VIABILITY SELECTION IN JUVENILE POPULATIONS OF EUROPEAN BEECH (FAGUS SYLVATICA L.)

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ABSTRACT

Changes of genetic structures among seedlings of European beech (*Fagus sylvatica* L.) were studied under nonmanipulated and meliorated site conditions. Genotypic structures were compared between two different stages: pre-germinated seed nuts and surviving juvenile plants. Five different environmental conditions were addressed: a former spruce site: (1) without melioration and substantial soil acidification, (2) meliorated by surface fertilization and liming, (3) by deep ploughing, (4) by deep ploughing as well as fertilization and liming, and as a reference environment, (5) an adult beech stand at a distance of 1 km from the melioration experiment. Two seed samples were exposed to each of these different conditions, one (Uslar sample) originating from a single stand of the same region, the other (mixed sample) a mixture from five stands of different regions. 13 enzyme coding gene loci were applied for genetic monitoring.

Population survival rates varied substantially between the different environmental conditions. With surface fertilization and liming, the highest survival abilities were observed as well as relatively high proportions of heterozygotes and large multiple locus genetic diversities. Viability selection is suggested for the enzyme gene loci Mdh-B, Lap-A, Idh-A, Got-B, and Mdh-C. Viability coefficients were estimated for populations and particular genotypes and illustrated for Lap-A, Idh-A, Got-B, and Mdh-C. Loss of rare alleles is indicated for the gene locus Skdh-A. The results show that melioration measures in order to improve soil conditions can substantially affect genetic structures and eventually lead to modified adaptational potential of juvenile beech material.

Key words: Fagus sylvatica, viability selection, allozymes, heterozygosity, genetic diversity, air pollution, fertilization

INTRODUCTION

In central Europe, European beech (*Fagus sylvatica*) and oak species (*Quercus robur, Q. petraea*) are increasingly subject to forest dieback. Although coniferous species such as Norway spruce (*Picea abies*) (*e.g.* ANONYMOUS 1995) show slight reductions of the proportions of damaged trees, these trends often correspond to annual peculiarities of water and temperature regimes and do not permit general conclusions on the future development of forest dieback.

The genetic response of forest tree populations to environmental stress has been studied in various populations of significant forest tree species such as Norway spruce (e.g. SCHOLZ & BERGMANN 1987, BERGMANN & SCHOLZ 1989, GEBUREK & SCHOLZ 1992), Scots pine (*Pinus sylvestris*) (GEBUREK *et al.*1987, MEJNARTOWICZ & PALOWSKI 1989, PRUS-GLOWACKI & GODZIK 1991, BAHTIYAROVA *et al.* 1994), silver fir (*Abies alba*) (e.g. SCHROEDER 1989, KONNERT 1992, SCHOLZ *et al.* 1994), and European beech (e.g. MÜLLER-STARCK 1989, 1993, MÜLLER-STARCK & ZIEHE 1991).

The corresponding experimental studies can be classified into three categories: firstly, fumigation and hydroponic experiments, which aim at the monitoring of the genetic response of seedlings and juvenile populations to certain stress components; secondly, studies on juvenile populations under field stress conditions, which mostly quantify changes between the genetic structures at different ontogenetic stages; thirdly, studies in adult tree stands, which compare genetically tolerant and sensitive subsets after longterm exposure to complex environmental stress. These experiments verified various non-random impacts of environmental stress on the genetic structures of forest tree populations and on reproductive processes. Among parameters of genetic variation, particularly genetic diversities and heterozygosities were subject to change. Viability selection and loss of genetic variation were obvious.

Various methods for the improvement of environ-

mental conditions have been suggested and experimentally applied (MATZNER *et al.* 1983, MATZNER *et al.* 1985, or KREUTZER 1995). One particular focus was on the improvement by deacidification via fertilization and liming. It is the aim of the present study to verify genetic consequences of environmental stress on juvenile populations under different field conditions which include exposure to stress following acidification as well as improved environmental conditions following different fertilization and liming regimes and deep ploughing.

The present study focusses on the dynamics of genetic structures between two particular stages of beech populations, pre-germinated seeds and juvenile survivors, exposed to environmental stress. The genetic comparisons between these two stages allows investigation of viabilities of genotypes, which may depend on environmental conditions.

