existing and approved references of adaptedness may therefore be of limited use. Operational methods must explicitly consider the relation between changes in genetic structures, viability selection, and the assessment of adaptedness. Since population persistence is the primary criterion of adaptedness, and since this depends critically on the degree of population reduction that is inevitably associated with viability selection, the latter two aspects deserve special attention in any attempt to assess adaptational processes.

The present paper tries to establish and apply an approach towards this aim by developing, in a first step, a concept of adaptational optimality that relates viability selection to population reduction. In a second step, this concept is used to derive a set of indices of adaptational optimality which can be applied to observations on changes of genetic structures over several stages of selection. The paper then concludes with an application of the thus obtained analytic tool to the results of a study on the effects of the production process on reproductive material from an approved beech seed stand.

Viability selection and adaptedness

As a rule, adaptedness to variable but sufficiently regular environmental conditions requires the preservation of genetic variability on which selection can continually operate. Adaptedness that is achieved by viability selection basically shows in the extent of population reductions from the zygotic to the adult (reproductive) stage. These reductions leave enough adult individuals for avoiding sizable random losses (drift) in the transmission of genetic variation to the next generation. High degrees of adaptedness to the prevailing conditions can, in this sense, be achieved by restricting the population reduction to an extent that is indispensable for the selective adjustments to be made. Of course, maximum adaptedness is reached if all population members survive. If selective adjustments are made and the population is reduced, these adjustments become manifest in a change of relative frequencies of genotypes during each stage of selection.

Gregorius and Degen (1994) showed that the minimum population reduction required for changing genotypic frequencies P_i at the beginning of a viability selection stage to frequencies P_i' at the end of this stage is,

$$L := 1 - \min_i \frac{P_i}{P_i'}.$$

L is frequently called the "selection load" but will more explicitly be referred to as *minimum mortality.* Accordingly,

$$S := 1 - L = \min_i [P_i / P_i']$$

equals the maximum fraction of survivors realizable for the given selective change. By analogy, S will be termed *maximum survival.*

Making use of the concept underlying L and S, three constituent features can be distinguished which relate viability selection to adaptedness. The first refers to the fact that any reduction of the population size exceeding L results from the absence of capacity for adaptation to the extant environmental conditions. The implied *nonadaptive deaths* are thus an indication of suboptimal adaptedness. One basic criterion for the assessment of adaptedness is therefore provided by the difference between the overall population mortality and the minimum mortality.

The second feature is to be found in the *selection process*, i.e. in the ways in which selection changes between selection stages. If, for example, a genotype is selectively advantageous at a particular stage and disadvantageous at the following stage, its relative frequency increases first and then decreases again with the possible result of no change from the beginning of the first to the end of the second stage. Hence, the population would in this case of opposing selection have experienced a reduction with no effect on the distribution of the genotypes. The two-stage selection process is thus adaptationally suboptimal. Selective neutrality in each of the two stages could have avoided this loss. This establishes a second criterion for the assessment of adaptedness, which will be elaborated in more detail.

The third feature accounts for the fact that for a given viability selection regime, the minimum mortality depends on the *initial frequencies*, i.e. the zygotic frequencies, P_i. The lowest minimum mortality is then achieved through adjustment of the zygotic frequencies towards concentration on the genotypes with the largest viabilities. However, complete adjustment could lead to genetic fixation, which is undesirable because of the implied loss of adaptability. The constraints imposed by the mechanisms of the mating system and by the modes of inheritance provide, however, efficient means of preventing genetic fixation. In the case of constant genotypic viabilities, these constraints may imply the existence of a stable genotypic equilibrium distribution. The equilibrium situation then specifies the maximum realizable adaptedness of the population for the given selection regime. Since the equilibrium is a dynamic one, adaptedness includes permanent adaptability to regular environmental condi-

tions. The adaptedness decreases with losses of the genetic variation that is required for preserving the adaptability to these conditions.

In principle, each of these three features of adaptational optimality of viability selection can be studied for any gene locus or combination of gene loci. If no frequency changes are observed at a set of gene loci, these loci can be stated to be not involved in the adaptational process and thus provide no adaptational capacity. Otherwise, the loci can be directly (functionally) involved in the selection process or they may be affected by stochastic (or structural) associations with the former (random changes need not be considered, since they can always be traced back to random or chaotic changes in the selective environment). The selection effects that are transported through stochastic or structural associations will generally be smaller than those observable at the directly involved loci. The selection observable at any locus or combination of loci may therefore be conceived of as a lower bound for the actual sum of the effects at the functional loci. The analysis of our experimental results will be based on this principle.

