in Forestry. Lecture Notes in Biomathematics 60. Springer-Verlag, Berlin, Heidelberg, New York. p. 253—266 (1985). —— Müller-Starck, G. and Gregorius, H. R.: Monitoring genetic variation in forest tree population. Proceedings 18th World Congress IUFRO, Yugoslavia. September 7 to 21. Division 2. Vol. II. p. 589—599 (1986). —— Padutov, V. E., Goncharenko, G. G. and Podzharova, Z. S.: Genetic variability in *Pinus sylvestris*. Doklady Acad. Sci. of Byelorussia 33: 1039—1042 (in Russian) (1989). —— Prakash, S., Lewontin, R. C. and Hubby, J. L.: A molecular approach to the study of genic heterozygosity in natural populations. IV. Patterns of genic variation in central, marginal and isolated populations of *Drosophila pseudoobscura*. Genetics 61: 841—858 (1969). —— Pravdin, L. F.: Scotch pine. Variability, intraspecies taxonomy and breeding. Nauka, Moscow (in Russiae) (1964). —— Rudin, D. and Ekberg, I.: Linkage studies in *Pinus sylvestris* L. — using macro-gametophyte allozymes. Silvae Genet. 27: 1—12 (1978). —— Starova, N. V., Yanbayev, Yu. A., Yumadilov, N. Kh., Adler, E. N., Dukharev, V. A. and Shigapov, Z. Kh.: Genetic variability of *Pinus sylvestris* in age classes. Genetika 26: 498—505 (in Russian) (1990). —— Sukhachyov, V. N.: Dendrology with foundations of forest geobotany. Goslestekhizdat, Leningrad (in Russian) (1938). —— Szmidt, A. E.: Genetic studies of Scotch pine (*Pinus sylvestris* L.) domestication by means of isozyme analysis. Ph. D. diss., Swedish University of Agricultural Sciences, Umea (1984). —— Szmidt, A. E. and Muona, O.: Linkage relationship of allozyme loci in *Pinus sylvestris*. Hereditas 111: 91—97 (1989).

Allozyme Variation in Populations of Pinus sylvestris L. from a 1912 Provenance Trial in Pulawy (Poland)

By W. Prus-Glowacki and E. Bernard

Adam Mickiewicz University, Faculty of Biology,
Department of Genetics, ul. Dąbrowskiego 165,
60—594 Poznań Poland

(Received 8th December 1993)

Summary

Study of the genetic variation and genetic structure of 13 populations of *Pinus sylvestris* from Eastern Europe and Turkey has shown significant genetic differentiation of the populations. The average genetic differentiation (index GST) is high (0.076), but it is about 50 % lower in populations from the area covered by ice during the last glaciation (GST = 0.035). The mean multilocus heterozygosity for 8 loci (Ho = 0.357) and the average number of alleles per locus are similar to those from the other parts of Europe. The genetic similarities of populations (Nei) are not correlated with the geographical localities of the studied stands.

Key words: Pinus sylvestris, genetic structure, isoenzymes, provenance.

FDC: 165.3; 165.5; 232.12; 174.7 *Pinus sylvestris*; (438).

Introduction

The experiment in Pulawy was established in the year 1912 and is the oldest provenance trial in Poland. This experiment was discovered in 1980 and described in detail by Oleksyn ad Giertych (1982, 1984). The trial comprises seed lots from 13 provinces of imperial pre-revolutionary Russia. The seed sample origins ranged from Latvia and Ukraine to Western Siberia and Turkey, and so, it covered a relatively large natural range of *Pinus sylvestris* in Eastern Europe. This experiment has also some additional advantages. Seeds collected in the beginning of 20th century were more likely to be from autochtonous stands, because there was no major practice in pre-revolutionary Russia to transfer seeds from one region to another for reforestation proposes. However, in relation to the IUFRO 1938 provenance trials, the trial in Pulawy has some disadvantages. The seeds did not originate from single stands but the material was collected from different localities and pooled together, because at that time, the province was regarded as the basic forest unit (Giertych and Oleksyn, 1981). On the other hand this kind of material could be useful for investigation of geographic races of the species because seeds originated from different geographical regions. This work aimed at describing genetic structure and level of genetic variation as well as geographical differentiation of *Pinus sylvestris* in Eastern Europe. The knowledge concerning this matter remains still largely incomplete (Prus-Glowacki, 1991; Müller-Stark et al., 1992).