MATERIAL AND METHODS

Experimental plots

Plots were established at two locations in the Solling hills, which are located northwest of the city of Göttingen. A cleared and meliorated former Norway spruce site was provided for these experiments by the Research Center on Forest Ecosystems of the University of Göttingen. The material was exposed to four different environmental conditions at this site: Non-manipulated ground, ground with surface fertilization and liming (4 t·ha⁻¹ dolomite), deep ploughing with fertilization and liming (soil cultivation up to 70 cm with 18.5 t·ha⁻¹ calcium carbonate, up to 20 cm with 4 t·ha⁻¹ dolomite, phosphate/potassium fertilization with 50 kg K·ha⁻¹ as K₂SO₄ and 50 kg P·ha⁻¹ as semi disintegrated phosphate), as well as deep ploughing without fertilization. A further control plot is located in an adult beech sstand without any ground manipulations at a distance of approximately 1,000 m from the other.

Four of the five field experiments consist of two 3 $m \times 6 m$ plots. The variant with surface fertilization is represented by only one 3 $m \times 3 m$ plot. All plots were protected against mice by metal fences and against birds by nets. In addition, soil from the non-manipulated variant and the two fertilized variants was transported into a greenhouse and used as reference environment in order to observe the influence of the soils on growing behavior under temperate environmental conditions.

Material

Pre-germinated seeds were sown in each of the experimental plots on the ground and covered by beech-litter in order to imitate as much as possible natural growing conditions (field experiments). Approximately 3,500 seeds were sown per variant.

The material was sown in April, 1991. Two seed samples were exposed to these conditions, the first of which originated from collections over the whole area of a single stand in the forest district of Uslar, the second (referred as the mixed sample) represents a mixture of five different samples from the forest districts of Driedorf, Weilburg, Hatzfeld, Winterberg and Schlüchtern. The material was taken from commercial seed lots supplied by the "Staatsklenge Wolfgang". Prior to the transfer of the material to the field and the greenhouse, samples were taken at random in order to characterize the initial population before exposure to environmental stress. These initial populations are designated as "seeds", while the survivors are designated as "juvenile plants". The material is surveyed in Table 1.

Table 1 Genetically examined material of beech nuts and juvenile plants

Category	Number of studied individuals		
	Uslar	Mixed sample	
Seeds	300	312*)	
Juvenile plants			
Non-manipulated ground	228	245	
Surface fertilization	287	260	
 Deep ploughing with fertilization 	97	203	
Deep ploughing without fertilization	33	5	
Adult beech stand	16	10	

*) Driedorf - 60, Weilburg - 60, Hatzfeld - 60, Winterberg - 60, Schlüchtern - 60

Enzyme system	E.C. No	Structure, metabolic category	Enzyme coding polymorphic gene loci
Diaphorase	1.6.99 <i>.</i> -	te, II	Dia–A
Glutamate oxaloacetate transaminase	2.6.1.1	di, I	Got-B
Isocitrate dehydrogenase	1.1.1.42	di, I	Idh-A
Leucine aminopeptidase	3.4.11.1	mo, II	Lap-A
Malate dehydrogenase	1.1.1.37	di, I	Mdh-A, Mdh-B, Mdh-C
6-Phosphogluconate dehydrogenase	1.1.1.44	di, I	6-Pgd-A, 6-Pgd-B, 6-Pgd-C
Phosphoglucomutase	2.7.5.1	mo, I	Pgm-A
Phosphoglucose isomerase	5.3.1.9	di, I	Pgi-B
Shikimate dehydrogenase	1.1.1.25	mo. II	Skdh–A

Table 2 Enzyme systems and structure (mo – monomeric, di – dimeric, te – tetrameric), metabolic category (I – primary, II – secondary) and enzyme coding gene loci.

 $^{1)}$ = Aspartate transaminase

Identification of multilocus-genotypes

Thirteen enzyme coding gene loci were utilized for multilocus genotyping. Genetic control and mode of inheritance of the respective enzyme systems were verified previously (MÜLLER-STARCK & STARKE 1993). Enzymes were separated from crude homogenate by standard horizontal starch gel electrophoresis (for details see STARKE 1996). For survey of enzyme systems and coding gene loci see Table 2.