Assessing adaptedness in the producing process of reproductive material

As was argued above, source populations are expected to show high degrees of adaptedness to their environmental conditions and should ideally fulfill the conditions for autochthony in order to be suitable for the production of reproductive material. The aim is then to make sure that the methods of production of reproductive material to not compromise the adaptedness inherent in its source.

A well-adapted source population is likely to be close to genetic equilibrium for many gene loci and to be adaptationally optimized for its selection processes. By this is minimizes its overall mortality as argued above. Hence, taking a sample of seed from the source population and subjecting it to a process of production of reproductive material, it should be warranted that the minimum mortalities realized at each stage of that process do not distinctly exceed the zygote-to-adult minimum mortality of the source population. Otherwise, some of the adaptedness of the source population is lost in the reproductive material. Therefore, minimum mortalities that remain below the zygote-to-adult minimum mortality of the source population during all stages of the production process are necessary in order to maintain the presumed high adaptedness of the source population.

However, the longevity of forest trees effectively prohibits direct estimates of zygote-to-adult minimum mortalities. Both stages are amenable to observation only through adult individuals and their offspring and thus in reversed order. An approach towards an indirect estimation of these mortalities can be derived from the expectation that a well-adapted source population is close to genetic equilibrium for many loci. In this case, genetic structures at specified developmental stages recur over the generations. This fact allows us to project the genetic structure of the present seed production back into the past so that the genetic structure of the present adult stage can be viewed as resulting from viability selection that acted on this projection. In the above representation of the minimum mortality L, the P_i and P_i' would then refer to genotypic frequencies among the seed and among the adults producing these seed, respectively. While this approach may help in studying the second and third of the above-listed features of adaptational optimality, it provides no information about the overall population mortality and, therefore, allows for no conclusions as to the first feature.

Characterization of adaptationally optimal selection processes

To arrive at a formal representation of the above necessary condition for preservation of the adaptedness of the source population in the reproductive material, let L° be the zygote-to-adult minimum mortality in the source population, and the $P_i(k)$ and $P_i'(k)$ be the genotypic frequencies at the beginning and at the end of the k-th selection stage. At this point no distinction need to be made between stages in the source population and stages in the production process of the reproductive material. Then the minimum mortality in the k-th stage equals $L_k=1-\min_i[P_i(k)/P_i'(k)]$. Similarly, the minimum mortality from the first (the zygotic stage) to the n-th stage equals $L_n^\circ=1-\min_i[P_i(1)/P_i'(n)]$. Moreover, let $S^\circ=1-L^\circ$, $S_k=1-L_k$ and $S_n^\circ=1-L_n^\circ$ denote the maximum fractions of survivors resulting as the complement of the respective minimum mortalities. By the above convention these quantities constitute proportions of maximum survival of or to the respective stages. It follows that

$$S_n^\pi := \prod_{k=1}^{n} S_k$$

equals the maximum survival to the n-th selection stage considering all intermediate stages. The actual rate of survival can under no circumstances exceed S_n^π. In the following, S_k, S_n° and S_n^π will be referred to as amounts of *primary*, *gross* and *net maximum survival*, respectively.

It is also intuitively obvious that $S_n^\pi \le S_n^\circ$, since the intermediate stages of selection included in S_n^π can decrease but never increase maximum survival to stage n (see Appendix for a mathematical proof and further details). Thus, *an n-stage selection process is adaptationally optimal if* $S_n^\circ=S_n^\pi$; the selection process is adaptationally suboptimal if S_n° distinctly exceeds S_n^π. The quotient

$$\zeta_n := S_n^\pi / S_n^\circ$$

can therefore be used as an *index for measuring the adaptational optimality of the selection process* up to the n-th stage. This index summarizes the above second and third feature of adaptational optimality.

