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Demographic Processes in Pinus sylvestris Populations from Regions under strong and weak Anthropogenous Pressure

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Summary

In two naturally regenerating populations of Pinus sylvestris, one under strong influence of pollution from smelting work and the second from an area under relatively weak anthropogenous pressure the isoenzyme variability in the age groups was studied. Some of the alleles and genotypes showed directional changes of frequencies in the studied age groups. This phenomenon may point to selection processes taking place in the studied populations. In the case of the population subjected to industrial pollution the changes of genetic structure are more intense in the groups of embryos and young individuals. In the population from an area without pollution changes in the genetic structure in the older groups of trees are observed. Adaptation strategy of the studied populations is connected with the increased level of genetic variability.

Zusammenfassung

Die Variabilität von Isoenzymen in verschiedenen Altersgruppen von zwei Pinus sylvestris Populationen wurde untersucht. Eine Population ist im oberschlesischen Industriegebiet in unterschiedlichem Maße Luftverunreinigungen, die andere ist neben Poznan, ausgesetzt. Eine der beiden Populationen wurde stark, die andere nur gering durch Immissionen belastet.

Es wurden Allele und Genotypen gefunden, die eine gesicherte Selektion in Altersgruppen anzeigen. Sie scheint in schwer belasteten Populationen mehr an frühe Entwicklungsstadien (Embryos und junge Pflanzen) gebunden zu sein. In Populationen geringer Immissionsbelastun-

gen machte sich die Veränderung der genetischen Struktur vor allem in höheren Altersklassen bemerkbar. Die Anpassungsstrategie der untersuchten Populationen ist mit einer Vergrößerung der genetischen Variabilität verbunden.

Introduction

In regions polluted or changed by industrial activities, populations of forest trees modify their genetic structure in response to the altered environmental conditions (SINCLAIR, 1969; MEJNARTOWICZ, 1984; SCHOLZ and BERGMANN , 1984; GREGORIUS et al., 1985; MÜLLER-STARCK, 1985). The populations attain adaptation to the changed environmental conditions due to an appropriate adaptative strategy which may be determined studying relations between demographic and genetic parameters in the populations (BRADSHAW, 1976; CLEGG et al., 1978; HARPER, 1978; PRUS-GLOWACKI, 1982; ZHIVOTOVSKI, 1984). Studies of this type should take into account the allele and genotype frequencies in various generations or, in long lived plants such as trees, in the age groups of naturally regenerating populations. Directional changes in allele and genotype frequencies may point to selection processes which eliminate from a population individuals of defined genetic properties. Detection of changes in indices of heterozygosity, fixation and of genotype polymorphism coefficients in age groups of naturally regenerating populations may point to an adaptive strategy realized by the studied populations.

The paper presents results of studies on the adaptive strategy of *Pinus sylvestris* populations in areas under strong anthropogenous pressure, in which adaptive processes should be particularly intense and in areas under a relatively weak anthropogenous pressure.

Material and Methods

For the studies we chose a naturally regenerating population of *Pinus sylvestris* (Bukowno), localized close to (10 km) heavy metals smelting works near Boleslaw (Upper Silesia) and a population from Zielonka Forest near Poznań under weak anthropogenous pressure.

In the two populations the age structure was analyzed and each of the populations was divided into three groups. Group S consisted of individuals aging 3 to 10 years, group Y - those aging 15 to 30 years, and group M included, maternal trees, aging more than 30 years. Potential genetic variability in the two populations was estimated analyzing a random sample of 100 embryos in each population. In each group of the trees, two-years old needles were collected and analyzed for the content of Pb, Cd, Cu, Zn, Ni and S.

Isozymes were studied in winter buds, collected from approximately 100 individuals chosen at random in each age group. Genetic parameters of individual age groups were estimated employing seven isozyme loci, i.e. GOT (E.C. 2.6.1.1) — two loci, GDH (E.C. 1.4.1.3), MDH (E.C. 1.1.1.37), ShDH (E.C. 1.1.1.14), Est F (E.C. 3.1.1.1) and beta-gal (E.C. 3.2.1.23)*.

Techniques of isozyme separation, staining and interpretation of the results corresponded to those described

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GOT — glutamate-oxalate transaminase
GDH — glutamic acid dehydrogenase
MDH — malic acid dehydrogenase
ShDH — shikimic acid dehydrogenase
Est F — fluorescence esterase
beta-gal — beta galactosidase

by RUDIN (1975), RUDIN and EKBERG (1978), YAZDANI and RUDIN (1982), SZMIDT and YAZDANI (1984).

