ISOENZYMATIC VARIABILITY IN SOME OF THE POLISH POPULATIONS OF NORWAY SPRUCE (*PICEA ABIES*) IN THE IUFRO – 1972 PROVENANCE TRIAL

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ABSTRACT

The isoenzymatic studies performed on nine *Picea abies* H. Karst populations from Poland, indicated considerable genetic variation among investigated stands. Genetic similarities have demonstrated a clear pattern of geographic variability. Three of the nine studied populations (Zwierzyniec, Nowe Ramuki and Orawa) have shown markedly diverse characteristics compared to the remaining populations. The mountain populations have formed one group with two related subgroups. The mean number of alleles per locus ($A/L = 2,22$) and level of heterozygosity ($H_O = 0,194$) for the lowland populations are within the range of these parameters for other Norway spruce populations from Finland and Lithuania. The populations from Carpathians and Sudety mountains are genetically more polymorphic ($H_O = 0,221$, $A/L = 2,34$) than the others. This pattern of genetic variation suggests the existence of two gene pools, one from southern and one from northern Poland formed during the glacial period and differentiated further in southern Poland into two subpools.

KEY WORDS: *Picea abies*, isoenzymes, genetic variation.

INTRODUCTION

Studies on genetic structure of the Norway spruce (*Picea abies* H. Karst) populations have been conducted by several investigators. Among them, studies of Lagerkranz and Ryman (1990), Liesebach et al. (1992) and those of Gömöry and Paule (1993) seem the most complex and involve the largest number of populations and enzymatic loci. The studies present isoenzymatic variability in 20-30 of Norway spruce stands from throughout the species range in Europe. In the studies, the authors have also included Polish populations. However, previous studies have bypassed certain interesting aspects of the subject, linked to biogeography and ecology of the species in Poland. In this respect, the post-glacial history of *Picea abies* in Europe and recolonisation pathways of areas freed by the subsiding continental glacier following the last glaciation present particularly interesting problems when confronted with the present genetic differentiation of Norway spruce populations.

According to Schmidt-Vogt (1974, 1977), Norway spruce colonized northern Poland from refuges in central Russia and penetrated the area of southern Poland from a refuge in the East Carpathian Mountains. Spreading of gene pools from

glacial refuges and potential intersections of the migration pathways undoubtedly could affect the genetic structure of the Polish Norway spruce populations. The so called middle Polish disjunction represents another interesting problem concerning spruce distribution in Europe. Some authors are of the opinion that the disjunction is a secondary phenomenon (Środoń 1967, Chylarecki and Giertych 1969, Ralska-Jasiewiczowa 1983). Other authors expect that the disjunction has historic background, linked to spruce migration pathways and ecological conditions unfavourable for the species in the middle of Poland (Schmidt-Vogt 1974, 1977). The southern limits of the range of Norway spruce in Poland coincide with the Sudety and Carpathian mountains. With the vast vertical range of Norway spruce diverse phenological and genotypic adaptations to the environmental (elevational) gradient are connected (Bergmann 1978, Modrzyński 1993, 1995, Oleksyn et al. 1997).

The above mentioned phenomena remain relatively unclarified from the genetical point of view, particularly in the micro-scale of specific mountain ranges. Broadly defined human activity also represents an important factor which shapes the specific gene pool of a population by introduction of foreign seed sources, by silvicultural practices as well as by the selective action of industrial pollution. On one hand, certain prac-

tices may enrich the gene pools of local populations but, on the other hand, contamination of forests and silvicultural activities may leads to an erosion of the gene pool of this species (Scholz and Bergmann 1984, Gregorius at al. 1985, Scholz 1986, Bergmann and Scholz 1987, Prus-Głowacki and Godzik 1995).

The aim of present study was to define the genetic structure and reciprocal taxonomic relations in nine *Picea abies* populations, originating from the northern, lowland portion of the species range in Poland and from the mountain regions in southern Poland. The studied populations are part of the international IUFRO-1972 provenance experiment with 20 Polish Norway spruce populations.