Material and Methods

Dormant winter buds were used for isoenzymatic analyses. Plant material was collected from 12 to 30 randomly choosen trees from each province. In cases when less than 30 individuals were available, the samples from all living trees were collected. The Tobolsk province was excluded from the isoenzymatic analyses to avoid the error of a small sample, because it was represented by only 7 trees. Detailed data on the geographical origin of the samples are given in *table 1* and *figure 1*. Variation of the following enzymatic loci was studied: fluorescent esterase FEST (E.C.3.1.1.1.), glutamate oxalo-acetate transaminase GOT 2 loci (E.C. 2.6.11.), diaforase DIA (E.C. 1.6.4.3.), glutamate dehydrogenase GDH (E.C. 1.4.1.3.), alcohol dehydrogenase ADH (E.C. 1.1.1.1.), shikimate dehydrogenase ShDH (E.C. 1.1.1.25.) and NADH — dependent dehydrogenase (NDH). The separation of isozymes on starch gels and the genetic interpretation of the results were performed as described in Muona and Szmidt (1985) and Prus-Glowacki (1986). The following genetic parameters for the studied groups of trees were calculated: the frequency of alleles and genotypes, number of alleles (A/L) and genotypes (G/L) per locus, number of effective alleles (ne), heterozygosity (Ho, He — observed and expected respectively), total (HT) and average (Hs) gene diversity between populations, genotypic polymorphism indices (Pg), fixation indices (F), genetic differentiation of populations DST = HT-Hs and GST = DST/HT and genetic similarity coefficients according to Nei and Hedrick (SN and SH). Based on genetic distances (DN = 1 — SN, DH = 1 — SH), dendrites and dendrograms illustrating mutual systematic positions (cluster analysis UPGMA) of the populations were con-

Table 1. — Data on the provenances used in the study (after OLEKSYN, 1987).

Denotat.	Region	Forest Range	Coordinates N	E
KS	Kars	Songalugskoe and Boržomskoe	40°30'	42°00'
AR	Arkhangelsk	Verkoleskoe and Lasskoe	63°50'	45°10'
CH	Kharkov	Majackoe and Kent's estate	50°00'	36°20'
ON	Olonets	Karganopolskoe and Podomskoe	61°30'	39°00'
WR	Voronezh	Hrenovskoe	51°06'	40°17'
WL	Vologda	Georgievskoe	59°43'	36°52'
JN	Jenisiejsk	Jenisejskoe (Konsko-Jenisejskoe)	58°00'	62°00'
NO	Novogrod	Tihvinskoe	59°37'	33°33'
VL	Volyniya	Luckoe	50°45'	25°18'
UF	Ufa	Šajtanovskoe	55°00'	52°00'
KI	Kiev	Dymarskoe	50°50'	30°17'
TV	Tver	Viesiegonskoe	58°38'	37°13'
KU	Kurland	Rucavskoe	56°07'	21°08'

structed (EL-KASSABY, 1991; NEI und ROYCHOUDRY, 1974; NEI, 1975; HEDRICS, 1974; JAIN and WORKMANN, 1967; KAHLER and ALLARD, 1981).

Results

Gene diversity

The general number of alleles in the 8 analysed loci varied from 18 to 25 in particular populations. On the average for all 13 provinces 20.8 alleles per population were noted. The mean number of alleles per locus is 2.6 and the effective number of alleles 1.69. Detailed data for allele numbers and frequencies in a single population are presented in *tables 2* and *3*. The highest average numbers of alleles per locus is noted for populations from Kurland and Volyniya (3. 12 and 3.0 respectively) and the lowest for Olonets 2.25 A/L. The highest effective numbers of alleles per locus in populations were found from Kurland and Kharkov (1.8 and 1.73), the lowest for province Olonets and Novogrod (1.53 and 1.48). Regarding the highest number of particular genotypes in the populations, 30 of them were observed in populations from Kurland, Volyniya, Kharkov and Arkhangelsk and the lowest — 21 in provenance Ufa. On the average for all populations 3.3 genotypes per locus were observed. In individual populations the genotype number per locus fluctuates from 2.62 (Ufa) to 3.75 for Arkhangelsk, Kharkov, Volyniya and Kurland (*Table 3*).

