TAXONOMIC POSITION OF *PINUS ULIGINOSA* NEUMANN AS RELATED TO OTHER TAXA OF *PINUS MUGO* COMPLEX

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ABSTRACT

Studies on taxonomic position of *Pinus uliginosa* Neumann, *P. uncinata* Ram. and *P. mugo* Turra, indicate a significant specificity of *P. uliginosa* population from Wielkie Torfowisko Batorowskie Peat Bog. *Pinus uncinata* in respect of genetic similarity is close to *Pinus mugo* Turra populations from the Tatra Mts. The time of divergence of *P. uliginosa* from the common ancestor, taking into account Nei's genetic distances, is twice as long as in the case of *Pinus uncinata*. In the view of the results the supposition that *Pinus uliginosa* from Wielkie Torfowisko Batorowskie Peat Bog is a marginal population of *P. uncinata* can be excluded, because of their significant difference in genetic structure. The presumable reasons of specificity of *P. uliginosa* population are discussed.

KEY WORDS: *Pinus uliginosa*, genetic structure, taxonomy, isoenzymes.

INTRODUCTION

Pinus uliginosa Neumann represents one of four native taxa of Polish pines. Its range is restricted to the Sudeten Mountains and submountainous regions, including foreland of the Sudeten Mts. Sudeten Mountains and their foreland mark the northern limits of the taxon range. The taxon was described for the first time by Neumann in 1837, in the area of the Great Peatbog "Batorowskie". The distribution of *P. uliginosa* in Poland has not been fully recognized yet due to the uncertain taxonomic position of the pine, extensive morphological variability and its disperse and "island" distribution in small stands (Boratyński 1994). For these reasons, *P. uliginosa* focused interests of multiple investigators. The studies on anatomical and morphological traits as well as chemotaxonomic investigations have failed to unequivocally determine the origin of the taxon or its relations to other native pine species. According to several authors, *P. uliginosa* should be included to the *Pinus mugo* complex and to *P. uncinata* subspecies which is growing in mountains of central Europe, the Alps and Pyrenees. In Poland, stands of *P. uliginosa* would represent marginal populations from northern limits of the *P. uncinata* range. On the other hand, some investigators are of the opinion that *P. uliginosa* represents a "minor" species within the *P. mugo* complex while still other treat it as an old hybrid between *Pinus mugo* Turra and *Pinus sylvestris* (Christensen 1987, Staszkiwicz 1993, Prus-Głowacki et al. 1978, 1981, Prus-Głowacki and Szweykowski 1979, 1983, Staszkiwicz and Tyszkiewicz 1972, Boratyński 1978, Krzakowa et al. 1984, Siedlewska and Prus-Głowacki 1995).

The chemotaxonomic and morpho-anatomical studies performed till now, pertaining to taxonomic relations of *P. uliginosa* have been restricted to a single enzymatic system, quantitative traits related to quercitine or a restricted number of morphological-anatomical traits (Krzakowa et al. 1984, Lauranson-Broyer et al. 1997). The present study is based on many more *P. mugo* and *P. sylvestris* populations and on higher numbers of individuals from *P. uliginosa* and *P. uncinata* populations, originating from the Pyrenees and they pertain to higher numbers of enzymatic loci.

The study aimed at determining taxonomic relations between three taxa of *P. mugo* complex, i.e., *P. mugo* Turra, *P. uliginosa* Neumann from populations of the locus classicus, *P. uncinata* Ram. from the Pyrenees and the species out of the complex of *P. mugo*, genetically most closer to the taxa, i.e. *P. sylvestris* L.