MATERIAL AND METHODS

The studies were performed on seeds of 9 *Picea abies* (Fig. 1) out of 20 Polish populations of the species included the IUFRO-1972 provenance experiment. The seeds were provided by Jon Dietrichsen (Department of Forestry, Agricultural University of Norway in As) at the beginning of 1985. The seeds were stored between 1971 and 1981 at 2°C and later at -10°C. Seeds were collected from cones obtained on at least 25 trees in each maternal population. Three of the populations (1, 6, 20) represented lowland habitats and the remaining ones originated from mountain stands. Geographic coordinates of the populations and their elevation are given in Table 1.

Approximately 150 to 250 seeds of each population were placed on a wet filter paper in Petri dishes, and incubated under controlled light and temperature conditions, which correspond to the day-night cycle, the temperature in the growth chamber was 25–27°C for 13 h and, then, 18–20°C for 11 h. The germinating seeds were illuminated for 16 h and this was followed by 8 h of darkness. The filter paper in Petri dishes and the seeds were moistened regularly using water containing Captan 50 W fungicide at 5 ml per 1000 ml distilled water.

For isoenzyme analysis, a random sample of 60 macrogametophytes was chosen from each population.

The macrogametophytes, following embryo removal, were placed on extraction plates at -15°C and on the following day enzymatic proteins were extracted. Macrogametophytes were

Fig. 1. Geographic location of the origin of seed samples used in the study.
NR – Nowe Ramuki, ZW – Zwierzyniec, BL – Bliżyn, TA – Tarnawa, OR – Orawa, RY – Rycerka, WI – Wisła, IS – Istebna, MI – Międzygórze.

ground in 0.2 M phosphate buffer (pH 7.5) consisting of 3.84 g monobasic sodium phosphate and 23.86 g dibasic sodium phosphate per liter of distilled water. Application strips of Whatman MM3 filter paper were soaked in the extract of an individual macrogametophyte and starch gel electrophoresis was conducted according to a modified procedure of Conkle et al. (1982). Genetic interpretation of electrophoretic patterns was based on preliminary experiments, in which allele segregation in mendelian ratios was tested (Prus-Głowacki and Modrzyński, 1998 in preparation). The examined enzymatic systems and numbers of loci are listed in Table 2. Using the Biosys 1 program (Swofford and Selander 1981) genetic parameters were calculated for the studied populations, including: frequency of alleles, number of alleles per locus, observed and expected heterozygosities, relatedness and ge-

TABLE 1. Data on geographic and topographic location of *Picea abies* populations studied.

No of population*	Forest district	Forest range	Geographical		Elevation m a s l
			longitude	latitude	
1	Zwierzyniec	Pogorzelce	52°48'	23°47'	160
6	Nowe Ramuki	Przykop	53°41'	20°34'	160
8	Międzygórze	Wodospad	50°13'	16°45'	580
10	Wisła	Malinka	49°38'	18°53'	710
12	Istebna	Zapowiedź	49°32'	18°58'	600
14	Rycerka	Praszywka	49°29'	19°00'	700
16	Orawa	Sokoliki	49°34'	19°33'	1050
18	Tarnawa	Stańcowa	49°05'	22°52'	750
20	Bliżyn	Świnia Góra	51°04'	20°41'	310

* Number used in provenance experiment trial IUFRO 72.

TABLE 2. List of analysed enzyme systems.

Enzyme systems	Abbreviation	EC number	Number of loci
Aconitase	ACO	4.2.1.3.	1
Acid phosphatase	ACP	3.1.3.2.	2
Alanine dehydrogenase	ALA	1.4.1.1.	1
Aldolase	ALD	4.1.2.13.	1
β -galactosidase	β GAL	3.2.1.22.	1
Catalase	CAT	1.11.1.6.	1
Fructose-1,6-diphosphatase	FDP	3.1.3.11.	2
Fluorescent esterase	FEST	3.1.1.1.	1
Fumarase	FUM	4.2.1.2.	1
Aspartate aminotransferase	GOT	2.6.1.1.	3
Isocitrate dehydrogenase	IDH	1.1.1.42.	2
Leucine aminopeptidase	LAP	3.4.1.1.	2
Malate dehydrogenase	MDH	1.1.1.37.	4
Menadione reductase	MNR	—	1
Phosphoglucosomerase	PGI	5.3.1.9.	2
Phosphoglucosomutase	PGM	2.7.5.1.	2
Glucose-6-phosphate isomerase	6PGI	5.3.1.9.	1
Uridine-5-glucose pyrophosphatase	UGPP	2.7.7.9.	1
Shikimate dehydrogenase	SKDH	1.1.1.25.	1

