

**GENETIC AND PHENOTYPICAL VARIATION OF SCOTS PINE  
(*PINUS SYLVESTRIS* L.) POPULATIONS DUE TO SEED ORIGIN  
AND ENVIRONMENTAL CONDITIONS AT EXPERIMENTAL SITES**

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**ABSTRACT**

Scots pine (*Pinus sylvestris* L.) is a tree species with a broad natural range. It is adapted to the subatlantic and continental climate in Central and Eastern Europe, Scandinavia and Asia. The objective of the investigation was to obtain information on the influence of the seed origin and of selection processes due to different environmental factors on the actual genetic structure of populations in a 20-year-old field trial.

There were visible and statistically significant differences between the provenances for height, diameter growth, and survival with a clear geographical trend. The growth performance of provenances from higher altitudes and Eastern Europe was poor under the conditions of the test locations. In addition, significant differences existed between the two test sites for all three traits. No site  $\times$  genotype interaction was found.

In contrast to the results for growth traits and survival, the differentiation of the provenances based on isozyme markers was low. The mean values for population genetic parameters fluctuated by random effects. The adaptation to different site conditions had significantly modified the genetic structure of populations at some single loci both for common and for rare alleles.

Several methods of data evaluation demonstrated that the predominant component of genetic variation depended more on the seed origin than on the local site conditions.

**Keywords:** *Pinus sylvestris*, provenance, selection, population genetics, isozyme markers

**INTRODUCTION**

Scots pine (*Pinus sylvestris* L.) is a tree species with a broad natural range. It is adapted to subatlantic and continental climate in Central and Eastern Europe, Scandinavia and Asia. Scots pine is an important tree for timber production in Germany. In the northeastern part of the country it covers more than 70 % of the forest area. It has a high adaptability and is growing under relatively dry conditions as well. Therefore Scots pine might become even more important for forestry if climate changes will happen.

Extensive afforestations and the trade with forest seeds have heavily altered the natural structures of this species in the last two centuries. The objective of this work was to investigate the influence of selection processes due to different environmental factors on the actual genetic structure of populations in comparison to the influence of seed origin and their adaptability for practical conclusions.

Provenance trials are one of the sources to get information on adaptation processes of forest tree species (MÁTYÁS 1996). Several provenances in a 20-

year-old provenance trial series were studied in order to investigate such processes in Scots pine populations.

**MATERIAL AND METHODS**

An experimental series at six different locations in the eastern part of Germany was established with a total of 76 provenances from Central and Eastern Europe in 1975 (KOHLSTOCK & SCHNECK 1992). The single trials are complete block designs with 4 blocks. 100 trees per plot were planted initially with a spacing of 2.0  $\times$  0.5 m. The sampled provenances were represented by at least of 25 trees.

The present investigations were carried out at two experimental sites in Neustrelitz and Weisswasser with different climatic but similar soil conditions (Table 1) when the plantations were 20 years old. At each site, diameter at 1.3 m was measured for 25 trees per plot (75 trees per provenance) and height was recorded for 5 trees per plot (15 trees per provenance) with a diameter near diameter of the mean basal area tree. In addition survival rate was ascertained. The trials were not thinned before measurement.

**Table 1.** Site conditions of the two experimental locations in Neustrelitz and Weisswasser.

	Neustrelitz	Weisswasser
Annual mean temperature	7.5 °C	8.9 °C
Average annual precipitation	599 mm	673 mm
Rainfall May–September	305 mm	341 mm
Soil type	sandy	sandy
Soil type group	oligotrophic, moderate water supply	oligotrophic, moderate water supply

For the analysis of field data plot means of 63 provenances grown at both sites were used (Table 2). Data were analyzed according the model:

$$Y_{ijk} = \mu + S_i + P_j + S*P_{ij} + E_{ijk},$$

where:  $\mu$  is grand mean,  $S_i$  is  $i^{\text{th}}$  site effect,  $P_j$  is  $j^{\text{th}}$  provenance effect,  $S*P_{ij}$  is interaction effect between  $i^{\text{th}}$  site and  $j^{\text{th}}$  provenance, and  $E_{ijk}$  represents residual.