Statistical Methods

Allele and genotypes frequencies were estimated in the two populations to establish genetic parameters characterizing the studied groups of individuals. In the analyzed age group, heterozygosity indices (H_0 and H_o) were calculated, according to the formula given by NEI and ROYCHOUDHURY (1974). The two indices were used to calculate WRIGHT's fixation index (JAIN and WORKMAN, 1967). Genotype polymorphism in individual age groups was calculated using the formula according to KAHLER et al. (1980). Significance of differences in allele and genotype frequencies in the studied age groups was evaluated using a chi² test and the U test for a significance of differences between two components of a set (pairs of age groups), assuming their equal frequency in the age groups (GREN, 1972).

Results

Analysis of demographic structure in the two populations demonstrated a similar age structure in each of them. The Zielonka population comprised approximately 6 000 individuals per ha while the Bukowno population comprised approximately 5 700 individuals per ha. Approximately 50% individuals were included into group Y (15 to 30 years of age). Distribution of individuals in age groups in the two analyzed populations can be presented by an almost symmetrical curve with a single apex, somewhat shifted toward the younger age groups.

Contents of heavy metals and sulphur in the needles of pines of two studied populations are presented in *Figure 1*. Contents of lead, cadmium and zinc were higher by approximately 85% in needle population from Bukowno while contents of copper and sulphur were higher in that population by 30% and 40% respectively. On the other hand, needles from Zielonka population showed higher content of nickel. The data indicated that the population from Bukowno remained under a much stronger anthropopression than the population from Zielonka Forest.

Genetic Structure

Alleles and genotypes most frequently observed in the two populations are presented in *Table 1* and *2*. In the case of MDH and beta-Gal, no satisfactory separation could be achieved in embryos and the data were not included in this study. Generally, in 7 loci 26 alleles were distinguished in the both populations.

Some of the alleles showed evident tendency for increased or decreased frequency in the studied age groups *(Table 1)*. In the Zielonka Forest and Bukowno populations there are alleles GOTA1, GOTA2, EstF4, MDH3, ShDH1 and ShDH4. Less evident the tendency for the alleles EstF1, EstF3 und ShDH3 is observed *(Table 1, Figure 2)*. In some cases, significance of differences in frequency between age groups was confirmed by chi² test.

Comparison of the two populations with respect to frequencies of individual alleles in the studied age groups showed that some alleles, for example alleles of GOT A locus exhibited for both populations the same tendencies of increased or lowered frequency. However the frequency of MDH 3 allele in Bukowno population decreased with age of studied individuals while it increased in Zielonka Forest population *(Table 1, Figure 2)*.

· Applying the test for significance of differences between two components of a set (U), statistically significant differences in allele frequencies were noted between the embryo group (E) and the remaining groups of trees for the Bukowno population and between Y and M age groups for the Zielonka population (see *Table 1*).

Genotypes most frequently noted in the two populations are presented in *Table 2*. Out of a total number of 52 genotypes in the two populations, 37 were observed in the Bukowno population and 44 in the Zielonka population. Differences in number of detected genotypes in the two populations pertained genotypes with low frequencies (GOT A22, GOT A13, GOT B0101, GOT B013, GOT B25, GOT B44, GOT B14, GOT B012, Est F0101, Est F011, Est F012, EST F013, and ShDH 0101, ShDH 101, ShDH 23, ShDH 24). Some of the genotypes showed directional changes in frequencies in the age groups. In some cases

the differences were statistically significant (*Table 2*). In both populations we noted, also, a number of genotypes in which directional changes in frequency we observed however, chi² test demonstrated no statistically significant differences between age groups. As shown in *Table 2*, this is true for genotypes GOT B22, GOT B12, Est F11, MDH 12, MDH 13, ShDH 11 and beta-Gal 12 in the Bukowno population and genotypes Est F14, MDH 11, MDH 12 and beta-Gal 12 in the Zielonka Forest population. The applied statistical test (U) demonstrated significant differences in genotype frequencies in the Bukowno population between embryos (E) on one hand and the other age groups (S, Y, M) on the other. In the Zielonka Forest population significant differences were observed most frequently between the group of the youngest individuals (S) and that of the oldest individuals (M) as well as between groups Y and M (*Table 2*).

Table 1. — Frequencies of alleles in the age groups in the population from Bukowno (polluted) and from Zielonka Forest, E — embryos, S — trees 3 to 10 years old, Y — 15 to 30 years, M — maternal trees over 30 years old, m̄ — mean values for whole populations, U — statistically significant differences in frequencies of alleles between pairs of age groups, * — statistically significant differences in frequency of alleles between studied age groups evaluated by chi² test.