netic distances according to Nei and Cavalli-Sforza-Rogers. Minimum spanning trees and dendrograms were constructed using UPGMA technique (Sneath and Sokal 1973). Deviation from Hardy-Weinberg equilibrium was tested, calculating the fixation index F according to Wright (1965). Measures of genetic diversity among and within populations were defined by calculating the following indices: total gene diversity (H_T),

gene diversity within populations (H_S) and among populations (DST). The relative degree of genetic differentiation among populations was also studied (GST).

RESULTS

Isoenzymatic analysis of 30 loci in nine Polish populations of *Picea abies* demonstrated presence of a total 106 alleles. A maximum number of 6 alleles per locus was noted for ACP1 and IDH1. Some of the loci were monomorphic. Among the 30 loci proved to be polymorphic at 95% and 99% criterion levels 73.33% and 57.78% loci respectively. At 95% criterion, the values ranged from 43.33% in Nowe Ramuki (6) population to 66.67% in Międzygórze population (8). At 0.99 criterion level, the highest number of polymorphic loci was noted in mountain population from Rycerka (14) – 83.33%, Istebna (12) – 80.0% and Międzygórze (8) – 80.0% and the lowest number of polymorphic loci in the population from Orawa (16) – 66.67%.

The mean number of alleles per locus ranged from 2.13 in Nowe Ramuki population (6) to 2.47 in Wisła population (10). The group containing a high mean number of alleles per locus (2.40 A/L) also included mountain population from Istebna (12) and Międzygórze (8). For all studied populations, the mean number of alleles per locus was 2.3 (Table 3).

The genetic differentiation of the studied populations, as expressed by the heterozygosity level, proved that the populations were not homogenous in this respect. The lowest level of heterozygosity was observed in lowland populations from northern Poland (Nowe Ramuki (6) – 0.196 and Zwierzyniec (1) – 0.185), the highest heterozygosity was found in the neighbouring populations from Wisła (10) and Istebna (12) ($H_0 = 0.230$ and 0.228 , respectively). The mean value of observed heterozygosity, H_0 , was 0.212 for the entire group (Table 3). The fixation index F , which demonstrates deviations from Hardy-Weinberg's equilibrium, showed that population Zwierzyniec (1) contained a significant excess of homozygotes, as compared to other populations. The mountain population from Międzygórze (8) also deviated from Hardy-Weinberg's equilibrium, demonstrating a high homozygosity. The Tarnawa population (18) from the Bieszczady Mountains showed an excess of heterozygotes. In general, however, the exami-

TABLE 3. Some of the genetic parameters for the studied populations of *Picea abies*. H_B – mean heterozygosity per locus (biased estimate), H_U – mean heterozygosity per locus (unbiased estimate), H_0 – observed heterozygosity, A/L – mean number of alleles per locus, F – fixation index, S_E – standard error, $\bar{x}$ – mean for the populations.

	Populations	H_B	S_E	H_U	S_E	H_0	S_E	A/L	S_E	Polymorphism at criterion		F
										95%	99%	
1	Zwierzyniec	0.205	0.037	0.209	0.038	0.185	0.034	2.33	0.23	56.67	73.33	0.115
6	Nowe Ramuki	0.198	0.042	0.202	0.042	0.196	0.042	2.13	0.24	43.33	60.00	0.030
8	Międzygórze	0.224	0.041	0.228	0.041	0.212	0.039	2.40	0.23	66.67	80.00	0.070
10	Wisła	0.231	0.042	0.235	0.042	0.230	0.042	2.47	0.25	63.33	76.67	0.021
12	Istebna	0.226	0.036	0.230	0.036	0.228	0.037	2.40	0.23	63.33	80.00	0.008
14	Rycerka	0.203	0.038	0.207	0.038	0.210	0.041	2.33	0.18	53.33	83.33	-0.014
16	Orawa	0.209	0.038	0.212	0.039	0.213	0.040	2.27	0.22	56.67	66.67	0
18	Tarnawa	0.216	0.040	0.220	0.040	0.234	0.044	2.17	0.18	56.67	70.00	-0.063
20	Bliżyn	0.200	0.036	0.204	0.037	0.202	0.036	2.20	0.21	60.00	70.00	0.010
	$\bar{x}$	0.212		0.216		0.212		2.30		57.78	73.33