Moreover, ζ_n decreases (not always strictly) with increasing number n of stages, and the quotient ζ_{n+1}/ζ_n

suggests itself as a measure for the differences between ζ-values in two successive stages. In fact, this quotient specifies the degree of optimality of selection *at* the $(n+1)^{st}$ stage (see Appendix). Through this property, ζ_{n+1}/ζ_n allows characterization of the selection process with respect to the relative effects of individual stages on the optimality of selection.

Preservation of adaptedness in the reproductive material

Recall that $S°$ denotes the gross maximum survival from the zygotic to the adult stage in the source population. Moreover, for reasons of comparability, consider the stages in the production process of the reproductive material as possible selection stages in the source population and assume that the adaptedness of the source population is preserved in the production process. One then expects that for the m, say, selection stages in the production process $\zeta_m=1$ both in the reproductive material and in the source population. Taking the last stage m as the start for a single large selection stage that covers the remaining period up to adulthood in the source population, the primary maximum survival in this final stage equals $S_{m+1}=\min_i[P_i'(m)/P_i^a]$, where P_i^a denotes the genotypic frequencies in the adult population. Thus, the assumption of adaptationally optimal selection in the source population yields $S_m^\pi \cdot S_{m+1}=S°=S_{m+1}^\circ$.

In summary, these considerations suggest an assessment of the preservation of the adaptedness of the source population in the reproductive material on two levels: (1) a level that is internal to the production process and uses the index ζ_m for assessment, and (2) a level that extends this to the whole zygote-to-adult phase of the source population and uses the index $\zeta=S_m^\pi \cdot S_{m+1}/S°=\zeta_{m+1}$ for assessment. If any of these quotients is distinctly smaller than 1, the production process of the reproductive material is unlikely to have preserved the adaptedness of the source population. In addition, since the actual overall fraction of survivors of the production process cannot exceed S_m^π, this quantity is an important indicator for the quality of the production process and the associated risks of random genetic drift.

Materials and methods

To study the production process of reproductive material in 1995 we chose to harvest seed, using a vibration harvester, from 127 trees of an approximately 120-year-old approved seed stand of beech (*Fagus sylvatica* L.) in Meinberg-Horn. Of the 1000 kg of seed harvested 3 kg was sown in a nursery in 1996 and subsequently analyzed for changes in genetic structure over several stages of the production process. There are seven stages: (1) harvesting of seed (starts with the overall seed production of the source population and ends with the harvest), (2) management of seed (cleaning, storage), (3) preparation of seed for sowing, (4) germination (6-week-old seedlings), (5) 2-year-old plants, (6) 3-year-old plants, (7) adult trees (in the source population, about 120 years old). For details of the sampling methods and sample sizes applied to the various stages, see von Werder (2000).

Genotypic structures are obtained for the following isoenzyme gene loci: IDH-A, MDH-B, MDH-C, 6PGDH-A, PGM-A, MNR-A, GOT-B, LAP-A and PGI-B. In the following an asterisk will be applied to MDH-B and LAP-A, i.e. MDH-B* and LAP-A*, in order to indicate lumping of the alleles 3 and 4 (at the locus MDH-B) and alleles 1 and 2 as well as 4 and 5 (at the locus LAP-A) (von Werder 2000). This proved to be useful in view of the statistical problems detailed in the following section.

Statistical problems

The estimates of S_n° and particularly of S_n^π may be subject to substantial statistical error on two successive levels. The first level concerns the sensitivity of the minimum quotients in the S_k's to sampling errors, and the second level refers to the multiplication of these errors through the formation of products in S_n^π. Sampling errors become most crucial in the estimation of S_k's when genotypes occur at low frequencies in the base population. Even if these genotypes are not selected so that there is no change in frequency, sampling errors may dominate S_k estimates. Moreover, rare genotypes are likely to yield observations that are at odds with the basic selection model in that a genotype is absent in a sample taken at the beginning of a selection stage but reappears in a sample taken at the end of this stage.

In order to minimize these problems with rare genotypes, and since efficient statistical methods for the analysis of multi-stage viability selection processes do not seem to be available, we decided to add 'rare' genotypes to those representing their alleles best (isoenzyme gene loci MDH-B and LAP-A). Herewith, a genotype is considered rare if for at least one selection stage it is absent at the beginning of that stage and reappears at the end of that stage or some later stage. If such a genotype is homozygous, it is lumped with the regularly occurring heterozygote carrying its allele. In the same way, a rare heterozygote is lumped with its regularly occurring homozygote. By this all genotypic classes are presumably sufficiently represented to exclude extreme sampling errors in our maximum likelihood estimates. Although statistical tests and estimates of confidence regions could have been carried out for some steps, we refrained from doing so since they cannot appropriately reflect the reliability of the estimates of our compound parameters.