	POPULATIONS											
ALLELES	ZIELONKA FOREST						BUKOWNO					
	E n=352	S n=204	Y n=204	M n=204	m̄	U, chi²	E n=286	S n=200	Y n=200	M n=200	m̄	U, chi² *
GOT A 1	0.972	0.961	0.971	0.828	0.935	E/M, S/M, Y/M	0.990	0.980	0.965	0.955	0.974	E/M, E/Y
GOT A 2	0.024	0.039	0.029	0.167	0.063	E/M, S/M, Y/M	0.010	0.015	0.035	0.045	0.024	E/M, E/Y
GOT A 3	0.004	0	0	0.005	0.002		0	0.005	0	0	0.002	
GOT B01	0	0	0	0	0		0.011	0.020	0	0	0.008	
GOT B 1	0.381	0.363	0.368	0.314	0.357		0.388	0.330	0.335	0.405	0.367	
GOT B 2	0.578	0.603	0.598	0.627	0.601		0.549	0.600	0.610	0.545	0.573	
GOT B 3	0.037	0.034	0.034	0.059	0.041		0.052	0.045	0.045	0.040	0.046	
GOT B 4	0.004	0	0	0	0.001		0	0	0.005	0.010	0.004	
GOT B 5	0	0	0	0	0		0	0.005	0.005	0	0.002	
Est F01	0.023	0	0.015	0.005	0.012		0	0	0	0	0	
Est F 1	0.729	0.737	0.701	0.740	0.727		0.797	0.710	0.705	0.735	0.736	E/Y, E/S
Est F 2	0.109	0.082	0.127	0.113	0.108		0.115	0.140	0.095	0.115	0.116	
Est F 3	0.043	0.057	0.083	0.069	0.062		0.072	0.085	0.150	0.080	0.097	E/Y, Y/S, Y/M
Est F 4	0.097	0.124	0.074	0.074	0.092		0.016	0.065	0.050	0.070	0.051	E/S, E/M
MDH 1	-	0.763	0.762	0.697	0.741		-	0.719	0.695	0.758	0.724	
MDH 2	-	0.168	0.158	0.145	0.157		-	0.189	0.226	0.187	0.201	
MDH 3	-	0.069	0.079	0.158	0.102	S/M, Y/M	-	0.092	0.079	0.056	0.075	
GDH 1	0.344	0.338	0.333	0.304	0.330		0.407	0.420	0.350	0.405	0.397	
GDH 2	0.656	0.662	0.667	0.696	0.670		0.593	0.580	0.650	0.595	0.603	
Gal 1	-	0.549	0.456	0.544	0.516		-	0.520	0.525	0.485	0.510	
Gal 2	-	0.451	0.544	0.456	0.484		-	0.480	0.475	0.515	0.490	
ShDH 01	0	0	0	0	0		0.021	0.010	0.020	0	0.013	
ShDH 1	0.805	0.819	0.843	0.765	0.808	Y/M	0.889	0.855	0.820	0.810	0.846	E/Y, E/M
ShDH 2	0.030	0.020	0.005	0.078	0.033	E/M, S/M, Y/M	0.008	0	0.005	0.075	0.022	E/M, S/M, Y/M
ShDH 3	0.127	0.136	0.127	0.078	0.117		0.053	0.125	0.130	0.100	0.099	E/S, E/Y *
ShDH 4	0.038	0.025	0.025	0.079	0.042	S/M, Y/M *	0.029	0.010	0.025	0.015	0.020	

Table 2. — Frequencies of more common genotypes noted in the age groups in the populations from Bukowno and Zielonka Forest. The rest of explanations as in *Table 1*.