MATERIAL AND METHODS

The material for the studies involved winter buds, collected in 6 populations of *P. mugo* Turra from the Tatra Mountains, in 9 populations of *P. sylvestris* from central and western Europe originated from provenance trials and natural stand (Table 1), in one population of *P. uncinata* from the Pyrenees and in one locus classicus population of *P. uliginosa* from the Great Peatbog "Batorowskie" in the Sudeten. Detailed data on localisation of the populations and on numbers of examined individuals were presented in Table 1. In the study, variability was examined in the following enzymatic loci: alcohol dehy-

drogenase (ADH, E.C.1.1.1.1.), diaphorase (DIA, E.C.1.6.4.3.), fluorescent esterase (Fest, E.C.3.1.1.1.), glutamate dehydrogenase (GDH, E.C.1.4.1.3.), glutamate-oxalacetic transaminase (GOT, E.C.2.6.1.1. – 2 loci), malate dehydrogenase (MDH, E.C.1.1.3.7. – 2 loci), shikimate dehydrogenase (ShDH, E.C.1.1.1.25 – 2 loci). The analysis of isozyme variability was performed using starch gel electrophoresis, according to the procedure described by Gulberg et al. (1982), Rudin and Ekberg 1978), Szmidt and Yazdani (1984), Yazdani et al. (1985) and used in studies on *P. sylvestris*. Data on isoenzymatic variability of some populations were taken from earlier studies, performed in our Department (Siedlewska and Prus-Głowacki 1995, Szweykowski et al. 1994, Prus-Głowacki and Nowak-Bzoway 1991, Wojnicka-Półtorak 1997).

For the studied populations, the following genetic parameters were calculated: frequencies of alleles and of genotypes, mean number of alleles and of genotypes per locus (A/L, G/L), observed and expected heterozygosity (H_o and H_e), F coefficient, genetic distances and similarities according to Nei (1972), indirect estimates of gene flow (N_m) and genetic diversity among and within populations (GST and DST).

RESULTS

Frequencies of alleles in the examined populations are presented in Table 2. Populations of individual taxa markedly differed in frequencies of alleles in some enzymatic loci, as well as in presence of private alleles. The alleles for which individual taxa exhibited significantly different frequencies are shown in Table 3. They included ADH1, ADH2, GOTB1, GOTB2, MDHC1, MDHC2, GDH1, ShDHA1 and ShDHA2. In most cases, within allele frequencies which differentiated

TABLE 3. Mean frequencies of some common alleles in particular taxa. M – *Pinus mugo*, S – *P. sylvestris*, UL – *P. uliginosa*, UN – *P. uncinata*. Differences in the frequency of alleles were tested by chi-square test assuming the homogeneity of frequencies in the samples

locus/allele	M	S	UL	UN	chi square $p=0.01$
ADH 1	0.047	0.611	0.015	0.360	***
ADH 2	0.932	0.361	0.940	0.640	***
GOTB 1	0.820	0.581	0.850	0.370	***
GOTB 2	0.160	0.371	0.150	0.460	***
MDHC 1	0.206	0.702	0.735	0.120	***
MDHC 2	0.788	0.297	0.265	0.880	***
GDH 1	0.544	0.650	0.190	0.440	***
ShDHA 1	0.596	0.810	0.225	0.620	***
ShDHA 2	0.355	0.143	0.745	0.320	***

taxons, frequencies of the alleles (ADH1, ADH2, GOTB1, GOTB2) in *P. mugo* and *P. uliginosa* resembled each other. In *P. sylvestris* and *P. uncinata* there are alleles GOTB1 and GOTB2 and in *P. sylvestris* and *P. uliginosa* alleles MDHC1 and MDHC2. The most different allele frequencies were noted for the pairs of taxa *P. uliginosa* – *P. uncinata* and *P. mugo* – *P. sylvestris*.

The private alleles, manifested at low frequencies in individual taxa, included ADH3 observed in the two *P. mugo* populations and in *P. uliginosa* but absent in the remaining populations, ADH4 and ADH5 noted only in the Tatra Mountains populations of *P. mugo*, DIAF3, present in *P. uncinata* and in the mountain population of *P. sylvestris* from Szczelińiec in the Sudeten Mountains, and GDH3 allele, which, simi-

TABLE 4. Genetic parameters in the studied populations of *Pinus mugo* – M., *P. sylvestris* – S., *P. uliginosa* – UL. and – *P. uncinata* – UN. A/L – mean number of alleles per locus, G/L – genotypes per locus, H_e – heterozygosity expected, H_o – heterozygosity observed, Pg – genotypes polymorphic indices, F – fixation index