In fact, according to system analytical principles (see Gregorius 1998), a suitable statistical method of analysis should be based on a model that reflects the relevant consequences of multi-stage viability selection. For the present purpose, such a model simply consists of a sequence of genotypic frequency distributions (relative frequencies), which obey the above-mentioned condition that $P_i'(k)>0$ implies $P_i(k)>0$ for each stage k of selection and for each genotype i. All these admissible frequencies are to be considered as free model parameters which are estimated from samples taken independently from each stage. Since $P_i'(k)=P_i(k+1)$ in a sequence of genotypic frequencies, each sample taken at the end of a stage also estimates the frequencies at the beginning of the next stage of selection. Consequently, model calibration takes place by adjusting admissible genotypic frequency sequences to the frequencies observed in the sequence of samples. This yields all required estimates, and their confidence regions are obtained on the basis of the product-multinomial distribution of the sample sequence.

The lack of such methods of statistical analysis classifies the interpretations of our results as preliminary with the possibility of presenting tendencies in the adaptational optimization of viability selection processes.

Results

Table 1 is organized such that the different stages of development appear in columns 3–9, and the gene loci appear in rows. For each gene locus and selection stage n, the index ζ_n of adaptational optimality of viability selec-

Table 1 The indices ζ_n of adaptational optimality of variability selection up to the *n*-th developmental stage, its constituent parameters S_n^{π} and S_n°, and the stage-specific measures of optimality ζ_{n+1}/ζ_n in the reproductive material

Gene locus	Parameter	Developmental stages[a] (*n*)						
		1	2	3	4	5	6	7
IDH-A (Isocitrate dehydrogenase)	S_n^{π}	0.834	0.649	0.481	0.458	0.382	0.367	0.361
	S_n°	0.834	0.901	0.885	0.843	0.958	0.973	0.958
	ζ_n	1.000	0.720	0.543	0.543	0.399	0.377	0.377
	ζ_{n+1}/ζ_n		0.720	0.755	1.0000	0.735	0.944	1.000
MDH-B* (Malate dehydrogenase)	S_n^{π}	0.933	0.714	0.537	0.470	0.464	0.464	0.447
	S_n°	0.933	0.962	0.987	0.863	0.904	0.991	0.983
	ζ_n	1.000	0.743	0.544	0.544	0.514	0.468	0.455
	ζ_{n+1}/ζ_n		0.743	0.732	1.000	0.944	0.912	0.972
MDH-C (Malate dehydrogenase)	S_n^{π}	0.736	0.457	0.368	0.196	0.181	0.154	0.144
	S_n°	0.736	0.457	0.844	0.450	0.469	0.849	0.927
	ζ_n	1.000	1.000	0.436	0.436	0.387	0.181	0.155
	ζ_{n+1}/ζ_n		1.000	0.436	1.000	0.887	0.469	0.856
6PGDH-A (Phospho-gluconate dehydrogenase)	S_n^{π}	0.963	0.943	0.914	0.888	0.404	0.393	0.383
	S_n°	0.963	0.943	0.914	0.888	0.999	0.976	0.952
	ζ_n	1.000	1.000	1.000	1.000	0.404	0.403	0.403
	ζ_{n+1}/ζ_n		1.000	1.000	1.000	0.404	0.996	1.000
PGM-A (Phospho-glucomutase)	S_n^{π}	0.956	0.813	0.580	0.500	0.337	0.297	0.231
	S_n°	0.956	0.813	0.924	0.880	0.810	0.729	0.818
	ζ_n	1.000	1.000	0.628	0.569	0.416	0.407	0.283
	ζ_{n+1}/ζ_n		1.000	0.628	0.906	0.731	0.979	0.695
MNR-A (Menadione reductase)	S_n^{π}	0.853	0.849	0.698	0.670	0.662	0.587	0.594
	S_n°	0.853	0.875	0.719	0.958	0.992	0.949	0.977
	ζ_n	1.000	0.970	0.970	0.699	0.667	0.618	0.598
	ζ_{n+1}/ζ_n		0.970	1.000	0.721	0.954	0.927	0.967
LAP-A* (Leucine amino-peptidase	S_n^{π}	0.659	0.521	0.324	0.264	0.153	0.117	0.091
	S_n°	0.659	0.521	0.546	0.483	0.533	0.423	0.576
	ζ_n	1.000	1.000	0.594	0.546	0.277	0.277	0.158
	ζ_{n+1}/ζ_n		1.000	0.594	0.920	0.507	1.000	0.572
PGI-B (Phospho-glucose isomerase)	S_n^{π}	0.956	0.111	0.111	0.109	0.108	0.062	0.060
	S_n°	0.956	0.929	0.926	0.984	0.976	0.996	0.958
	ζ_n	1.000	0.119	0.119	0.110	0.110	0.062	0.062
	ζ_{n+1}/ζ_n		0.119	1.000	0.923	1.000	0.564	1.000