GENO-TYPES	ZIELONKA FOREST						BUKOWNO					
	E n=176	S n=102	Y n=102	M n=102	m	U, chi²	E n=143	S n=100	Y n=100	M n=100	m	U, chi²
GOT A 11	0.943	0.921	0.941	0.667	0.868	E/M, S/M, Y/M x	0.980	0.960	0.930	0.910	0.945	E/Y, E/M
GOT A 12	0.049	0.079	0.059	0.314	0.125	E/M, S/M, Y/M x	0.020	0.040	0.070	0.090	0.055	E/Y, E/M
GOT B 11	0.131	0.118	0.088	0.098	0.109		0.147	0.140	0.130	0.190	0.152	
GOT B 22	0.336	0.363	0.324	0.402	0.356		0.301	0.370	0.420	0.340	0.358	
GOT B 12	0.451	0.451	0.520	0.382	0.451	Y/M	0.448	0.390	0.350	0.390	0.395	
GOT B 13	0.041	0.039	0.039	0.049	0.042		0.056	0.030	0.060	0.030	0.044	
GOT B 23	0.033	0.029	0.029	0.069	0.040		0.049	0.070	0.040	0.050	0.052	
Est F 11	0.550	0.515	0.520	0.539	0.531		0.637	0.500	0.460	0.530	0.532	E/Y
Est F 12	0.163	0.144	0.147	0.176	0.158		0.198	0.200	0.170	0.200	0.192	
Est F 13	0.054	0.093	0.088	0.118	0.088		0.088	0.110	0.230	0.120	0.137	E/Y, S/Y, Y/Mx
Est F 14	0.124	0.206	0.108	0.098	0.134	S/M x	0.033	0.110	0.090	0.090	0.081	
MDH 11	-	0.594	0.564	0.461	0.540		-	0.520	0.500	0.560	0.527	
MDH 22	-	0.010	0	0.013	0.007		-	0.040	0.050	0	0.030	S/M, Y/M
MDH 12	-	0.257	0.277	0.224	0.253		-	0.250	0.290	0.330	0.290	
MDH 13	-	0.079	0.119	0.250	0.149	S/M, Y/M	-	0.140	0.080	0.070	0.097	
MDH 23	-	0.059	0.040	0.039	0.046		-	0.040	0.050	0.040	0.043	
GDH 11	0.131	0.098	0.147	0.098	0.110		0.167	0.200	0.150	0.140	0.164	
GDH 12	0.426	0.480	0.373	0.412	0.423		0.480	0.440	0.400	0.530	0.463	
GDH 22	0.443	0.422	0.480	0.490	0.458		0.353	0.360	0.450	0.330	0.373	
ShDH 11	0.644	0.706	0.716	0.647	0.678		0.836	0.750	0.670	0.670	0.732	E/Y, E/M
ShDH 12	0.059	0.029	0.010	0.069	0.042	E/Y, Y/M	0.016	0	0.010	0.090	0.029	E/M, S/M, Y/M
ShDH 13	0.186	0.147	0.196	0.059	0.147	E/M, S/M, Y/Mx	0.057	0.210	0.240	0.160	0.167	E/S, E/Y, E/Mx
ShDH 14	0.079	0.049	0.049	0.108	0.071		0.025	0.020	0.050	0.030	0.031	
ShDH 33	0.034	0.059	0.029	0.049	0.043		0.025	0.020	0.010	0.020	0.019	
β-Gal 11	-	0.265	0.206	0.304	0.258		-	0.220	0.270	0.230	0.240	
β-Gal 12	-	0.569	0.500	0.480	0.516		-	0.600	0.510	0.510	0.540	
β-Gal 22	-	0.166	0.294	0.216	0.225	S/Y	-	0.180	0.220	0.260	0.220	

Changes in heterozygosity level (H_0) for individual enzymatic loci and mean values in individual age groups of the two populations are shown in *Figure 3*.

In some loci the level of heterozygosity was increasing and in the other it was decreasing with increasing age. In the same loci, differences were observed between populations from Bukowno and the Zielonka Forest. In the Zielonka Forest population for instance heterozygosity of the ShDH locus was decreasing with progressing age while it was increasing in the population from Bukowno. On the average, however, the value of H_0 coefficient was increasing in both populations from the youngest group of embryos (E) to the oldest age group (M). Between the two populations differences were observed both in the heterozygosity level and in the dynamics of its increase. In the Zielonka Forest population heterozygosity was maintained at a similar level in the first three age groups and in-

creased subsequently by approximately 6% in the oldest group (in relation to the embryos population). In the Bukowno population, the main increase in heterozygosity level (by approximately, 12%) was noted on transition from group E to groups S (embryos and the youngest individuals).

The WRIGHT's fixation index F, illustrating whether the individual groups remain in Hardy-Weinberg proportions, demonstrated an excess of homozygotes among embryos in both populations. In the Bukowno population the excess was noted in all age groups. On the other hand, in the Zielonka Forest population the value of the F index is close to the Hardy-Weinberg proportions in the group of the youngest individuals (S) and it is showing an excess of homozygotes in the older age groups. Overall values for the whole studied sample showed that the population from Zielonka was in Hardy-Weinberg proportions
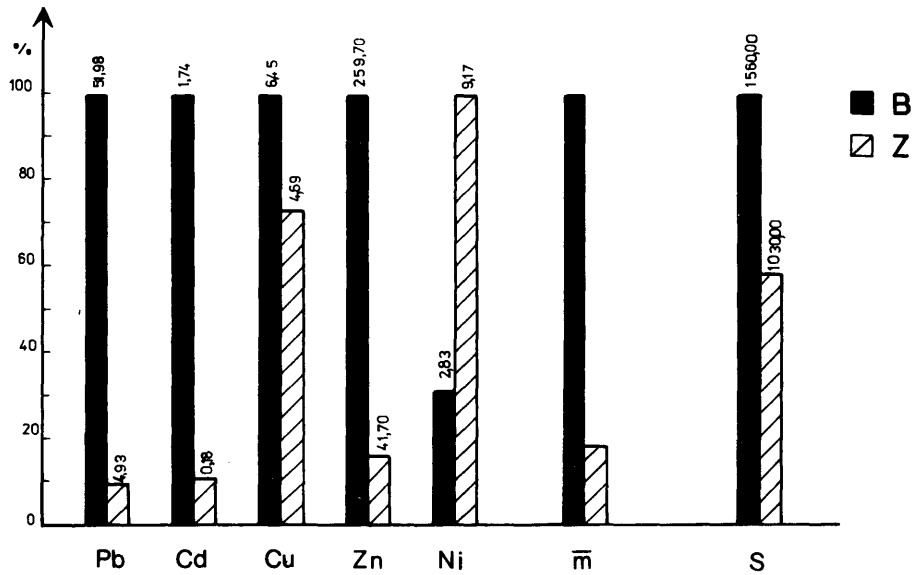
m — mean value for the heavy metals.