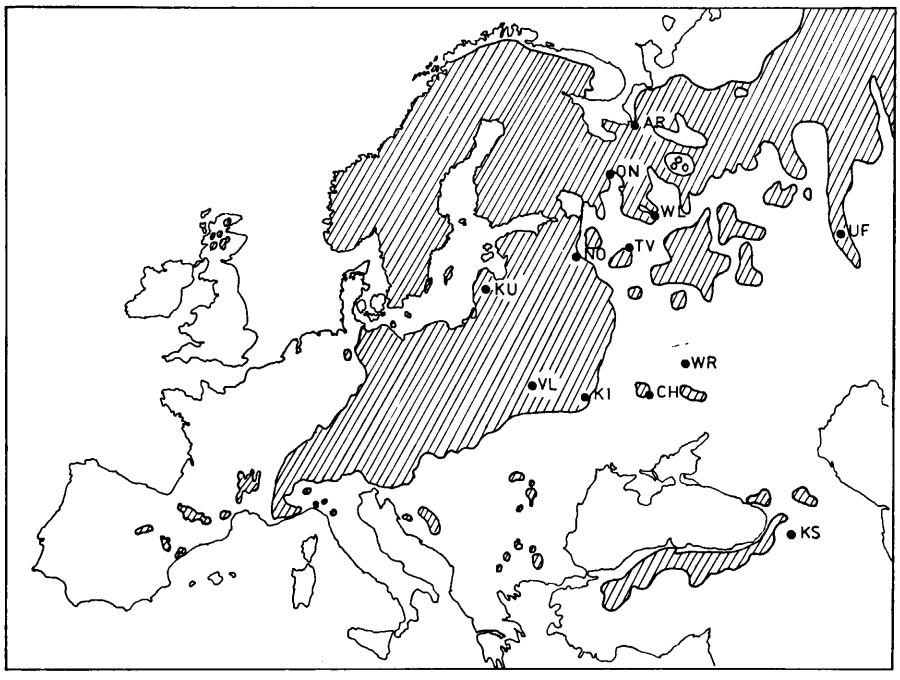

Figure 1. — Location of provinces from which the seed samples originated.

Genetic structure

The multilocus heterozygosity (Ho and He), fixation index (F) and genotype polymorphism (Pg) indices for the populations studied are given in *table 3*. The highest heterozygosity (Ho) and genotypes polymorphic indices (Pg) are noted for populations from Tver and Kurland (Ho = 0.470 and 0.452; Pg = 0.470 and 0.452), the lowest for population from Novogrod (Ho = 0.270, Pg = 0.423). The mean multilocus heterozygosity for all populations studied is Ho = 0.357 and genotype polymorphism index Pg = 0.480. The fixation indices indicate that the several populations are not in a HARDY-WEINBERG equilibrium. In populations from Kharkov and Jenisiejsk excess of homozygotes is noted (F = 0.168) while in the populations from Kurland, Ufa and Tver heterozygosity is higher than predicted from the HARDY-WEINBERG formula, however for the whole group the F value is close to 0 (—0.001). The GST coefficients indicate that genetic differentiation between the provenances studied reach 7.05 % (*Table 4*). For particular loci these values fluctuate between 1.5 % (Got B) and 12.5 % (Got A).

Genetic similarities

The dendrogram based on allele frequencies (NEI's genetic similarity coefficients) indicates that the populations form several groups (*Fig 2*). The main cluster consists of 12 populations falling into 4 subgroups: the trees from provenances of Arkhangelsk, Voronezh, Kiev, Olonets, Novogrod (1st subgroup), Volyniya, Ufa and Tver (2nd subgroup). To these subgroups a pair of populations from Kars and Kurland (3rd subgroup) is connected and further still Vologda and Jenisiejsk (4th subgroup). Most distinct from the whole group is the population from Kharkov. Dendrite based on the method of closest neighbourhoods shows a similar relationship as can be seen from the dendrogram (*Fig. 2*). HEDRICK's similarity coefficients based on frequencies of genotypes show essentialy the same pattern of genetic similarities as is the case for alleles frequencies (data not shown).

Discussion and Conclusions

Gene diversity

Number of alleles per locus as a measure of genetic

Table 2. — Frequencies of alleles in the *P. sylvestris* populations.
m — mean value, SD — standard deviation.