[a] The numbering of stages refers to: 1, seed harvesting; 2, seed management; 3, sowing of seed; 4, germination; 5, 2-year-old plants; 6, 3-year-old plants; 5, adult trees. Values underlined in the S_n^{π}- and S_n°-rows indicate statistically significant inhomogeneity among the underlying genetic structures

tion up to the *n*-th developmental stage, its constituent parameters S_n^{π} (net maximum survival) and S_n° (gross maximum survival), as well as the stage-specific measures of optimality ζ_{n+1}/ζ_n are computed for the reproductive material. In addition, the ζ_n-values are illustrated in Fig. 1 using a logarithmic scale in order to display the differences between stages measured by ζ_{n+1}/ζ_n.

Disregarding statistical aspects, Table 1 and Fig. 1 demonstrate substantial deviations from optimal selection during the production process of the reproductive material. In the last stage, ζ_7-values range from 0.06 to 0.6 between the enzyme loci. This is paralleled very much by the amounts S_6^{π} of net maximum survival to the last stage of the production process. The smallest S_6^{π}-value equals 0.062, which thus indicates a reduction during the production process that is very likely to have distinctly exceeded 94%.

With the exception of two loci, gross maximum survivals S_n° are consistently high across stage. The exceptions are MDH-C, which shows large variation for the S_n°'s among stages, and LAP-A*, which shows consistently low gross maximum survivals. Despite this difference between the two loci, they show about the same degree ζ_7 of overall selective optimality, and this degree is next to the lowest.

Recalling that large changes in ζ between stages, as measured by the quotient ζ_{n+1}/ζ_n, indicate stages of strongly suboptimal selection, our data reveal that such selection is more or less unevenly distributed over the stages. The stages of strongest sub-optimality differ among loci. For the step from the last stage in the production process to the adult stage in the source population remarkably high selective optimality is realized at five loci ($\zeta_7/\zeta_6 \geq 0.967$). Only at loci PGM-A, LAP-A* and MDH-C do degrees of optimality ($\zeta_7/\zeta_6 = 0.695$, 0.572, 0.856) appear that reach values as low as those observed for stages within the production process.

Considering each stage separately, it turns out that across the loci there is no stage which shows consistently