Quantification of genetic variation and viability selection

Intrapopulation variation was studied by means of the observed proportion of heterozygotes (H_a), the genetic diversity (v, GREGORIUS 1978, 1987) and the total differentiation within populations (δ_T , GREGORIUS 1987): In order to quantify the potential to form different gametic types, the hypothetical gametic multilocus diversity (v_{gam} , GREGORIUS 1987) was determined for each sample. Differences among frequency distribution were tested statistically by utilizing the log likelihood ratio test (*G*-test) of homogeneity in contingency tables.

Viabilities of populations or particular genotypes were determined as proportions of those population members or individuals of the corresponding type which survived till the age of two. The initial number of individuals of a particular genotype was estimated by its proportion in the additional sample of seed material.

RESULTS AND DISCUSSION

Germination success under greenhouse and field conditions

In a pilot experiment, height growth of seedlings from

the Uslar sample and the mixed sample was tested in the greenhouse. Material was sown on 30 cm deep soil, which originated from three of the five field locations in the Solling hills (see Table 1): Non-manipulated ground, surface fertilization and liming, deep ploughing with fertilization and liming. Sample size is 12 pregerminated seeds per soil variant, *i.e.* 36 individuals for the Uslar sample and 180 individuals for the mixed sample (5 subsets with 36 individuals each). All seedlings survived until census after three weeks except 22 of the subset Schlüchtern (equivalent to a loss of 61%).

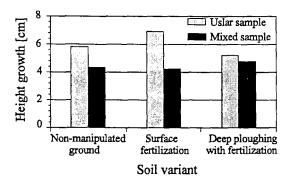


Figure 1 Average height growth of seedlings of the Uslar sample and the subsets of the mixed sample under three different soil conditions in the greenhouse at the age of three weeks.

As can be seen from Figure 1, seedlings of the Uslar sample showed superior height growth under all studied soil conditions. Since the Uslar seedlings originated from a stand of the same forest district, it may be suggested that the Uslar material is better adapted to the relatively extreme soil acidification of the Solling hills than the seedlings of the mixed sample descending from other regions of Germany. Concerning height Table 3 Range of pH-values (H_2O) among the five soil variants

Soil category	pH-values
Non-manipulated ground	2.80-2.86
Surface fertilization	3.68-4.51
Deep ploughing with fertilization	4.15-4.63
Deep ploughing without fertilization	4.02
Adult beech stand	3.00-3.29

growth, the Uslar sample indeed showed superiority when planted in the greenhouse in soil from the field plots. Especially in the meliorated soil variant with surface fertilization, the Uslar material is capable of gaining a substantial growth advantage during the first three weeks.

In order to evaluate impacts of acidity on height growth, pH-values (H_2O) were measured in the upper layer of the mineral soil in each of the three studied soil variants and the two remaining ones (deep-ploughing, adult beech stand). Results are compiled in Table 3. From this and from Figure 1 it can be concluded that under the conditions given there is no evidence that height growth is correlated with the pH-value of the soil variants.

The observed pH-values demonstrate that acidification is most severe in the plots with non-manipulated ground. This location was formerly stocked by a planted stand of Norway spruce (*Picea abies* L. Karst.). The comparison with the experimental plots in adult beech clearly demonstrate that acidification is less pronounced in this mixed deciduous tree stand as compared to the former Norway spruce stand. The pHvalues of the adult beech stand are representative for areas in higher elevations of the Solling hills which are subjected to more severe atmospheric deposition than to other regions of Germany (*e.g.* HUETTL 1993). The three remaining plots reveal considerably higher pH- values. In the two fertilized variants, the range of pHvalues is larger than in all the others. This clearly indicates that the input of fertilizer does not result in homogeneous soil conditions. The relatively high pHvalues under the condition of deep ploughing without fertilization can be explained by the local soil conditions: The deeper soil layers reveal higher pH-values due to the acidification in the upper soil segments and corresponding fluxes of matter. Obviously, deep ploughing tends to reverse this process.

Germination success under field conditions is surveyed in Table 4. Data refer to two inventories. The first took place on October 30, 1991, *i.e.* six months after establishment, and the second on May 8, 1992 (after 12 months). An increasing number after 12 months can be easily explained by low mortality between 6 and 12 months and additionally germinated seed nuts.

Substantial losses are evident in all soil variants and both seed samples. Losses tend to be slightly smaller in the mixed sample in comparison with the Uslar sample. At present, there is no evidence that the Uslar sample (local origin) is better adapted than the mixed sample. It cannot be ruled out that the adaptedness of the Uslar sample will become evident in succeeding stages.