Loci/ All./	Populations						
	KS	AR	CH	ON	WR	WL	JN
FEst							
1	0.679	0.640	0.611	0.778	0.520	0.719	0.633
2	0.143	0.180	0.167	0.037	0.240	0.156	0.200
3	0.179	0.160	0.222	0.185	0.220	0.125	0.167
5	0.000	0.020	0.000	0.000	0.020	0.000	0.000
Got A							
1	1.000	1.000	0.982	1.000	1.000	1.000	1.000
2	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	0.000	0.018	0.000	0.000	0.000	0.000
Got B							
1	0.571	0.480	0.556	0.593	0.640	0.594	0.600
2	0.393	0.460	0.407	0.407	0.360	0.313	0.400
3	0.036	0.060	0.037	0.000	0.000	0.063	0.000
4	0.000	0.000	0.000	0.000	0.000	0.031	0.000
Diaf.							
1	0.893	0.820	0.556	0.815	0.906	0.920	0.867
2	0.107	0.100	0.426	0.093	0.094	0.060	0.000
3	0.000	0.080	0.019	0.093	0.000	0.020	0.100
4	0.000	0.000	0.000	0.000	0.000	0.000	0.033
GDH							
1	0.250	0.580	0.741	0.648	0.680	0.594	0.633
2	0.750	0.420	0.259	0.352	0.320	0.406	0.367
ADH							
1	0.615	0.520	0.574	0.537	0.500	0.813	0.800
2	0.385	0.480	0.000	0.463	0.500	0.156	0.200
3	0.000	0.000	0.426	0.000	0.000	0.031	0.000
4	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ShDH A							
1	0.714	0.860	0.832	0.907	0.917	0.469	0.667
2	0.214	0.040	0.093	0.037	0.042	0.469	0.267
3	0.072	0.040	0.019	0.000	0.000	0.031	0.000
5	0.000	0.060	0.056	0.000	0.042	0.000	0.066
6	0.000	0.000	0.000	0.056	0.000	0.031	0.000
NDH							
1	0.654	0.840	0.796	0.885	0.800	0.750	0.833
2	0.231	0.060	0.185	0.077	0.180	0.125	0.100
3	0.115	0.100	0.000	0.039	0.020	0.125	0.067
5	0.000	0.000	0.019	0.000	0.000	0.000	0.000

Loci/ All./	Populations							
	NO	VL	UF	KI	TV	KU	- m	SD
FEst								
1	0.750	0.817	0.885	0.717	0.735	0.707	0.707	0.094
2	0.083	0.083	0.039	0.050	0.059	0.086	0.117	0.067
3	0.167	0.100	0.077	0.233	0.177	0.190	0.169	0.046
5	0.000	0.000	0.000	0.000	0.029	0.017	0.007	0.010
Got A								
1	1.000	1.000	1.000	1.000	0.971	1.000	0.996	0.009
2	0.000	0.000	0.000	0.000	0.029	0.000	0.002	0.008
3	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.005
Got B								
1	0.667	0.450	0.615	0.583	0.588	0.650	0.584	0.061
2	0.292	0.517	0.385	0.383	0.412	0.283	0.386	0.065
3	0.042	0.033	0.000	0.033	0.000	0.067	0.029	0.025
4	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.008
Diaf.								
1	0.792	0.833	0.731	0.883	0.735	0.850	0.815	0.098
2	0.083	0.033	0.039	0.050	0.059	0.117	0.097	0.104
3	0.083	0.117	0.231	0.050	0.206	0.033	0.079	0.072
4	0.042	0.017	0.000	0.017	0.000	0.000	0.008	0.014
GDH								
1	0.750	0.617	0.539	0.617	0.588	0.450	0.591	0.129
2	0.250	0.383	0.462	0.383	0.412	0.550	0.409	0.129
ADH								
1	0.625	0.617	0.731	0.450	0.647	0.567	0.615	0.110
2	0.375	0.383	0.269	0.550	0.353	0.300	0.340	0.154
3	0.000	0.000	0.000	0.000	0.000	0.100	0.043	0.118
4	0.000	0.000	0.000	0.000	0.000	0.033	0.003	0.009
ShDH A								
1	1.000	0.650	0.808	0.833	0.853	0.650	0.782	0.144
2	0.000	0.167	0.154	0.133	0.088	0.133	0.141	0.124
3	0.000	0.033	0.000	0.033	0.000	0.183	0.032	0.050
5	0.000	0.133	0.000	0.000	0.059	0.017	0.033	0.040
6	0.000	0.017	0.039	0.000	0.000	0.017	0.012	0.018
NDH								
1	0.875	0.810	0.731	0.700	0.529	0.717	0.763	0.098
2	0.042	0.155	0.231	0.217	0.441	0.150	0.169	0.103
3	0.083	0.017	0.039	0.083	0.029	0.133	0.065	0.044
5	0.000	0.017	0.000	0.000	0.000	0.000	0.003	0.006

richness of populations, indicates that populations from Kurland and Volyniya are the most polymorphic. Also the number of genotypes and the level of heterozygosity are high in these populations. It is also true that other populations from this geographic region belong to the most heterozygotic and rich in alleles (PRUS-GLOWACKI et 1993).