Figure 1. — Contents of heavy metals and sulphur in two year old needles of the studied populations from Bukowno (B) and from the Zielonka Forest (Z). (μg per 1 g of dry matter). In percent the relative contents of the elements in the needles.
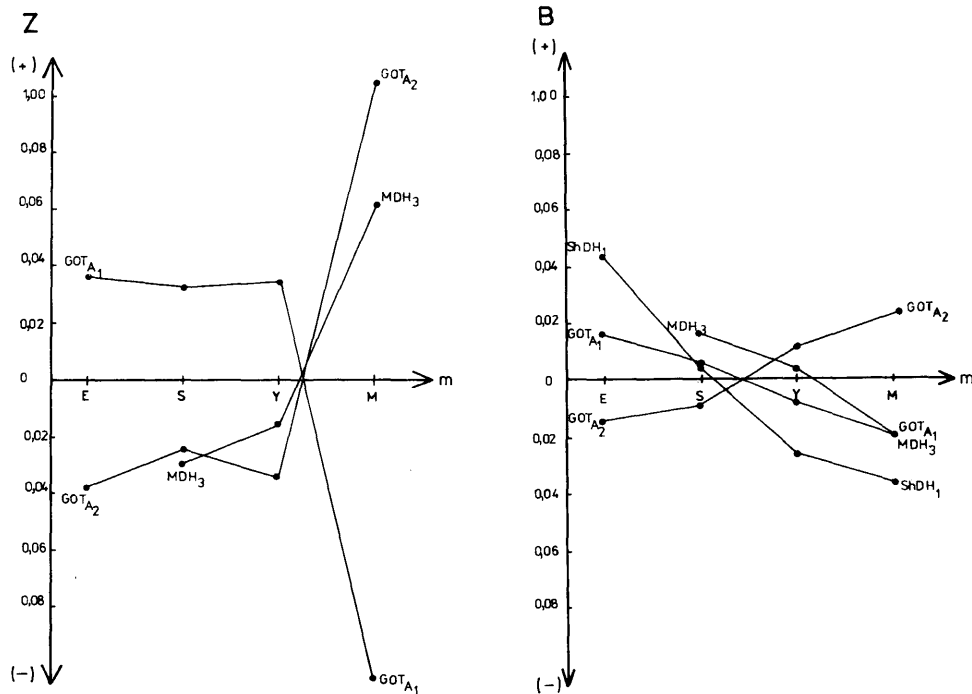

Figure 2. — Dynamics of changes in frequencies of some alleles in age groups of the studied populations. E — group of embryos, S — trees 3 to 10 years old, Y — 15 to 30 years and M — maternal trees over 30 years old. Z — population from the Zielonka Forest, B — from Bukowno For details see text.

(F = 0) while the Bukowno population contained an excess of homozygotes (F = 0.059) (*Fig.* 4).

Changes in values of genetic polymorphism indices (Pg) in age groups of both populations are illustrated in *Figure 5*. The greatest increase in polymorphism, reaching 80%, was noted in the GOT A locus in both the Zielonka Forest and the Bukowno populations. Significant increase in polymorphism was noted also for the ShDH loci (approximately 45%) and those of Est F (approximately 20%)