For both samples, surface fertilization results in the highest survival rates. Deep ploughing with fertilization reduces survival percentages. This may be a consequence of the reduction of humus soil in favour of mineral soil (modified surface conditions in case of drought. The substantial investment for this method of soil treatment does not seem to result in a correspondingly large benefit in terms of increasing survival rates. In contrast, deep ploughing without fertilization results in a substantial decrease of survival rates in the case of the mixed sample. This trend is not obvious in the case of the Uslar sample. The reason for this phenomenon cannot be explained satisfactorily at present. It cannot be excluded that it is the consequence of a better

	Uslar sample			Mixed sample		
Soil category	No. of pre- germinated seeds	No. of survivors	Survivors %	No. of pre- germinated seeds	No. of survivors	Survivors %
Non-manipulated ground	3040	355/371	11.7 / 12.2	3160	436 / 430	13.8/13.6
Surface fertilization	3040	488 / 489	16.1 / 16.1	3160	594 / 620	18.8 / 19.6
Deep ploughing with fertilization	3040	274 / 267	9.0 / 8.8	3160	475 / 459	15.0/14.5
Deep ploughing without fertilization	370	36/35	9.7 / 9.5	384	6/5	1.6/1.3
Adult beech stand	6144	113/96	1.8/1.6	6408	64 / 59	1.0/0.9
Total	15634	1266 / 1258	8.1 / 8.0	16272	1575 / 1573	7.0 / 9.7

Table 4 Success in germination of two seed samples on five different soil categories under field conditions; data refer to inventories after 6 months / 12 months of exposure

Category	Ha	υ	Ugam	δτ
Uslar sample				
Pre-germinated seeds	0.226	1.358	49.0	0.264
Juvenile plants:				
Non-manipulated ground	0.260	1.375	55.2	0.273
Surface fertilization	0.263	1.383	60.0	0.278
Deep ploughing with fertilization	0.249	1.361	50.3	0.267
Deep ploughing without fertilization	0.237	1.340	39.8	0.258
Adult beech stand	0.233	1.311	27.3	0.245
Mixed sample				
Pre-germinated seeds	0.242	1.372	55.2	0.271
Juvenile plants:				
Non-manipulated ground	0.260	1.375	53.0	0.273
Surface fertilization	0.276	1.390	62.4	0.281
Deep ploughing with fertilization	0.249	1.375	54.9	0.273
Deep ploughing without fertilization	0.273	1.294	23.3	0.253
Adult beech stand	0.336	1.462	86.7	0.333

 Table 5 Survey of variation parameters for two germinating seed samples and corresponding survivors under five different environmental conditions (further explanation see article)

genetic adaptation of the local Uslar sample. Results suggest the general conclusion that fertilization in combination with deep ploughing tends to slightly increase survival rates. Surprisingly, the non-manipulated ground reveals relatively high survival percentages. In contrast to this, smallest values were obtained in the adult beech stand. This can be explained mainly by disadvantageous light conditions and possibly also by higher humidity, which favors disposition for fungal attack.

Genetic variation within samples

In Table 5, the following variation parameters are shown for two samples and five environmental variants. The average heterozygosity H_a , the gene pool diversity v, the hypothetical gametic multilocus diversity v_{gam} , and the total differentiation δ_T . Due to an overlap in the zymograms of 6Pgdh-B and -C and possible misclassification of genotypes (see MULLER-STARCK & STARKE 1993), these two gene loci will be excluded from the multilocus compilations of data.

In the interpretation of data, small sample sizes must be taken into account, especially in the case of the variants "adult beech stand" (Uslar sample and mixed sample) and deep ploughing without fertilization in case of the mixed sample (see Table 1). Surprising is the fact that the heterozygosities among the survivors are on the average not smaller than among the initial populations (*i.e.* germinating seeds). Apparently, there is no viability advantage in favor of homozygotes.

In the case of the diversities, a reduction is obvious among the survivors as compared to the initial populations. This is obvious especially for the experimental plots with substantial losses of individuals. An exception is the mixed sample in the adult beech stand. This trend is more pronounced in the case of the hypothetical gametic multilocus diversity. If experimental plots of minimum sample sizes are omitted, the experimental plots with surface fertilization reveal the largest values for v_{gam} , *i.e.* the largest potential to form different gametic types and thus to be able to adapt to changing environmental conditions.