These populations could gain the high genetic variability (high number of alleles per population and per locus and high heterozygosity), as a result of post-glacial migration of genetically diverse populations from South-European and West-Central Asiatic refugia. During this time intense mixing of the different gene pools was possible.

Studies of morphological characters such as volume production indicate that trees from Kurland and Volyniya are characterised by great plasticity (GIERTYCH and OLEKSYN, 1981; OLEKSYN and GIERTYCH, 1984). This is in good agreement with LERNER's (1954) hypothesis about higher adaptability to the environment and higher vitality of the more heterozygotic and genetically richer populations. It is worth mentioning that the average number of alleles per locus (2.6) and the average level of heterozygosity (Ho = 0.357) for the Pulawy provenance trial are very similar as in populations of *Pinus sylvestris* from Central and Western Europe (PRUS-GLOWACKI et al., 1993; PRUS-GLOWACKI and STEPHAN, 1994).

Some of the populations from Pulawy deviate from HARDY-WEINBERG equilibrium (Jenisiejsk, Kharkov, Ufa, Tver and Kurland F = 0.168; 0.168; —0.273; —0.212; —0.111 respectively). This can be explained by the high selection pressure of the local environmental conditions in the Pulawy provenance trial, or by the special genetic structure of marginal populations where the excess of homozygotic trees was noted (Kharkov, Jenisiejsk). The deviations from the HARDY-WEINBERG equilibrium were reported also for marginal populations of coniferous trees by TIGERSTEAD (1973) and RUDIN et al. (1974).

Genetic differentiation between populations is high (GST = 0.07) as compared to other European populations of *Pinus sylvestris* (ranging from 0.020 to 0.028) PRUS-GLOWACKI and STEPHAN, 1994; PRUS-GLOWACKI et al., 1993; GULLBERG et al., 1985; MEJNARTOWICZ and BERGMANN, 1985; MUONA and SZMIDT, 1985). WANG et al. (1991) reported unexpectedly low genetic differentiation of populations of *Pinus sylvestris* from northern Sweden var. *lapponica* compared to China var. *mongolica* (GST = 0.028) in spite

Table 3. — Mean number of alleles (n) and genotypes (G) per locus and effective numbers of alleles (ne), heterozygosity observed (Ho) and expected (He), fixation index (F) and genotype polymorphism index (Pg) in the studied provenances from the trial Puławy. The denotation of provenances as in *Table 1.*

Provenance	n A/L	ne	G G/L	Ho	He	F	Pg	Tree no.
Kars	2.37	1.69	2.87	0.385	0.373	-0.031	0.459	14
Arkhangelsk	2.75	1.68	3.75	0.370	0.364	-0.014	0.498	25
Kharkov	2.75	1.73	3.75	0.324	0.389	0.168	0.528	27
Olonets	2.25	1.53	3.00	0.283	0.312	0.091	0.440	27
Voronezh	2.37	1.64	3.37	0.309	0.334	0.074	0.460	25
Vologda	2.87	1.68	3.62	0.340	0.362	0.061	0.490	16
Jenisiejsk	2.37	1.63	3.50	0.291	0.350	0.168	0.458	15
Novogrod	2.37	1.48	2.87	0.270	0.287	0.057	0.423	12
Volyniya	3.00	1.67	3.75	0.368	0.366	-0.005	0.518	30
Ufa	2.37	1.58	2.62	0.432	0.339	-0.273	0.449	12
Kiev	2.62	1.64	3.37	0.354	0.358	-0.011	0.501	30
Tver	2.62	1.71	3.12	0.470	0.388	-0.212	0.478	17
Kurland	3.12	1.80	3.75	0.452	0.407	-0.111	0.543	30
m	2.60	1.69	3.33	0.357	0.356	-0.001	0.480	21

of the very large geographical distance of the 2 groups of populations. The latest paper of SZMIDT and WANG (1993) confirmed these findings also for a group of populations of *P. sylvestris* var. *armeana* from Turkey, *P. sylvestris* var. *lapponica* from Sweden and *P. sylvestris* var. *mongolica* from China. The high value of the GST coefficient in our studied populations could have 2 explanations: 1) the large area covered by the study, from Jenisiejsk to Kurland and from Kars to Arkhangelsk with isolated stands of Scots pine restricting gene flow between populations and in this way maintaining genetic differences, and 2) different history of the "old" populations from the south not covered by ice during the latest glaciation and from the north, where after glaciers receded *Pinus sylvestris* immigrated from several refugia and intensive gene mixing between populations took place, causing decrease

Table 4. — Relative measure of gene diversity and of genetic differentiation between (GST) and within populations from the Puławy (provenance trial).