Population	A/L	G/L	H_e	H_o	Pg	F
M01	2.80	3.80	0.246	0.246	0.357	0.001
M02	3.20	4.30	0.278	0.262	0.407	0.059
M03	3.20	4.10	0.241	0.230	0.372	0.047
M04	2.90	3.90	0.254	0.238	0.370	0.064
M05	2.90	3.70	0.230	0.221	0.345	0.037
M06	2.80	3.40	0.236	0.257	0.343	-0.090
Mean M	2.96	3.86	0.248	0.242	0.365	0.020
S01	2.40	3.30	0.341	0.340	0.466	0.002
S02	2.30	2.70	0.280	0.287	0.407	-0.023
S04	2.40	2.90	0.291	0.320	0.411	-0.101
S07	2.20	2.90	0.275	0.240	0.390	0.126
S14	2.50	2.90	0.278	0.290	0.380	-0.042
S16	2.40	3.00	0.304	0.287	0.432	0.058
S21	2.40	2.90	0.267	0.257	0.368	0.038
S22	2.40	3.10	0.306	0.319	0.423	-0.044
S23	2.40	3.10	0.310	0.327	0.452	-0.054
Mean S	2.37	2.97	0.295	0.296	0.413	-0.004
UL	2.40	3.20	0.237	0.202	0.356	0.146
UN	2.90	3.90	0.308	0.298	0.430	0.033

larly to GOTA4, was noted exclusively in populations of *P. mugo*, *P. uliginosa* and *P. uncinata*. The ShDHA3 allele was absent in populations of *P. uliginosa* and *P. uncinata* but was observed in most populations of *P. sylvestris* and all populations of *P. mugo* (Table 2). We are fully aware of the fact that the numbers of the compared populations of particular taxa are not the same, but we believe that the random samples of *P. uliginosa* (40 trees) from locus classicus and *P. uncinata* (50 trees) from the Pyrenees represent an "average" genetic structure of the studied taxa. The span of the studied genetic parameters of populations within the taxon of *P. sylvestris* and taxon *P. mugo* is small and not significant for inter-species comparisons (Table 4).

The mean number of alleles per locus (A/L) showed the highest value in populations of *P. mugo* and amounted to 2.96 and the lowest value in populations of *P. sylvestris*, in which it was 2.37. In *P. uliginosa* population an average of 2.4 allele was noted per locus which resembled closely the value for *P. sylvestris*. In *P. uncinata* as well as in *P. mugo* the value was 2.9 allele per locus. The mean number of genotypes per locus (G/L) in the examined taxa showed values very similar in proportions to the mean number of alleles per locus. The mean number of genotypes per locus was 3.86 for *P. mugo*, 2.97 for *P. sylvestris*, 3.2 for *P. uliginosa* and 3.9 genotypes for *P. uncinata* (Table 4). The mean observed heterozygosity (H_o) for the studied loci (Table 4) showed the lowest value for *P. uliginosa* (0.202) and the value was by about 30% lower than those for *P. sylvestris* and *P. uncinata* ($H_o=0.296$ and 0.298 , respectively). *P. mugo* populations were intermediate in this respect ($H_o=0.242$). The values of genotype polymorphism index showed a similar, level in *P. sylvestris* and *P. uncinata* ($Pg=0.413$ and $Pg=0.429$) similar values of Pg are also noted for pairs of taxa, *P. mugo* ($Pg=0.365$) and *P. uliginosa* ($Pg=0.356$). Fixation index (F) indicated that the populations are in Hardy-Weinberg's equilibrium, except of *P. uliginosa* population which demonstrated a marked excess of homozygotes ($F=0.146$).