Twelve provenances were selected from the total of 63 along the east west gradient of their geographic origin to analyze the genetic structure. 50 randomly selected individual trees per population at each of the two sites were characterized by isozyme markers. The following 18 polymorphic loci were used: alanine aminopeptidase (*Aap*–C), alcohol dehydrogenase (*Adh*–B), aspartate aminotransferase (*Aat*–A, –B, –C), formate dehydrogenase (*Fdh*), glutamate dehydrogenase (*Gdh*), leucine aminopeptidase (*Lap*–A, –B), malate dehydrogenase (*Mdh*–A, –C), menadione reductase (*Mnr*–A), NADH dehydrogenase (*Ndh*–B), phosphoglucomutase (*Pgm*–A), 6-phosphogluconate dehydrogenase (*Pgdh*–shikimate dehydrogenase (*Skdh*–A, –B). Electrophoretic methods and analysis of inheritance are given in HERTEL (1997).

The observed and expected heterozygosity and the effective number of alleles were used to describe the genetic variation within population. The parameters to estimate the differentiation between populations were calculated according to NEI (1973) and GREGORIUS (1984). These population genetic parameters were calculated as average values over 18 polymorphic loci. The principal component analysis with allele frequencies of several loci as variables used the additional information of correlation between isozyme loci to visualize genetic similarities.

All data were computed by the Statistical Analysis System (SAS Institute Inc.). Special SAS Macros (STAUBER 1997) were used for computation of population genetic parameters.

## RESULTS

### Phenotypical traits

There were visible and statistically significant differ-

ences between the provenances and between the sites for height, diameter growth, and survival (Table 3). No statistically significant interaction between sites and provenances could be observed for all three traits. About a half of total variance for height and diameter was caused by the influence of provenance. The portion of site was low. For survival, by contrast, variance component ‘site’ had the largest amount on total variance (55 %).

A clear geographical trend could be detected. Provenances from higher altitudes and Eastern Europe have grown not so well under the conditions of the test sites (Figure 1). Also their survival rate was usually lower than that of the provenances from Poland and German lowlands. Height growth and survival rate were lower for all provenances under the more unfavorable conditions at Neustrelitz (Table 2). Because of the strong influence of spacing on diameter growth the mean values of this trait for most of the provenances are higher at Neustrelitz where density was lower due to higher mortality.

### Genetic structure

#### Population genetic parameters

The analysis of 13 enzyme systems with 18 polymorphic loci allowed the detection of a total of 93 alleles. Only 30 alleles were present in all 24 populations, the remaining alleles were rare or not common in all populations. The mean number of alleles per locus did not differ significantly between provenances and between sites.

The estimations of genetic parameters of the two experimental locations like the average levels of observed and expected heterozygosity and effective number of alleles were nearly identical (Table 4). There were some irregular differences between the populations, which might be caused by random effects. The only geographic trend was the higher genetic variation of the four most eastern provenances Gorodok (50), Gomel (48), Voronezh (66) and Angasjak (38) at the site ‘Weisswasser’ in comparison to the site ‘Neustrelitz’.

**Table 2. Geographical data, mean heights, diameters and survivals of the analysed provenances at two locations (N – Neustrelitz, W – Weisswasser); (SO – seed orchard).**