Fig. 2. A – genetic distances acc. to Wagner Tree Procedure, B – dendrite based on Cavalli-Sforza-Rogers similarity coefficients.

ned populations seemed to approximate Hardy-Weinberg's equilibrium (Table 3).

The analysis of gene diversity of the individual loci, is illustrated in Table 4. The mean total gene diversity, H_T , was 0.223, gene diversity within populations, H_S , was 0.215 and gene diversity among populations, D_{ST} , was 0.008. The value of the G_{ST} coefficient, accepted as a relative index of genetic differentiation of studied populations, was 6.3%.

Genetic relationships among the studied populations within individual loci is demonstrated in the minimum spanning tree in Fig. 2A.

Cluster analysis according to Cavalli-Sforza and Edwards (after Swofford and Selander 1981) showed that populations from Zwierzyniec (1), Nowe Ramuki (6) and Orawa (16) differed the most from each other compared to the remaining populations. Populations from the Beskidy Mountains formed a single group and were most closely related to Międzygórze population (8) in the Sudety Mountains. The geographically distant populations from Tarnawa (18) in the Bieszczady Mountains and from Bliżyn (20) in the Świętokrzyskie Mountains formed a separate pair.

The dendrite (Fig. 2B), constructed on the basis of minimum genetic distances and illustrating reciprocal taxonomic relations between populations by the closest neighbourhood method, demonstrated a central position for the Bliżyn population (20), with the related populations from Orawa (16), Tarnawa (18), Rycerka (14) and Wisła (10). The population from Istebna (12) and the lowland population from Nowe Ramuki (6) related to the population from Rycerka (14). Another lowland population from Zwierzyniec (1) was linked to the population from Międzygórze (8) and the latter one with the mountain population from Wisła (10).

Analysis of genetic relatedness using Cavalli-Sforza and Edwards coefficient (Swofford and Selander 1981) and the Distance Wagner Tree Procedure (Fig. 2A) demonstrated that the two lowland populations, Zwierzyniec (1) and Nowe Ramuki (6), formed a single cluster with the high mountain population from Orawa (16). The mountain populations formed another cluster with Międzygórze population (8) referring to the population from Wisła (10). The population from Bliżyn (20) and the genetically distant population from Tarnawa (18) in Bieszczady Mountains were closely related to the group (Fig. 2A).

Analysis of genetic relatedness on the basis of Nei's distances demonstrated population clusters similar to those detected by the Cavalli-Sforza-Edwards and Distance Wagner Tree procedures described above.

DISCUSSION AND CONCLUSIONS

The percentage of polymorphic loci, used as a measure of population differentiation, has indicated that the lowland populations possess a lower number of polymorphic loci (with the mean of about 58%), as compared to the mountain populations (mean of around 67%). This is particularly evident at criterion level of 0.95. This pattern in variability may reflect the ecological differentiation of mountain populations which inhabit various mountain ranges (Table 3).

Calculated genetic parameters were in a rank noted by other authors. The observed heterozygosity, H_O , was 0.212 (minimum value of 0.185 and maximum value of 0.234) for the nine Polish populations. The value resembles that obtained for populations from Finland, $H_O = 0.23$ (Muona et al. 1987). On the other hand, Goncharenko et al. (1993) and Krutowski and Bergmann (1993) found H_O values of 0.185 and 0.254 for 5 populations in Lithuania and 6 populations in other regions of Europe from Central Russia to Germany and Sweden, respectively. Thus, the H_O value obtained in our studies for 30 loci is somewhat lower than the estimate of Krutowski and Bergmann (1993) but slightly higher than those for Lithuanian populations. Giannini et al. (1991) studied 17 enzymatic loci in 9 populations of *Picea abies* in northern Italy and obtained H_O mean value of 0.179. Gömöry and Paule (1993), on the other hand, obtained markedly higher H_O values for Norway spruce populations in the Slovak Carpathians: 0.27 to 0.40 for 10 and 15 polymorphic loci, respectively. The authors explained a high heterozygosity level relative to the post-glacial history of Slovakian Norway spruce originating from more than one glacial refuge in the Southern Carpathians and in Rumania. The high value of H_O in Gömöry and Paule (1993) studies is a result of analysing exclusively polymorphic loci (only GOT A was monomorphic in some populations). The populations studied in this project, including the lowland populations from the northern range limits in Poland, have shown heterozygosity values closely related to values published for the geographically adjacent populations from Lithuania ($H_O = 0.185$ and $H_O = 0.196$) but lower than values for the Carpathians and Sudety Mountains.