Gene flow between the studied populations (N_m) as well as differentiation between the populations (GST) and within the

TABLE 5. Some of genetic parameters in the studied groups of populations: H_T – total heterozygosity, H_S – heterozygosity in the samples, D_{ST} – genetic diversity among samples, G_{ST} – proportion of the total genetic diversity among samples, N_m – estimated numbers of migrants per generation

	H_T	H_e	D_{ST}	G_{ST}	N_m
All populations (17)	0.3133	0.2675	0.0458	0.1463	1.459
<i>P. sylvestris</i> (9 populations)	0.3027	0.2945	0.0082	0.0271	8.982
<i>P. mugo</i> (6 populations)	0.2519	0.2476	0.0043	0.0172	14.264
<i>P. mugo</i> <i>P. uliginosa</i> <i>P. uncinata</i> (8 populations)	0.2697	0.2502	0.0195	0.0723	3.207
<i>P. mugo</i> <i>P. uliginosa</i> (7 populations)	0.2629	0.2460	0.0169	0.0642	3.646
<i>P. mugo</i> <i>P. uncinata</i> (7 populations)	0.2603	0.2523	0.0080	0.0307	7.894
<i>P. uliginosa</i> <i>P. uncinata</i> (2 populations)	0.3000	0.2604	0.0396	0.1319	1.646
<i>P. sylvestris</i> <i>P. mugo</i> (15 populations)	0.3089	0.2684	0.0405	0.1310	1.658
<i>P. sylvestris</i> <i>P. uliginosa</i> (10 populations)	0.3197	0.2845	0.0352	0.1102	2.018
<i>P. sylvestris</i> <i>P. uncinata</i> (10 populations)	0.3123	0.2958	0.0165	0.0528	4.484

populations (D_{ST}) are presented in Table 5. Within populations of particular species, gene flow for *P. sylvestris* amounted to 8.98 individuals per generation while in populations of *P. mugo* it was almost twice as high ($N_m=14.26$). When intensity of migration was studied in the entire complex of *P. mugo* (*P. mugo* Turra, *P. uliginosa*, *P. uncinata*), the index decreased significantly to 3.20 migrants per generation. Between *P. mugo* and *P. uncinata* populations, 7.89 migrants were observed per generation and the value resembled that observed between *P. sylvestris* populations. A relatively small gene flow was observed between *P. uliginosa* and *P. uncinata* and between *P. sylvestris* and *P. mugo* populations ($N_m=1.64$ and 1.65, respectively) as well as between *P. sylvestris* and *P. uliginosa*, in which case the index amounted to 2.01 migrants per generation. A twofold higher gene flow was observed between *P. sylvestris* and *P. uncinata* ($N_m=4.48$).

G_{ST} indices, which reflect genetic differentiation between populations, were relatively low for *P. sylvestris* (0.0271) and even lower for *P. mugo* (0.0172). Upon comparisons between taxa within *P. mugo* complex (*P. mugo* Turra, *P. uliginosa*, *P. uncinata*) the value significantly increased (to 0.0723), which

points to a heterogenous character of the group. In comparisons of population pairs *P. mugo*/*P. uliginosa* and *P. mugo*/*P. uncinata*, the values amounted to 0.0642 and 0.0307 respectively. The latter value resembled that typical for *P. sylvestris*. In comparisons of *P. sylvestris* – *P. uliginosa* and *P. sylvestris* – *P. uncinata* pairs the indices amounted to 0.0201 and 0.0448, respectively. In comparisons of *P. uliginosa* and *P. uncinata* populations as well as *P. sylvestris* and *P. mugo* populations the genetic differentiation between the populations dramatically increased to 0.131 in each case (Table 5).

Genetic similarities according to Nei (1972), established on grounds of allele frequencies, are presented in Fig. 1. The studied populations evidently formed two clear-cut groups, of which one contained all *P. sylvestris* populations. The highest distance within the group of *P. sylvestris* populations was 0.0197 and was ascribed to the mountain population from Szczeliniec (Sudeten Mountains). The other, weakly differentiated group was formed by *P. mugo* populations from the Tatra Mountains. The *P. uncinata* population was linked to the latter group, at the distance of 0.0414 and also *P. uliginosa* which manifested a genetic distance from *P. mugo* population group of $DN=0.101$.

Fig. 1. Dendrogram showing the genetic similarities of studied taxa, based on genetic distances according to Nei. M – populations of *Pinus mugo*, UN – population of *P. uncinata*, UL – population of *P. uliginosa*, S – populations of *P. sylvestris*.