Locus	HT	HS	DST	GST	Within populations %
FEst	0.458	0.443	0.015	0.032	96.8
GOT A	0.008	0.007	0.001	0.125	87.5
GOT B	0.509	0.501	0.008	0.015	98.5
Diaf	0.320	0.297	0.023	0.072	92.8
GDH	0.483	0.451	0.032	0.066	93.4
ADH	0.504	0.458	0.046	0.091	91.9
ShDH A	0.368	0.328	0.040	0.108	89.2
NDH	0.385	0.364	0.021	0.054	94.6
Mean	0.371	0.345	0.026	0.070	93.0

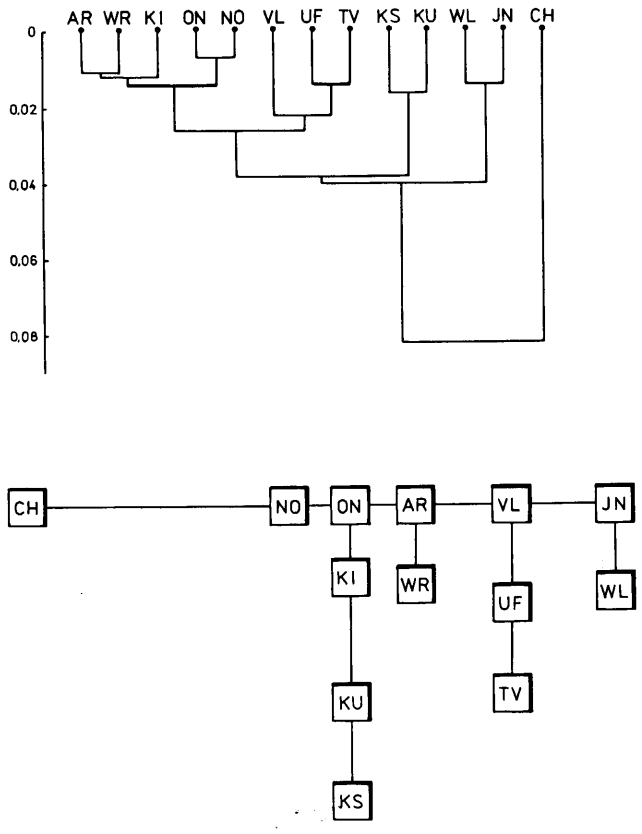

Figure 2. — Dendrogram showing the genetic similarities of *Pinus sylvestris* populations from the Puławy provenance trial (UPGMA) based on NEI's genetic distances.

of genetic specificity. The comparison of these 2 groups is presented in *table 5*. The populations from the south are twice as differentiated (GST = 0.076) as those from the north (GST = 0.035), having at the same time fewer alleles per locus. This phenomenon was discussed by GULLBERG et al. (1985) for several coniferous species from the area covered by a glacier versus areas free of ice during the latest glaciation.

Geographical differentiation

The studied material forms 1 heterogenous cluster consisting of several groups of populations not correlated with their geographical origin. Only 2 geographically close populations from Olonets and Novogrod are genetically similar. The most distinct population from the others is the population from Kharkov. This stand is isolated from the continous range of the species and thus it could have gained and maintained its own specificity. The specificity of Scots pine from this region was indicated also by PRAVDIN (1964). In conclusion it can be pointed out that the studied populations, in spite their great differentiation and very complex pattern of variation, are similar to other populations from the western and northern part of the range of the species in several genetic parameters such as heterozygosity, number of alleles per locus and genotype polymorphism indices (PRUS-GLOWACKI and STEPHAN; 1994; PRUS-GLOWACKI et al., 1993) A more extensive study on the Eastern part of the range of *Pinus sylvestris* is necessary to fill the gap in our knowledge about the genetic pools and the genetic differentiation of the species.