The mean numbers of alleles per locus have proven similar for populations from northern Poland and from Lithuania and were 2.26 in Lithuanian populations and 2.3 in Polish populations against the range of the index between 2.13 and 2.47. In Italian populations showed generally a lower mean number of alleles per locus (1.83, ranging from 1.66 to 2.04 A/L). The similar pattern of genetic variability in the Polish and Lithuanian Norway spruce populations may originate from a common

TABLE 4. Genetic differentiation of *Picea abies* populations from Poland in the studied loci.

Locus	No. of alleles	H _T	H _S	D _{ST}	G _{ST}
ACO	5	0.470	0.460	0.010	0.021
ACP 1	6	0.636	0.605	0.031	0.048
ACP 2	4	0.443	0.441	0.002	0.004
ALA 2	3	0.080	0.078	0.002	0.025
ALD 1	2	0.128	0.125	0.003	0.023
βGAL	2	0.037	0.032	0.005	0.135
CAT	2	0.008	0.007	0.001	0.125
FDP 1	4	0.338	0.321	0.017	0.050
GDP 2	3	0.069	0.068	0.001	0.014
Fest	2	0.033	0.072	0.011	0.333
FUM	4	0.396	0.385	0.011	0.027
GOT 1	3	0.063	0.060	0.003	0.047
GOT 2	3	0.012	0.011	0.001	0.083
GOT 3	3	0.497	0.490	0.007	0.014
IDH 1	6	0.098	0.089	0.009	0.091
IDH 2	2	0.012	0.011	0.001	0.083
LAP 1	5	0.573	0.564	0.009	0.015
LAP 2	6	0.374	0.374	0.000	0.000
MDH 1	3	0.151	0.134	0.017	0.112
MDH 3	2	0.164	0.157	0.007	0.042
MDH 4	6	0.507	0.494	0.013	0.025
MDH 5	3	0.055	0.053	0.002	0.036
MNR 2	3	0.041	0.039	0.002	0.048
PGI 1	2	0.004	0.003	0.001	0.250
PGI 2	4	0.464	0.455	0.009	0.019
PGM 1	3	0.044	0.043	0.001	0.022
PGM 2	3	0.377	0.364	0.013	0.034
6PGI	2	0.048	0.043	0.005	0.104
UGPI	5	0.467	0.445	0.022	0.047
ShDH	5	0.108	0.106	0.002	0.018
Mean	Σ = 106	0.223	0.215	0.008	0.063

post-glacial origin and similar climatic conditions existing in northern Poland and Lithuania (Chylarecki and Giertych 1969, Schmidt-Vogt 1974).

Within population genetic differentiation, D_{ST} was relatively low (0.008) while the G_{ST} index, which reflects relative inter-population genetic variability, was relatively high averaging 0.063 for all populations and 0.061 for the mountain populations. Thus, the latter index has proven markedly higher than that obtained by Goncharenko et al. (1993) for Lithuanian populations of Norway spruce from a relatively restricted geographic region (0.018). For Italian populations of the species, the G_{ST} index has been higher than for Lithuanian populations but lower than in Polish populations, averaging 0.042 (Giannini et al. 1991). Studies of Krutowski and Bergmann (1993) on spruce populations ranging from Germany to Central Russia have demonstrated a G_{ST} index value higher by about 2% (0.084), compared to our results.