No	Provenance	Country	Longitude (°E)	Latitude (°N)	Altitude (m)	Height (m)		Diameter (cm)		Survival (%)	
						N	W	N	W	N	W
2	Kolpin	D	14°16'	52°14'	40	7.8	8.6	7.8	7.9	38.3	53.3
3	Meiningen	D	10°19'	50°42'	350	7.0	8.0	6.6	7.1	33.0	61.3
4	Rathenow	D	12°47'	52°18'	40	7.4	7.9	8.3	8.0	37.3	45.3
6	Hildburghausen	D	10°44'	50°14'	310	7.2	7.9	7.3	7.0	30.3	64.3
9	Oranienburg	D	13°16'	52°50'	40	8.1	8.8	7.8	7.6	39.0	57.3
10	Neustrelitz	D	13°11'	53°19'	60	7.7	8.6	8.0	7.9	39.0	53.3
11	Mirow	D	12°47'	53°13'	50	7.5	8.5	7.8	7.8	35.0	56.0
12	Gransee I	D	13°06'	53°11'	50	7.5	8.1	7.9	7.4	47.0	54.3
13	Oelsnitz	D	12°14'	50°24'	460	7.7	8.3	6.9	7.0	39.7	60.0
14	Schleiz	D	11°56'	50°56'	470	8.0	7.5	8.1	7.2	37.7	45.7
15	Potsdam	D	13°06'	52°37'	50	8.1	8.5	8.4	7.7	32.7	64.0
16	Perleberg	D	11°41'	53°16'	40	8.5	8.2	8.7	7.9	40.7	54.0
17	Colbitz	D	11°36'	52°19'	90	8.0	8.8	8.2	7.5	50.3	66.7
18	Rostock I	D	12°17'	54°12'	20	7.9	9.0	8.4	7.2	39.3	68.7
19	Bad Berka	D	11°18'	50°53'	340	7.6	8.3	7.7	7.5	33.0	61.0
20	Tharandt	D	13°32'	50°59'	400	7.5	8.0	7.8	7.2	43.3	68.3
21	Niesky	D	14°51'	51°19'	130	8.3	8.3	8.0	7.6	42.0	60.7
22	Güstrow	D	12°15'	53°45'	20	8.2	8.2	7.6	7.4	48.3	58.0
23	Peitz I	D	14°31'	51°58'	90	8.6	7.9	8.8	7.6	35.7	63.7
27	Eibenstock	D	12°26'	50°27'	710	6.9	7.1	6.3	6.0	35.3	50.3
28	Jena	D	11°48'	50°54'	325	8.3	8.4	7.1	7.0	45.0	64.0
29	Neubrandenburg	D	13°16'	53°30'	60	8.3	8.2	8.0	7.9	44.7	60.0
30	Finsterwalde	D	13°43'	51°38'	110	7.7	7.9	8.2	7.8	31.0	63.7
31	SO* Finsterwalde	D	–	–	–	7.9	8.0	8.3	8.0	43.0	44.0
32	Rosslau	D	12°15'	51°54'	65	8.3	8.2	9.1	8.3	41.3	53.7
33	SO* Rosslau	D	–	–	–	7.6	8.1	8.0	7.8	42.0	64.3
34	Rostock II	D	12°09'	54°06'	16	7.9	8.2	7.5	7.8	52.3	59.7
35	SO* Rostock	D	–	–	–	7.9	7.5	8.0	7.4	33.0	50.0
36	Gransee II	D	13°09'	53°01'	80	8.1	8.0	8.4	7.5	39.0	56.0
37	SO* Gransee	D	–	–	–	8.2	8.5	8.2	8.0	41.0	53.3
38	Angasjak 1	RUS	55°51'	55°37'	200	6.3	7.0	6.5	5.9	34.0	53.3
39	Angasjak 2	RUS	55°51'	55°37'	200	6.2	6.9	6.3	6.3	31.0	39.7
40	Borisov	BEL	28°23'	54°15'	200	7.6	7.8	7.8	6.8	34.3	66.7
41	Kiew	UK	29°56'	50°31'	200	6.9	8.0	7.8	7.5	34.7	59.3
42	Melekesse	RUS	49°41'	54°11'	150	6.5	7.3	6.5	7.0	28.7	46.3
43	Jurbarkas	LIT	22°30'	55°05'	50	7.3	7.9	7.2	7.7	46.7	49.3
44	Kaunas	LIT	24°12'	54°59'	120	8.0	8.1	8.1	7.5	39.3	51.7
45	Riga 1	LAT	23°22'	56°30'	60	7.2	7.7	7.0	7.6	55.0	52.7
46	Riga 2	LAT	27°20'	56°15'	180	7.7	7.8	7.0	7.1	46.7	55.3
47	Riga I	LAT	24°05'	56°45'	20	7.0	7.7	7.0	6.7	32.0	49.7
48	Gomel	BEL	30°53'	52°23'	120	7.7	7.9	7.6	8.0	38.7	58.3
49	Welikie Luki	RUS	30°28'	55°58'	250	6.2	8.1	6.5	7.0	35.7	57.3
50	Gorodok	BEL	30°00'	55°18'	220	7.2	8.5	8.2	7.4	32.7	71.3
52	Riga 4	LAT	26°00'	57°25'	140	6.6	6.8	6.7	6.2	31.7	59.0
54	Riga II	LAT	25°50'	56°40'	100	7.3	7.5	6.9	7.1	45.7	60.0
55	Plaska	POL	23°16'	53°54'	170	7.6	8.1	8.0	7.5	41.3	64.7
56	Rychtal	POL	17°58'	50°11'	200	7.9	8.0	8.0	7.9	47.0	60.3
57	Suprasl	POL	23°22'	53°14'	170	7.5	8.3	7.5	8.0	39.3	60.7
58	Rytel	POL	18°01'	53°40'	190	7.9	8.6	7.8	7.6	38.7	71.0
59	Pokoj	POL	17°52'	50°54'	160	8.0	8.5	8.1	7.4	31.7	66.0
60	Tarda	POL	20°00'	53°48'	120	7.6	8.6	7.3	7.4	43.0	66.7