Acknowledgements

We are grateful to Prof. M. GIERTYCH for constructive comments on the paper and to ROMANA NOWAK-BZOWY M. Sc. for her skilful technical assistance and computer processing of data.

This work was supported by the Polish Academy of Sciences (grant CPBP no. 04.04.9.0204).

Literature Cited

BZOWY, P. and NOWAK-BZOWY, R.: Gen — computer program. (unpublished) (1986). —— EL-KASSABY, Y. A.: Genetic variation

Table 5. — Relative measure of genetic differentiation between populations (GST) from area covered by land-ice during the last glaciations and from an area free of land-ice and verge numbers of alleles per locus (A/L).

Loci	A Populations from area not covered by land-ice		B Populations from area covered by land-ice	
	GST (%)	Alleles A/L	GST (%)	Alleles A/L
FEst	5.10	3.10	0.90	3.50
GOT A	0.03	1.14	0.02	1.16
GOT B	1.50	2.57	2.10	2.83
Diaf	12.40	3.00	3.20	3.16
GDH	9.20	2.00	3.40	2.00
ADH	13.00	2.00	4.80	2.50
ShDH A	17.5	3.42	4.20	3.33
NDH	2.20	3.14	9.60	3.00
Mean	7.60	2.54	3.52	2.68

A — provenances KS, CH, WR, UF, JN, VL, KI;
B — provenances KU, NO, TV, ON, AR, WL.
Denotation of the provenances as in *table 1.*

within and among conifer populations: Review and evaluation of methods. In: Biochemical markers in the population genetics of forest trees. Eds. Fineschi, Malvolti, Cannata and Hattemer. SPB Academic Publishing, Hague. pp. 61—76 (1991). —— Giertych, M. and Oleksyn, J.: Summary of results on Scots pine (*Pinus sylvestris* L.) volume production in Ogievskij's prerevolutionary Russian provenance experiments. Silvae Genetica **30**(2—3) 56—74 (1981). —— Gullberg, U., Yazdani, R., Rudin, D. and Ryman, N.: Allozyme variation in Scots pine (*Pinus sylvestris* L.) in Sweden. Silvae Genetica **34**(6), 193—201 (1985). —— Hedrick, P. W.: Genetic similarity and distance; comments and comparisons. Evolution **29** (2), 362—366 (1974). —— Jain, S. K. and Workman, P. L.: Generalized F-statistics and the theory of inbreeding and selection. Nature **214**, 674—678 (1967). —— Kahler, A. L. and Allard, R. W.: Worldwide patterns of genetic variation among four esterase loci in barley (*Hordeum vulgare* L.). Theor. Appl. Genet. **59**, 101—111 (1981). —— Lerner, I. M.: Genetic homeostasis. Ed. Oliver and Bayd, Edinburgh. (1954). —— Mejnartowicz, L. and Bergmann, F.: Genetic differentiation among Scots pine populations from the lowland and the mountains in Poland. In: Population genetics in Forestry. Lecture Notes in Biomathematics **60**. Springer Verlag, Berlin, Heidelberg. 253—266 (1985). —— Müller-Starck, G., Baradat, P., and Bergmann, F.: Genetic variation in European tree species. New Forests **6**, 23—28 (1992). —— Muona, O. and Szmidt, A. E.: A multilocus study of natural populations of *Pinus sylvestris*. Lect. Notes Biomath. **60**, 226—240 (1985). —— Nei, M.: Molecular population, genetics and evolution. North-Holland, Amsterdam (1975). —— Nei, M. and Roychoudhry, A. K.: Sampling variances of heterozygosity and genetic distance. Genetics **76**, 379—390 (1974). —— Oleksyn, J.: Air pollution effects of 15 European and Siberian Scots pine (*Pinus sylvestris* L.) provenances growing in a 75-year old experiment. Arboretum Kórnickie **32**, 151—162 (1987). —— Oleksyn, J. and Giertych, M.: Odnaleziono najstarsze polskie doświadczenie proweniencyjne z sosną zwyczajną. Las Polski **1**, 27—28 (1982). —— Oleksyn, J. and Giertych, M.: Results of a 70 years old Scots pine (*Pinus sylvestris* L.) provenance experiment in Puławy, Poland. Silvae Genetica **33**(1), 22—27 (1984). —— Pravdin, L. F.: Scots pine. Variation, intraspecific taxonomy and selection. Izdatel'stvo "Nauka", Moskva, 1—177 (1964). —— Prus-Glowacki, W.: Demographic processes in population of *Pinus sylvestris* from industrial polluted area. Proc. Genepool of forest woody species its conservation and utilization. Nitra, CSSR, 1986. Eds. Kormutak, and A. Uzak, D.. 107—122 (1986). —— Prus-Glowacki, W.: Biochemical polymorphism. In Giertych, M. and Matyas, C. (eds). Genetics of Scots Pine. Elsevier Sci. Publ., Amsterdam. 73—86 (1991). —— Prus-Glowacki, W. and Stephan, R.: Genetic structure of *Pinus sylestris* L. from Spain in relation to other European populations. Silvae Genetica **43** (1), 7—14 (1994). —— Prus-Glowacki, W., Urbaniak, L. and Zubrowska-Gil, M.: Allozyme differentiation in Mid-European and Scandinavian populations of Scots pine (*Pinus sylvestris* L.). Genetica Polonica **34**(2), 159—176 (1993). —— Rudin, D., Eriksson, G., Ekberg, I. and Rasmusson, M.: Studies of allele frequencies and inbreeding in Scots populations by the aid of the isozyme technique. Silvae Genetica **23**, 10—13 (1974). —— Szmidt, A. E. and Wang, X.-R.: Molecular systematics and genetic differentiation of *Pinus sylvestris* (L.) and *P. densiflora* (Sieb. et Zucc.). Theor. Appl. Genet. **86**, 159—165 (1993). —— Tigersteadt, P. M. A.: Studies on isozyme variation in marginal and central populations of *Picea abies*. Heredites **75**, 47—60 (1973). —— Wang, X.-R., Szmidt, A. E. and Lindgren, D.: Allozyme differentiation among populations of *Pinus sylvestris* L. from Sweden and China. Heredites **114**, 219—226 (1991).