in the population from Bukowno. On the average, genetic polymorphism level (Pg) increased in studied loci by 10% in the Zielonka Forest population and by 20% in the Bukowno population. As was the case with heterozygosity, the main increase in genetic polymorphism level was noted in the Zielonka Forest population between groups Y and M, and, in the Bukowno population, between embryos population and the youngest age group (groups E and S, respectively).
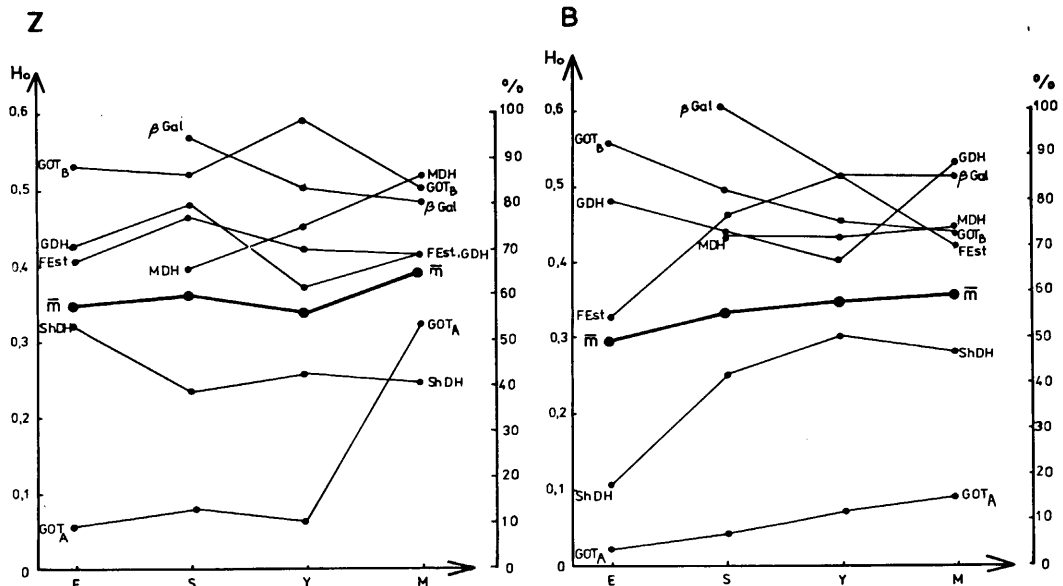
Figure 3. — Changes of indices of heterozygosity (H_0) in age groups of the studied populations. m — mean value for the all studied loci. Description of the age groups as in Figure 2.
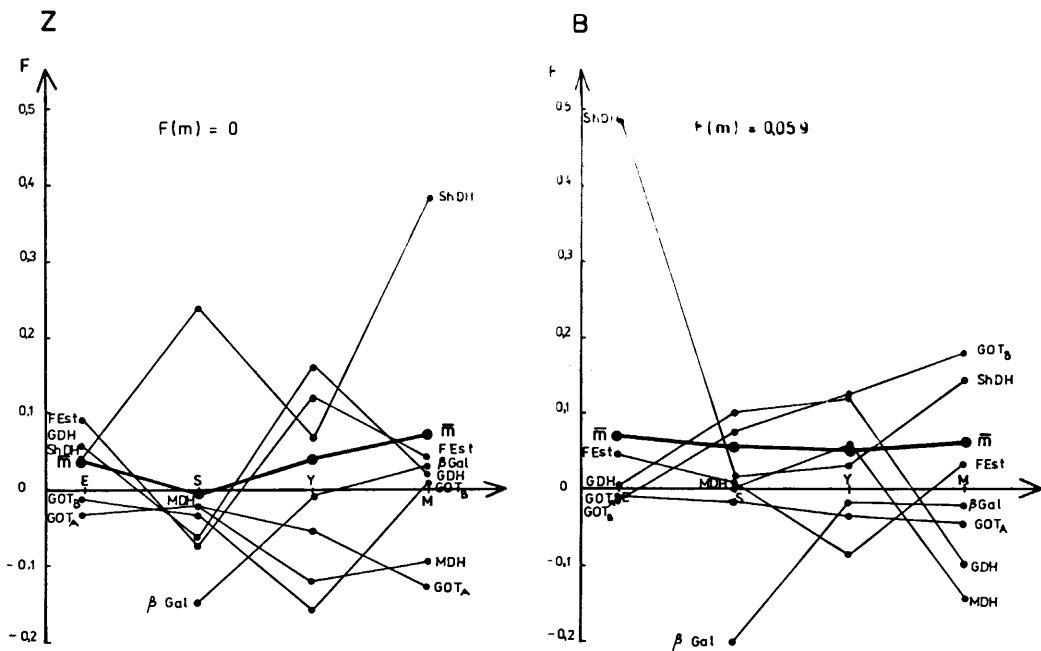

Figure 4. — Fixation indices (F) in age groups of the studied populations. F(m) — mean value for all investigated loci and the age groups. Other explanations as in Figure 2.