Six of the populations studied by us have remained in Hardy-Weinberg's equilibrium while three of the populations exhibited deviations from the equilibrium, expressed in the fixation index F (according to Wright 1965). Two of the lat-

ter populations (Zwierzyniec (1) and Międzygórze (8) populations) showed a marked excess of homozygotes, while the third one (Nowe Ramuki (6) population) much higher than expected homozygosity level (Table 3).

Genetic relatedness of the studied populations, calculated by three different methods, i.e. by Nei's cluster analysis (UPGMA), according to Cavalli-Sforza and Edwards (chord distance – not shown) or according to Wagner (Wagner tree Fig. 2A) have demonstrated a clear pattern of geographic variability. Three of the nine studied populations have shown markedly diverse characteristics compared to the remaining populations as well as between each other. The group contains two lowland populations (Nowe Ramuki (6) and Zwierzyniec (1)) and the high mountain population from Orawa (16). The remaining mountain populations have formed two related groups. This pattern suggests the existence of two gene pools, one from southern and one from northern Poland formed during the glacial period and differentiated further in southern Poland into two subgroups. The genetic similarity of the mountain populations may reflect their common origin and post-glacial migrations. However, we are not able to ex-

clude effects of other factors which might affect the gene pools in mountain populations.

One such influence might involve the geographic proximity of the studied populations and possible gene flow among them, which can result in an uniform genetic structure of gene pools. Another factor capable of inducing genetic similarity involves similar ecologic and climatic conditions in the examined geographic regions inducing directed selection and, thus shaping (in the similar manner) genetic composition of examined populations. Such effects could have taken place even in the case of seed introduction from other regions. This question seems to be, however, difficult to solve at present due to the lack of data which could document the autochthonous character of the populations or their introduction from other regions of Europe (Modrzyński 1991, 1993). In this respect, the clear differences of Orawa population (16) from the remaining mountain populations is of interest, as it grows at the highest elevation above sea level (1050 m) and in parallel shows certain similarities to populations from northern Poland. The genetic divergence of the population may reflect its high mountain character and its similarity to populations from northern Poland may originate from climatic similarities. It is

known that a 100 m difference in elevation above sea level is an equivalent of a 100 km northward shift of the habitat (Czarnowski 1993). On the other hand, a common artificial origin of populations from Orawa (16) and of those from northern Poland cannot be excluded, with the subsequent differentiation due to adaptive processes. The dendrite illustrating genetic relatedness based on the closest neighbourhood method, illustrates the specific intermediate position of Bliżyn population (20) in the Świętokrzyskie Mountains, located between northern Poland and mountains of southern Poland (Fig. 1). Also the remaining genetic parameters (Table 3) confirm the intermediate character of Bliżyn population. If the population is autochthonous, the geographic region may be regarded as a gene pool mixing pot for the northern pathway of migrating spruce in the post-glacial period on one hand and the spruce migrating from the South on the other (Chylarecki and Giertych 1969).

Our preliminary studies have demonstrated the existence of genetic differentiation among Polish *Picea abies* populations. Therefore, further studies are planned on more populations from a broader geographic range using a large number of polymorphic loci.

TABLE 5. Gene diversity (H_e) of 30 loci in specific populations of *Picea abies* from Poland. H_s — mean value for studied populations.