DISCUSSION AND CONCLUSIONS

The present studies have proven that principal differences between the studied taxa involved frequencies of some alleles. The differences were detected in ADH, GOTB, MDHC, ShDHA and GDH loci (Table 3). Additionally, in populations belonging to the studied taxa private alleles were detected, however generally present at low frequencies. The studied populations formed two genetically clearly distinct groups. One of them contained *P. mugo* populations, which were only imperceptibly differentiated, as indicated by the low value of genetic differentiation index (GST) (Table 4). The other group included *P. sylvestris* populations. The *P. mugo* group was linked to *P. uncinata* (Dn=0.041) and by much more distance with *P. uliginosa* (DN=0.100). Despite the relatively extensive distances from *P. mugo* population group, both taxa (*P. uncinata* and *P. uliginosa*) formed the same group of *P. mugo* complex (Fig. 1). In cases of *P. mugo* and *P. uncinata* the value of genetic distance coefficient was substantial (DN=0.041) and approached the value established by Nei (1987) for subspecies. In the case of *P. mugo* and *P. uliginosa*

the value corresponded to that established for species (DN=0.100). If genetic distances between the studied taxa are accepted to correlate with time of divergence (Nei 1972), the differentiation of the studied taxa from a common stem involved separation, at first, of *P. uliginosa* and, then, of *P. uncinata*. Timing of *P. uncinata* divergence took place by 50% later than separation of *P. uliginosa* from a common ancestor. The significantly distinct genetic character of *P. uliginosa* from 'Batorowskie' Peatbog, as compared to *P. mugo* and *P. uncinata*, has been surprising, but the result is consistent with conclusions of Lauranson-Broyer et al. (1997), who have examined reciprocal taxonomic relations of *P. mugo* Turra, *P. uliginosa*, *P. uncinata* and *P. sylvestris* on the basis of analysis of flavonoid compounds and have found that *P. mugo* Turra from the Tatra Mountains and *P. uncinata* from French Jura and the Pyrenees form a single group, while *P. uliginosa* from "Batorowskie" Peatbog has proven to be clearly distinct from *P. mugo*-*P. uncinata* complex.

In the light of our present results, *P. uliginosa* from "Batorowskie" Peatbog does not seem to represent a marginal population of *P. uncinata*, as was suggested earlier (Krzakowa et al. 1984, Siedlewska and Prus-Głowacki 1995, Staszkievicz and Tyszkiewicz 1972).

The Nm coefficient (Table 4) of gene flow between the studied taxa (Sladkin 1985) has pointed to the potential for the intense ongoing or past hybridization between *P. mugo* Turra and *P. uncinata* as well as between *P. sylvestris* and *P. uncinata*. Judging by the low Nm value, such hybridization would involve *P. mugo* and *P. uliginosa* less frequently. In the context, it seems possible that *P. uliginosa* represents an old, stabilised hybrid between *P. uncinata* and *P. sylvestris* or an introgressant with marked admixture of *P. sylvestris* genes (Siedlewska and Prus-Głowacki 1995, Christensen 1987, Neet-Sarqueda et al. 1988).

However the specific genetic structure of *P. uliginosa* populations from "Batorowskie" Peatbog cannot be excluded as result of isolation of the population, genetic drift or founders effect, as indicated by the high homozygosity of the population (F=0.146).

In turn, Nm indices, analysed for individual enzymatic loci in taxa pairs *P. mugo*-*P. uliginosa*, *P. mugo*-*P. uncinata*, *P. uncinata*-*P. uliginosa*, *P. sylvestris*-*P. uliginosa* (Table 6) point to a possibility of directional selection, which would provide a specific, distinct character of the examined population. According to Sladkin (1985), Nm value lower than 1.0 in a defined locus indicates an intense selection directed at the locus. Values of the index are much lower for ADH, MDHC

TABLE 6. Some genetic parameters in pairs of studied taxa for particular enzymatic loci. The denotations of parameters as in Table 5