Number of Lethal Loci and Lethal Equivalents in Willow, Salix viminalis

By H. Kang[1]), J. Lee[2]) and E. V. Nordheim[3])

(Received 9th December 1993)

Abstract

Two methods of estimating lethal equivalents have been examined in this paper: A combinatorial method (COMB) and a method developed by Morton, Crow and Muller (MCM). Both methods produce similar estimates of lethal equivalents. However, the 2 methods differ in 2 respects: (1) COMB makes inferences to particular individual(s) in the population, while MCM makes inferences to the entire population; and (2) COMB estimates the number of lethal loci which is translated into lethal equivalents, while MCM directly estimates lethal equivalents. In a previous paper Kang et al. (1992) failed to recognize the second difference between COMB and MCM, and overestimated lethal equivalents in *Salix viminalis*. The revised estimate of lethal equivalents using COMB is 1.8, which is similar to that (1.69) estimated by MCM previously.

Key words: lethal equivalent, inbreeding, selfing, full-sib crossing, willow, *Salix viminalis*.

FDC: 165.3; 165.41; 161.6; 176.1 *Salix viminalis*.

[1]) North Central Forest Experiment Station and Department of Forestry, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706—1598, USA

[2]) Department of Statistics, University of Wisconsin-Madison, WI 53706, USA

[3]) Department of Statistics and Department of Forestry, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

Introduction

Two different methods of estimating lethal equivalents have been widely used in forest genetics literature. Some authors (Sorensen, 1969; Fowler and Park, 1983; Park and Fowler, 1984) used a method (MCM) developed by Morton et al. (1956). Others (Koski, 1971; Bramlett and Pepper, 1974; Bishir and Pepper, 1977; Bishir and Namkoong, 1987) used a combinatorial approach (COMB). There are different variations of these 2 methods. For example, using MCM, Sorensen (1969) removed the proportion of mortality due to environmental effects and outcrossing by taking the ratio between the viable seeds of selfed vs outcrossed. Bishir and Namkoong (1987) devised a least square method to remove environmental/maternal effects when using COMB. Salvolainen et al. (1992) also proposed a model which extends COMB to incorporate environmental causes of death. A general conclusion one can draw from these different variations of COMB and MCM is that both methods result in similar estimates of lethal equivalents.

More important distinctions that should be made between COMB and MCM are: (1) in COMB inferences are made to particular individuals, while in MCM inferences are made to the entire population; and (2) COMB estimates the number of lethal loci in the particular individual(s), while MCM estimates the lethal equivalents of the entire population. In case of selfing, the number of lethal loci in a parent is the same as the lethal equivalents of the