Locus	1	2	3	4	5	6	7	8	9	H_s
ACO	0.414	0.344	0.445	0.553	0.463	0.510	0.495	0.467	0.453	0.460
ACP 1	0.566	0.411	0.745	0.763	0.512	0.668	0.572	0.615	0.595	0.605
ACP 2	0.437	0.477	0.341	0.446	0.414	0.472	0.460	0.398	0.526	0.441
ALA 2	0.033	0.000	0.097	0.098	0.098	0.097	0.000	0.215	0.066	0.078
ALD 1	0.127	0.033	0.127	0.183	0.097	0.066	0.000	0.259	0.235	0.125
βGAL	0.259	0.033	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032
CAT	0.000	0.000	0.000	0.033	0.000	0.033	0.000	0.000	0.000	0.007
FDP 1	0.097	0.499	0.305	0.345	0.325	0.450	0.345	0.259	0.264	0.321
FDP 2	0.000	0.000	0.033	0.000	0.264	0.129	0.158	0.033	0.000	0.068
Fest	0.000	0.066	0.033	0.033	0.000	0.033	0.000	0.000	0.033	0.072
FUM	0.396	0.567	0.216	0.292	0.373	0.324	0.382	0.581	0.333	0.385
GOT 1	0.033	0.033	0.066	0.127	0.155	0.033	0.000	0.000	0.100	0.060
GOT 2	0.000	0.000	0.000	0.000	0.033	0.000	0.033	0.033	0.000	0.011
GOT 3	0.488	0.494	0.508	0.503	0.520	0.521	0.463	0.413	0.500	0.490
IDH 1	0.033	0.000	0.127	0.000	0.066	0.155	0.159	0.098	0.167	0.089
IDH 2	0.000	0.000	0.066	0.000	0.000	0.033	0.000	0.000	0.000	0.011
LAP 1	0.613	0.573	0.521	0.505	0.506	0.488	0.606	0.634	0.551	0.564
LAP 2	0.382	0.352	0.434	0.420	0.389	0.345	0.389	0.389	0.259	0.374
MDH 1	0.660	0.440	0.127	0.066	0.282	0.098	0.066	0.066	0.000	0.134
MDH 3	0.183	0.000	0.282	0.259	0.210	0.066	0.000	0.210	0.210	0.157
MDH 4	0.546	0.580	0.707	0.528	0.471	0.432	0.728	0.432	0.321	0.494
MDH 5	0.000	0.000	0.098	0.155	0.097	0.033	0.000	0.000	0.097	0.053
MNR 2	0.000	0.000	0.000	0.098	0.066	0.000	0.155	0.000	0.033	0.039
PGI 1	0.000	0.000	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.003
PGI 2	0.427	0.474	0.508	0.506	0.481	0.440	0.490	0.377	0.398	0.455
PGM 1	0.066	0.000	0.097	0.033	0.000	0.000	0.129	0.066	0.000	0.043
PGM 2	0.259	0.183	0.364	0.499	0.440	0.332	0.452	0.364	0.381	0.364
6PGI	0.259	0.000	0.000	0.000	0.066	0.066	0.000	0.000	0.000	0.043
UGPI	0.406	0.457	0.493	0.437	0.508	0.345	0.282	0.581	0.494	0.445
ShDH	0.164	0.033	0.098	0.098	0.066	0.033	0.273	0.098	0.097	0.106
Mean	0.228	0.201	0.227	0.234	0.216	0.206	0.222	0.219	0.203	0.217

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ZMIENNOŚĆ ISOENZYMATYCZNA
NIEKTÓRYCH POLSKICH POPULACJI ŚWIERKA POSPOLITEGO (*PICEA ABIES*)
Z DOŚWIADCZENIA PROWENIENCYJNEGO IUFRO – 1972

STRESZCZENIE

Badanie zmienności izoenzymatycznej dziewięciu populacji *Picea abies* H. Karst. wskazuje na ich znaczne zróżnicowanie genetyczne. Podobieństwa genetyczne badanych populacji wskazują na ich wyraźną zmienność geograficzną. Trzy z badanych populacji (ze Zwierzyńca, Nowych Ramuk oraz Orawy) odbiegają znacznie od pozostałych. Populacje górskie tworzą jedną grupę z dwoma bliskimi genetycznie podgrupami. Średnia liczba alleli na locus ($A / L = 2,22$) i poziom heterozygotyczności ($H_o = 0,194$) w populacjach niżowych mieszczą się w zakresach wartości notowanych dla populacji z Finlandii i Litwy. Populacje z Karpat i Sudetów są genetycznie bardziej zmienne ($H_o = 0,221$, $A / L = 2,34$) niż pozostałe. Taki obraz zmienności genetycznej sugeruje obecność u tego gatunku z badanego terenu dwóch pul genowych, jednej w południowej Polsce zróżnicowanej na dwie podgrupy, a drugiej w Polsce północnej ukształtowanych w czasie epoki lodowcowej i czasie późniejszych procesów specjacyjnych.

SŁOWA KLUCZOWE: *Picea abies*, izoenzymy, zmienność genetyczna.