The parameters characterizing differentiation within populations reveal pronounced deviations only in those cases where sample sizes are lowest.

Viability selection

Quantification of viability selection is based on the initial populations of pre-germinated seeds from two different samples and the corresponding survivors under field stress conditions. The frequencies of the initial populations were estimated from samples drawn at random before exposure of the material to field conditions.

At the single loci, the following trends for the estimated viabilities of the different genotypes were observed:

Mdh–B: The genotypic structures of the surviving seedlings differed extremely from those of the estimated initial structures. The differences were highly significant (significance level <.001) for all plots with more than 30 surviving juvenile plants and several others. The most drastic changes were observed for the

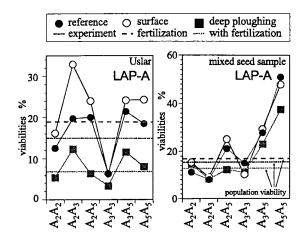


Figure 2 Viabilities of genotypes at the gene locus Lap-A for two samples and three environmental conditions (population viabilities are also indicated)

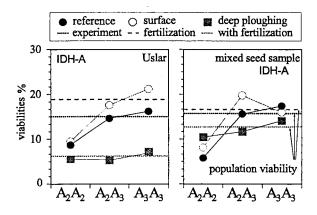


Figure 4 Viabilities of genotypes at the gene locus *Idh–A* for two samples and three environmental conditions (population viabilities are indicated)

genotype B_3B_4 . The frequencies of this genotype in the initial structures are estimated with proportions below 3% for both the Uslar and the mixed sample. However, for all experiments, the observed frequencies of B_3B_4 among the surviving juvenile plants are larger than 18 %. Hence, even if the corresponding frequencies in the initial structures were slightly underestimated, a substantial or even extreme proportion of those individuals carrying B3B4 must have survived under the field conditions. This also contributes to the relatively large average heterozygosity of the surviving plants. However, since the estimated initial frequencies of B_3B_4 are relatively low, estimation of viabilities is not sufficiently reliable and is not illustrated for this gene locus. Although the observed changes in genotypic structures at Mdh-B are drastic, they are in accordance with other studies. Whereas TUROK (1995) reported frequencies of B₃B₄ mostly between 0 and 8 % among beech nuts from

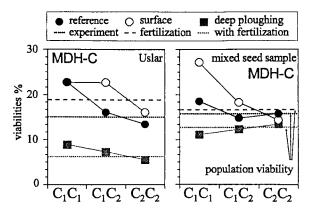


Figure 3 Viabilities of genotypes at the gene locus *Mdh–C* for two samples and three environmental conditions (population viabilities are indicated)

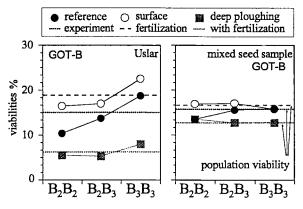


Figure 5 Viabilities of genotypes at the gene locus *Got–B* for two samples and three environmental conditions (population viabilities are indicated)

different stands in Nordrhein-Westfalen, Germany, B_3B_4 has been found with frequencies mostly between 15 % and 25 % in several adult beech stands in Rheinland-Pfalz (STARKE *et al.* 1995). It may be concluded that strong selection in favor of B_3B_4 already operates during the early ontogenetic stages considered in the present paper.

Lap–A: The results are compiled in Figure 2. The most pronounced viability differences are observed for the mixed sample at *Lap–A*. Here it can be concluded that carriers of allele A_5 reveal above-average viabilities. This is particularly evident for the genotype A_5A_5 . This trend confirms observations of earlier studies under different environmental conditions (see MÜLLER-STARCK 1993). Since the mixed sample is expected to show a larger variation in the genetic background and the Uslar sample presents a different pattern with large viability of A_2A_3 under surface fertilization, it may be

suggested that for the Uslar sample particular multiple locus associations and selection regimes hold.

KIM (1985) found that homozygotes at the gene locus Lap-A had a strong viability advantage under homogeneous greenhouse conditions, while heterozygotes were superior under field conditions. In the present case heterozygotes at Lap-A are observed with frequencies of 41% in the Uslar sample and 61% in the mixed sample. Under homogeneous greenhouse conditions, the Uslar sample indeed showed superior growth.