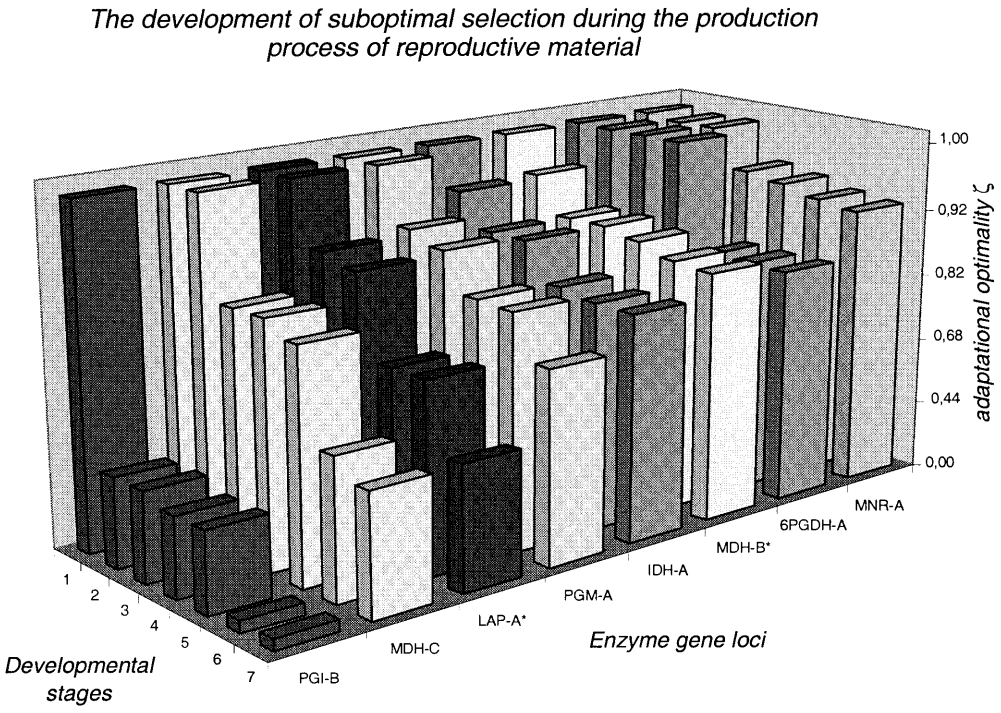

Fig. 1 The development of suboptimal selection during the production process of reproductive material. The indices ζ_n of adaptational optimality of viability selection up to the *n*-th developmental stage in the reproductive material

high or consistently low optimality of selection. On the other hand, with the exception of the locus PGI-B, if pronounced suboptimal selection occurs at one stage, then the ζ_{n+1}/ζ_n-values are about equal at all such stages. For example, at the locus IDH-A, stages 2, 3 and 5 show the lowest amounts of stage-specific optimality, varying between 0.720 and 0.755. The remaining stages show $\zeta_{n+1/}\zeta_n$-values above 0.944 (see Table 1).

In order to get a rough idea about possible sampling effects on the ζ_n's, we performed several tests of homogeneity among the genotypic structures observed in the different stages. Corresponding to the two components S_n° and S_n^π of ζ_n, these tests involved comparisons between the first and the *n*-th stage as well as comparisons for all intermediate stages jointly. Except for MDH-B and MNR-A, the genetic structures of the seven stages showed significant differences at all loci. With the exception of 6PGDH-A and PGI-B, this significance vanished when the last stage was excluded from the test. However, this did not continue consistently when the number of stages is reduced further. Various significant differences between the pairs of genetic structures used for S_n° occurred, however, without showing any consistency. The significances are marked in Table 1 by underlining the respective values in the rows corresponding to S_n^π and S_n°.

Concluding remarks

It was emphasized above that the lack of suitable methods of statistical analysis restricts conclusions to be derived from our observations to preliminary statements which help in outlining tendencies. Considerably adaptational sub-optimality of the selection processes acting during the production process of reproductive material is such a tendency realized to various degrees over the gene loci. Another tendency is to be seen in alternating phases of strong sub-optimality (steep steps in Fig. 1) and near-optimality (plateaus in Fig. 1; ζ_{n+1}/ζ_n close to 1 in Table 1). of the selection process as measured in terms of ζ_{n+1}/ζ_n. This tendency is, however, less pronounced at some loci, such as IDH-A, where the overall degree of sub-optimality (measured by ζ_7) is more evenly distributed over the stages.

The most consistent tendency across loci concerns the high degree of optimal selection between the third and fourth stage (ζ_4/ζ_3 close to 1). The fourth stage is the stage of germination, and it is preceded by drastic reductions in population size caused by both natural and anthropogenic factors (harvesting, seed management, sowing of lots). In contrast, of all the stages in the production process, germination is least affected by human interference. It is thus conceivable that the artificial reductions inactivate or replace the natural selection processes in a counter-adaptive way. If natural forms of selection become dominant again, the forces of adaptation optimization are reactivated.

As has been emphasized earlier, it has to be taken into account that the present isoenzyme gene loci are likely to not be directly subjected to selection but are only stochastically associated with the directly selected loci. Therefore, in order to develop the above suggestion into a testable hypothesis, explicit modeling of the effects of variable viability selection regimes on the dynamics of genotypic structures at associated loci is required. On the

other hand, the indirect selection via stochastic genomic associations is a form of selection of its own kind (occasionally referred to as "hitchhiking" or "associative selection"), which differs from direct selection by its lower intensity. Hence, our observations can at least be claimed to reflect this form of selection.