Discussion

Studies of demographic processes in forest trees populations are of basic importance for the understanding of the complex adaptive processes taking place in such populations. The processes are particularly intense in naturally regenerating populations and involve drastic reduction in population density through elimination of seedlings and young individuals. For example a population consisting in the initial phase of 100,000 individuals per ha may end up with approximately, 100 trees (TIGERSTEDT et al., 1982). Examination whether the processes are stochastic or whether they result from selection of defined genotypes was not possible until isoenzymatic markers have been introduced to genetic and demographic studies (SCHALL

and LEVIN, 1976). Studies performed so far on the genetic structure of tree population in a demographic aspects have usually considered two age groups: the embryo population and the population of maternal trees, or have been conducted in such a way that they have not permitted monitoring changes. taking place during the formation of the genetic structure of a population (LINHARD et al., 1979; RUDIN and TIGERSTEDT, 1979; SHAW and ALLARD, 1982; TIGERSTEDT et al., 1982; YAZDANI et al., 1985).

Our studies on the genetic structure of different age groups in naturally regenerating pine populations from regions under strong or weak anthropogenous pressure have allowed us to define the dynamics of changing in their genetic structure, beginning at the embryos popu-
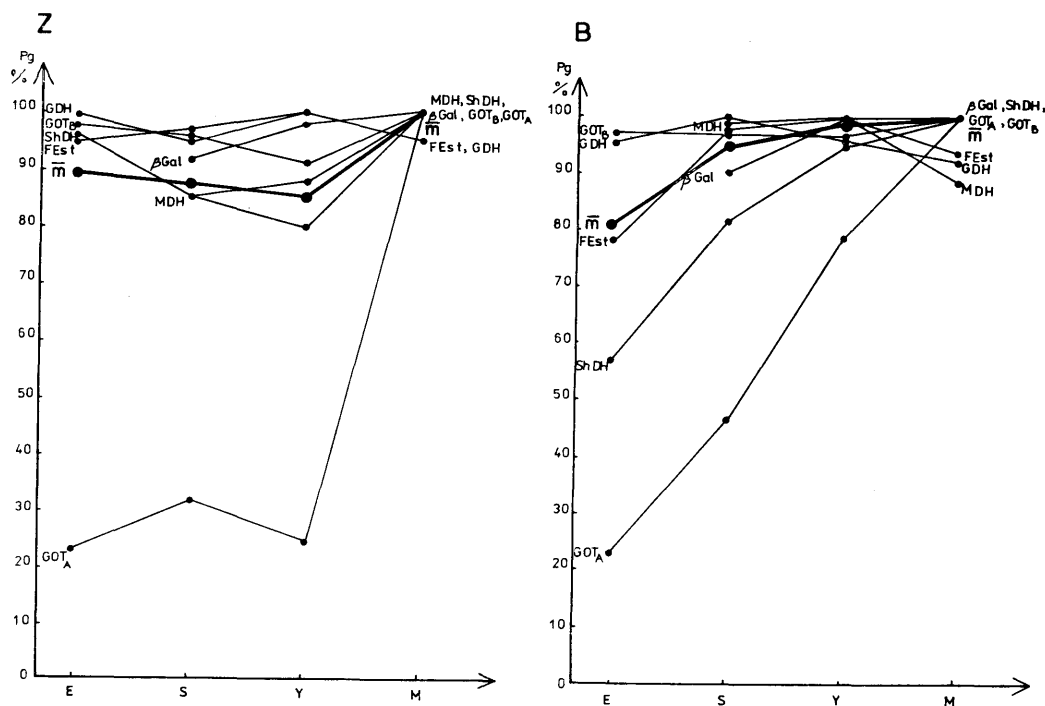
Figure 5. — Changes of genotypic polymorphism indices (Pg) in the age groups of investigated populations. Other explanations as in Figure 2.

lation and ending with maternal trees group. While it is difficult to compare directly adaptive strategies of the two populations due to their different origin and not equal environmental pressures, similar tendencies are observed in the two populations, as far as changes in the frequency of some alleles and genotypes in age groups. This concerns alleles of GOT A, GOT B and ShDH loci. Common tendencies observed in this study permit to suggest that in both populations a similar density selection operates, linked most probably to overcrowding of seedling and young trees populations. In the case of the Bukowno population, the selection is accelerated by additional action of the anthropogenic factors (Table 1, 2, Figure 5).