Table 2. (continued).

No	Provenance	Country	Longitude (°E)	Latitude (°N)	Altitude (m)	Height (m)		Diameter (cm)		Survival (%)	
						N	W	N	W	N	W
61	Rozpuda	PL	23° 10'	53° 50'	130	7.7	8.1	7.8	7.6	40.7	64.0
62	Zwierzyniec	PL	23° 00'	50° 40'	200	7.8	8.1	7.7	7.6	47.0	69.3
63	Taborz	PL	19° 59'	53° 47'	130	8.2	7.8	8.7	7.2	42.7	73.7
64	Starzyna	PL	23° 30'	52° 20'	150	8.1	8.0	7.8	7.5	37.7	67.3
65	Kliczkow	PL	15° 21'	51° 21'	200	7.8	8.5	8.3	8.9	39.7	42.3
66	Voronezh	RUS	39° 30'	51° 50'	180	7.0	7.7	7.0	7.1	31.7	55.0
67	Belica 417	BG	23° 31'	42° 03'	1900	5.3	5.5	6.0	5.5	15.3	26.0
68	Arramov 418	BG	23° 42'	42° 00'	1800	5.7	6.2	6.2	5.9	17.3	45.0
69	Bansko 419	BG	23° 31'	41° 49'	2000	5.4	6.9	5.3	6.7	21.7	36.3
70	Michalvova	BG	24° 26'	41° 51'	1600	4.9	5.9	4.4	5.8	30.0	38.0
71	Tscheditova	BG	24° 00'	42° 00'	1700	5.5	6.4	5.2	6.5	22.7	45.3
72	Antom Ivanov	BG	24° 18'	41° 56'	1650	4.8	5.9	4.7	5.4	22.7	50.0
<b>Site mean</b>						7.4	7.9	7.5	7.3	37.6	56.6

Table 3. Analysis of variance for tree height, diameter (1.3 m), and survival at age 20 (DF and MS are degrees of freedom and mean squares).

Source of variation	d.f.	Height			Diameter			Survival		
		MS	$\sigma$	F	MS	$\sigma$	F	MS	$\sigma$	F
Site	1	21.287	0.110	49.85*	2.840	0.012	5.57*	12098.305	63.776	333.13*
Provenance	62	3.575	0.525	8.37*	3.708	0.533	7.27*	122.923	13.061	3.38*
Site $\times$ provenance	62	0.371	0	0.87	0.506	0	0.99	44.556	2.746	1.23
Residual	252	0.427	0.427		0.510	0.510		36.317	36.317	

\* significant at 5 % level

Table 4. Average population genetic parameters based on 18 polymorphic isozyme loci.