The above considerations apply chiefly to the selection acting during the production of reproductive material, and they are largely independent of the initial assumption of adaptedness of the source population. In fact, no conclusive indication as to the validity of this assumption seems to be implied by our observations. Even the last step from the production process to the adult source population showed no consistent pattern of selective optimality across loci. This does, however, not affect the suggestion of strong adaptational sub-optimality of the selection process, no matter whether it resulted from insufficient adaptedness of the source population or from inadequacies of the production process. Hence, to lower the risk of reproducing inferior reproductive material, application of the above methods for the assessment of adaptedness should be extended to the approval of seed stands.

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Appendix

The validity of the inequality $S_n^{\pi} \le S_n^{\circ}$ will be proven by induction. For this purpose consider the fact that the genotypic frequencies between the selection stages are related by $P_i'(k)=P_i(k+1)$ and that $S_1^{\pi}=S_1^{\circ}=S_1$. Suppose that the inequality $S_n^{\pi} \le S_n^{\circ}$ holds for any $n>1$, then

$$S_{n+1}^{\pi} = S_n^{\pi} \cdot S_{n+1} \le S_n^{\circ} \cdot S_{n+1} = \min_i \frac{P_i(1)}{P_i'(n)} \cdot \min_i \frac{P_i(n+1)}{P_i'(n+1)}$$

$$\le \min_i \frac{P_i(1)}{P_i'(n)} \cdot \frac{P_i(n+1)}{P_i'(n+1)} = \min_i \frac{P_i(1)}{P_i'(n)} \cdot \frac{P_i'(n)}{P_i'(n+1)} = S_{n+1}^{\circ},$$

which proves the assertion.

In order to obtain $S_{n+1}^{\pi}=S_{n+1}^{\circ}$, both inequalitites in this proof must become equalities. This shows that $S_{n+1}^{\pi}=S_{n+1}^{\circ}$ if and only if $S_n^{\pi}=S_n^{\circ}$ and if there exists a genotype j with $S_n^{\circ}=P_j(1)/P_j'(n)$ and $S_{n+1}=P_j(n+1)/P_j'(n+1)$. Hence, if the equality $S_n^{\pi}=S_n^{\circ}$ holds for some stage n, it holds for all previous stages. Looking ahead, this result implies that if for each of the stages k, $k=1, \ldots, n-1$, there exists a genotype j with $S_k^{\circ}=P_j(1)/P_j'(k)$ and $S_{k+1}=P_j(k+1)/P_j'(k+1)$, then $S_l^{\pi}=S_l^{\circ}$ for $l=1, \ldots, n$. This is the condition for an adaptationally optimal selection process extending over $n \ge 2$ stages.

The general principle of the proof of the above inequality can also be applied to derive an important characteristic of the the index $\zeta_n=S_n^{\pi}/S_n^{\circ}$:

$$\frac{\zeta_{n+1}}{\zeta_n} = \frac{S_{n+1}^{\pi}}{S_{n+1}^{\circ}} \cdot \frac{S_n^{\circ}}{S_n^{\pi}} = \frac{S_{n+1} \cdot S_n^{\circ}}{S_{n+1}^{\circ}} \le 1$$

This shows that ζ_n decreases with increasing number n of selection stages.

In fact, $S_n^{\circ} \cdot S_{n+1}/S_{n+1}^{\circ}$ presents itself again as a measure of the ζ type if one conceives of S_n° as an amount of primary maximum survival of a hypothetical stage that extends from the beginning of the zygotic to the end of the n-th stage. The product $S_n^{\circ} \cdot S_{n+1}$ therefore constitutes an amount of net maximum survival based on two stages, and S_{n+1}° is the pertaining amount of gross maximum survival to the end of the $(n+1)^{st}$ stage. Hence, ζ_{n+1}/ζ_n measures the degree of adaptational optimality of selection *at* the $(n+1)^{st}$ stage. This makes sense, since the effect of the last stage considered should not depend on a more or less arbitrary subdivision into stages preceding this last stage.

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