Interestingly that the same alleles and genotypes have shown in some cases reciprocal tendencies in the two populations. This pertains, for instance, MDH 3 allele and MDH 13 genotype. In the Zielonka Forest population the number of trees carrying the alleles increases while it decreases in the Bukowno population. Frequency changes in MDH alleles may constitute a good index of the selective processes in P. silvestris populations polluted by SO_2 as already indicated by MEJNARTOWICZ (1983). Directional changes in allele frequencies from E to Y in Est F locus in the Bukowno population which have not been observed in Zielonka Forest population, allow to suggest that alleles in the locus may provide a marker of selective pressure resulting from industrial pollution. Comparing allele and genotype frequencies in individual age groups in Bukowno population one can note that most of the directional changes pertains the first three age groups (E, S, Y). In the group of maternal trees, the tendencies are not observed (Tables 1 and 2). This may point to existence in the population of two adaptive peaks. One of the peaks has been reached by the maternal trees (M) before intense industrial pollution started (approximately 30 years ago) while the other peak characterizes the group of progeny - trees subjected to strong anthropogenous pressure. As far as changes in the genetic structure of the two populations

are concerned, an increase in average heterozygosity level (H_0) and in genotypic polymorphism (Pg) have been observed (Fig. 3, 5), from the embryos group to the population of maternal trees. In the Zielonka Forest population, the increase has been observed upon transition from group Y to group M (by 5% H_0 and 10% Pg). In Bukowno population, H_0 and Pg values have increased most rapidly upon transition from embryos group (E) to the group of youngest individuals (S): by 10% H_0 and 20% Pg. The observed differences between populations most probably reflect differences in selective pressures which are stronger for the Bukowno population (and directed mainly to embryos and seedlings populations). Fixation index (F) (Fig. 4), shows that the whole Zielonka Forest population remains in a Hardy-Weinberg proportions (m F = 0) while the population from Bukowno is demonstrating some excess of homozygotes in all age groups (m F = 0.059). Deviation from Hardy-Weinberg proportions in the Bukowno population may point to directional selective processes.

Adaptive strategy of the two populations is connected with an increased level of genetic variability (H_0 and Pg), relatively higher (by approximately 100%) in the industrially polluted population (Fig. 3 and 5). The results correspond to those of MÜLLER-STARCK (1985), obtained for Fagus silvatica and for trees of Pinus sylvestris (GEBUREK et al., 1987) resistant and sensitive to air pollution. It is difficult to assume that the observed adaptive strategies are universal for most tree populations due to the complexity of factors which may affect the dynamics and direction of adaptive processes in these organisms. However, it seems that the obtained results provide indications as to directions for further studies on adaptive processes under anthroprogeneous pressure.

Acknowledgements

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Genetic Variance and "C" Effects in Balsam Poplar Rooting

By R. E. Farmer Jr., M. Freitag and K. Garlick[1])

Summary

Dormant cuttings of Populus balsamifera L. clones from six natural populations between latitudes 45⁰ N and 54⁰ N at longitude 90⁰ W were propagated to (1) evaluate the pattern of genetic variance in number of roots and (2) assess the influence of environmental preconditioning on variance in rooting. Geographical source accounted for less than 10 percent of variance in number of roots per cutting. Clonal variance within populations ranged from 15 percent to 81 percent of total variance, depending upon collection time between November and April. Physiologically dormant cuttings propagated in September rooted poorly. Environmental preconditioning associated with primary ramets in a nursery or in a long-term field test was not a statistically significant source of variance.

Key words: Rooting, genetic variance, environmental preconditioning.

Introduction

Rooting of cuttings via growth of preformed root primordia has been extensively studied in Populus mostly with interspecific hybrids, and variation in root development has been associated with cutting size and location on parent plant (e. g. Bloomberg, 1959, 1963; Smith and Wareing, 1972b), carbohydrate reserves (e. g. Smith and Wareing, 1972b; Fege and Brown, 1984), dormancy (Smith and Wareing, 1972a, b; Cunningham and Farmer, 1984), and rooting environment (see Zsuffa, 1976; and Fege, 1983 for reviews). However, since most of the studies have involved small numbers of clones, our knowledge of genetic variation in rooting is incomplete. A study in P. deltoides Bartr. ex Marsh (Wilcox and Farmer, 1968) revealed moderate genetic control over number of roots and demonstrated that rooting was positively correlated with resumption of shoot growth; environmental preconditioning, or "C" effects, (Lerner, 1958) accounted for about 10 percent variance in rooting. Thielges and Beck's (1976) observations in P. deltoides led them to hypothesize that growth of root primordia causes bud break. They reported variable broadsense heritabilities for both dates of root initiation (h^2 = .33 to .95) 2nd bud break (h^2 = .51—.98). While broad phenotypic variation in number of roots per cutting has been observed in balsam poplar (Populus balsamifera L.) by Cunningham and Farmer (1984), genetic control of this variation has not been reported.

Under natural conditions, the presence of preformed root primordia on balsam poplar probably has some fitness value under circumstances where flooding may deposit soil

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