Under field conditions the situation is partially reversed. In particular for the soil variant with deep ploughing and fertilization, the mixed sample leads to significantly larger proportions of survivors (Table 4). With the field variants of non-manipulated soil and surface fertilization, a slightly larger population viability can be observed. Thus the mixed sample seems to possess a larger adaptive capacity for these environmental conditions. Deep ploughing without fertilization, however, either permitted relatively large viabilities for the Uslar sample or caused relatively high mortality for the mixed material. In both cases very special adaptational effects are suggested to be responsible.

Mdh–C: As can be seen from Figure 3, viability advantages are clearly indicated with respect to the genotype C_1C_1 on the experimental plot with surface fertilization but not for deep ploughing with fertilization. The findings from a previous study under severe field stress conditions without fertilization indicating superior viabilities of heterozygotes (MÜLLER-STARCK 1993) cannot be confirmed under the present soil conditions.

Pgi-B: There is an drastic increase of the frequency of the rare genotype B_2B_3 in both samples and environmental conditions. The carriers of this genotype obviously reveal viability advantage. Due to small initial frequencies of B_2B_3 determination of viability parameters strongly depends on random effects and does not lead to reliable results.

Idh-A: Carriers of genotype A_2A_2 reveal a viability disadvantage as compared to other genotypes (compare Figure 4). For the mixed sample a slight heterozygote advantage can be observed which is more pronounced under strong stress conditions. This gene locus is of particular interest since significant differences have been observed between genotypic structures of adult beech trees attacked by beech scale and those not attacked (GORA *et al.*, 1994).

Got–B: In the Uslar sample, genotype B_3B_3 has superior viability under all studied experimental conditions(see Figure 5). This is particularly evident on the experimental plots with the lowest survival rates. In the mixed sample, this trend is not confirmed, but differen-

ces among the viabilities of genotypes are generally less pronounced than in the Uslar sample.

Skdh–A: Results confirm earlier statements (ZIEHE 1990), which verify pronounced minor polymorphisms at this gene locus and a corresponding reduction of rare alleles in the surviving populations as compared to the corresponding initial population. In particular for the Uslar sample the homozygote for the most frequent allele shows an increasing frequency in all field experiments.

Dia–A: At this gene locus, no uniform trend over the involved environmental conditions is observed neither for the Uslar sample nor the mixed sample. If only the reference environment, surface fertilization, and deep ploughing with fertilization are considered, a heterozygote viability advantage for the Uslar sample and an advantage of the homozygote A_2A_2 . for the mixed sample is estimated. This difference may be explained by different genetic backgrounds of the samples.

The occurrence of genomic associations may play a considerable role in the dynamics of genotypic structures. If seed applied in the experiments descends from only a limited number of trees, associations between alleles or genotypes over the gene loci are likely. Such effects can reduce genetic (multilocus) variation and adaptability of the seed material to environmental conditions not experienced by their ancestors. However, genomic associations as a consequence of selection operating at several gene loci in the parental generation may also be advantageous for the seed, if similar environmental conditions and selection regimes are encountered. In this context it is not surprising that the "native" Uslar sample shows a larger viability as compared to the mixed sample at those plots in the adult beech stand. On the other hand, the mixed sample, which is expected to show less specific associations, is superior under manipulated conditions, with the above-mentioned exception.

CONCLUDING REMARKS

The results indicate genotype-environment interactions: The ranking of survival abilities of genotypes at specific gene loci changes with the environmental and melioration conditions.

Previous results on viability selection were confirmed (*e.g.* for *Lap–A*) or supplemented. The genotype A_2A_2 at *Idh–A* for example showed inferior survival abilities at the early ontogenetic stage. On the other hand it is less likely to be attacked by beech scale as an adult beech tree. This emphasizes the importance of including components of several ontogenetic stages in considerations of fitness, since this influences the maintenance of genetic polymorphisms.

Modification of environmental conditions, such as melioration measures, modify selection regimes and lead to changing genetic structures. In general it is not clear whether this may eventually lead to loss of polymorphism and how the adaptational potential of populations is affected.

Results also indicate that methods to improve environmental conditions do not generally result in an increase of survival rates, less viability selection, nor protectedness of genetic variation. The pattern of genetic response to environmental stress and to different melioration regimes depends significantly on the genetic structures of the seed samples. Furthermore, the observed survival rates clearly demonstrate that even less intensive melioration measures, such as surface fertilization, can provide best survival conditions among the variants presently investigated.

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