Locus	H _T	H _S	DST	GST	Nm	H _T	H _S	DST	GST	Nm	H _T	H _S	DST	GST	Nm	H _T	H _S	DST	GST	Nm
	UL / UN					SYL / UL					SYL / UN					SYL / MUGO				
ADH	0.28	0.23	0.05	0.17	1.22	0.51	0.40	0.11	0.22	0.90	0.48	0.46	0.02	0.05	5.06	0.44	0.27	0.17	0.38	0.41
DIAF	0.09	0.09	0.00	0.01	17.66	0.18	0.18	0.01	0.05	5.08	0.21	0.20	0.01	0.04	6.29	0.19	0.19	0.00	0.02	9.95
FEst	0.24	0.24	0.00	0.00	80.97	0.38	0.36	0.02	0.05	4.90	0.39	0.37	0.02	0.05	5.24	0.36	0.35	0.01	0.03	6.98
GDH	0.61	0.59	0.02	0.04	6.29	0.51	0.46	0.06	0.11	1.99	0.46	0.44	0.01	0.03	7.78	0.50	0.48	0.01	0.03	9.58
GOTA	0.10	0.10	0.00	0.01	44.78	0.05	0.05	0.00	0.03	9.73	0.04	0.04	0.00	0.02	12.41	0.06	0.05	0.00	0.04	5.97
GOTB	0.46	0.38	0.08	0.17	1.20	0.51	0.48	0.03	0.05	4.34	0.55	0.53	0.01	0.03	9.50	0.43	0.40	0.03	0.08	2.92
MDHA	0.05	0.05	0.00	0.01	20.68	0.07	0.07	0.00	0.04	6.43	0.06	0.06	0.00	0.05	4.92	0.05	0.05	0.00	0.05	5.17
MDHC	0.50	0.33	0.17	0.34	0.49	0.42	0.42	0.00	0.01	21.06	0.46	0.40	0.06	0.13	1.65	0.49	0.37	0.12	0.24	0.77
ShDHA	0.51	0.43	0.08	0.15	1.44	0.42	0.31	0.11	0.26	0.70	0.33	0.31	0.01	0.04	6.48	0.45	0.41	0.04	0.09	2.51
ShDHB	0.18	0.18	0.00	0.00	328.38	0.15	0.14	0.01	0.07	3.23	0.15	0.14	0.01	0.08	2.94	0.12	0.12	0.01	0.07	3.51
Mean	0.30	0.26	0.04	0.13	1.65	0.32	0.28	0.04	0.11	2.02	0.31	0.30	0.02	0.05	4.48	0.31	0.27	0.04	0.13	1.66

and ShDH loci, which argues for a selection acting on "Batorowskie" Peatbog, possibly caused by specific environmental conditions in the peatbog.

Nevertheless, the data obtained in the presented study have still failed to unequivocally determine the taxonomic status of *P. uliginosa* and greater numbers of Polish *P. uliginosa* populations, populations of *P. uncinata* and *P. mugo* from the Tatra Mountains should be studied for a strict determination of *P. uliginosa* taxonomic position.

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POZYCJA TAKSONOMICZNA *PINUS ULIGINOSA* NEUMANN W RELACJI DO INNYCH TAKSONÓW Z KOMPLEKSU *PINUS MUGO*

STRESZCZENIE

Badania relacji taksonomicznych *Pinus uliginosa* Neumann, *Pinus uncinata* Ram. i *Pinus mugo* Turra, wykazały znaczną odrębność populacji *P. uliginosa* z Wielkiego Torfowiska Batorowskiego. *Pinus uncinata* pod względem podobieństwa genetycznego plasuje się blisko populacji *P. mugo* z Tatr. Czas dywergencji badanej populacji *P. uliginosa* od wspólnego pnia, przyjęty na podstawie odległości genetycznych Nei'a jest jeszcze raz tak długi, jak w przypadku *P. uncinata*. W świetle uzyskanych wyników wykluczyć można przypuszczenie, że *P. uliginosa* z Wielkiego Torfowiska Batorowskiego jest marginalną populacją *P. uncinata* ze względu na jej odmienną strukturę genetyczną. Dyskutuje się przypuszczalne przyczyny tak dużej jej odrębności w stosunku do innych badanych taksonów.

SŁOWA KLUCZOWE: *Pinus uliginosa*, struktura genetyczna, taksonomia, izoenzymy.