No	Provenance	Observed heterozygosity		Expected heterozygosity		Effective number of alleles	
		Neustrelitz	Weisswasser	Neustrelitz	Weisswasser	Neustrelitz	Weisswasser
3	Meiningen	0.21	0.24	0.21	0.24	1.26	1.32
9	Oranienburg	0.24	0.22	0.22	0.21	1.29	1.27
17	Colbitz	0.26	0.24	0.26	0.24	1.36	1.31
18	Rostock	0.24	0.24	0.24	0.25	1.31	1.33
21	Niesky	0.24	0.25	0.24	0.24	1.32	1.32
27	Eibenstock	0.27	0.24	0.26	0.23	1.34	1.31
38	Angasjak	0.23	0.27	0.24	0.27	1.32	1.36
48	Gomel	0.23	0.25	0.24	0.24	1.31	1.32
50	Gorodok	0.22	0.25	0.21	0.24	1.27	1.32
57	Suprasl	0.24	0.23	0.23	0.24	1.30	1.31
59	Pokoj	0.24	0.24	0.26	0.23	1.34	1.30
66	Voronezh	0.24	0.27	0.25	0.27	1.33	1.36
<b>Mean</b>		0.24	0.24	0.24	0.24	1.31	1.32

Table 5. Number of rare alleles in 12 provenances at two experimental sites.

No	Provenance	<i>Pgm-A</i>		<i>Lap-B</i>		<i>Skdh-A</i>	
		Neustrelitz	Weisswasser	Neustrelitz	Weisswasser	Neustrelitz	Weisswasser
3	Meiningen	0	0	1	0	0	0
9	Oranienburg	1	2	0	0	0	0
17	Colbitz	1	0	5	3	1	1
18	Rostock	1	1	1	0	0	0
21	Niesky	2	3	0	0	1	0
27	Eibenstock	1	2	1	0	0	0
38	Angasjak	0	0	0	0	1	0
48	Gomel	0	2	1	0	1	0
50	Gorodok	0	3	1	0	1	0
57	Suprasl	0	2	0	0	2	0
59	Pokoj	0	3	0	0	0	0
66	Voronezh	0	1	1	1	1	0
	Sum	6	19	11	4	8	1

Table 6. Estimation of components of genetic variation at the total variation by the method of NEI (1973) (average values of 18 polymorphic loci).

Subdivision by location		Subdivision by provenances	
Total genetic variation	$H_T = 0.2453$	Total genetic variation	$H_T = 0.2453$
Average value of two location	$H_S = 0.2451$	Average value of 12 provenances	$H_S = 0.2416$
Average value of 24 units	$H_C = 0.2399$	Average value of 24 units	$H_C = 0.2399$
Component of variation between the locations from the between-population variation	3 %	Component of variation between the locations from the between-population variation	69 %

## Genetic structure at single loci

Considering single loci, it was noticed a shift of frequencies of common alleles at five isozyme loci (*Aat-B*, *Mdh-A*, *Mr-A*, *Pgm-A* and *Skdh-A*) especially in the four eastern seed origins between the two locations (Figure 2). This shift was statistical significant for the total of 12 provenances for the loci *Mdh-A*, *Pgm-A* and *Skdh-A* (paired Wilcoxon rank test,  $p < 0.10$ ).

The identical sample size of all populations allowed a comparison of the presence of rare alleles (alleles with frequencies below 0.05 per population). Thus, a loss of rare alleles at the loci *Lap-B* and *Skdh-A* at 'Weisswasser' and a loss of rare alleles at the locus *Pgm-A* at 'Neustrelitz' was ascertained (Table 5). The comparison of the sums of rare alleles for each locus between the two locations was carried out by the paired Wilcoxon rank test ( $p < 0.05$ ).

## Estimation of components of variance due to seed origin and to environment

A possibility to estimate the effect of seed origin and of environmental conditions on the genetic structure of Scots pine populations is given by the method of NEI (1973). In this case, the hierarchical subdivision of the total variation was carried out for the two locations and for the 12 provenances (Table 6). The procedure resulted in a large component (69 %) of genetic variation related to the seed origin and a very small portion (3 %) related to the test site conditions. The remaining 28 % of total genetic variation might be assigned to an interaction between seed origin and experimental location.

A second method to compare the differentiation between populations is the calculation of subpopulation differentiation according to GREGORIUS (1984). This subpopulation differentiation measures the mean gene-

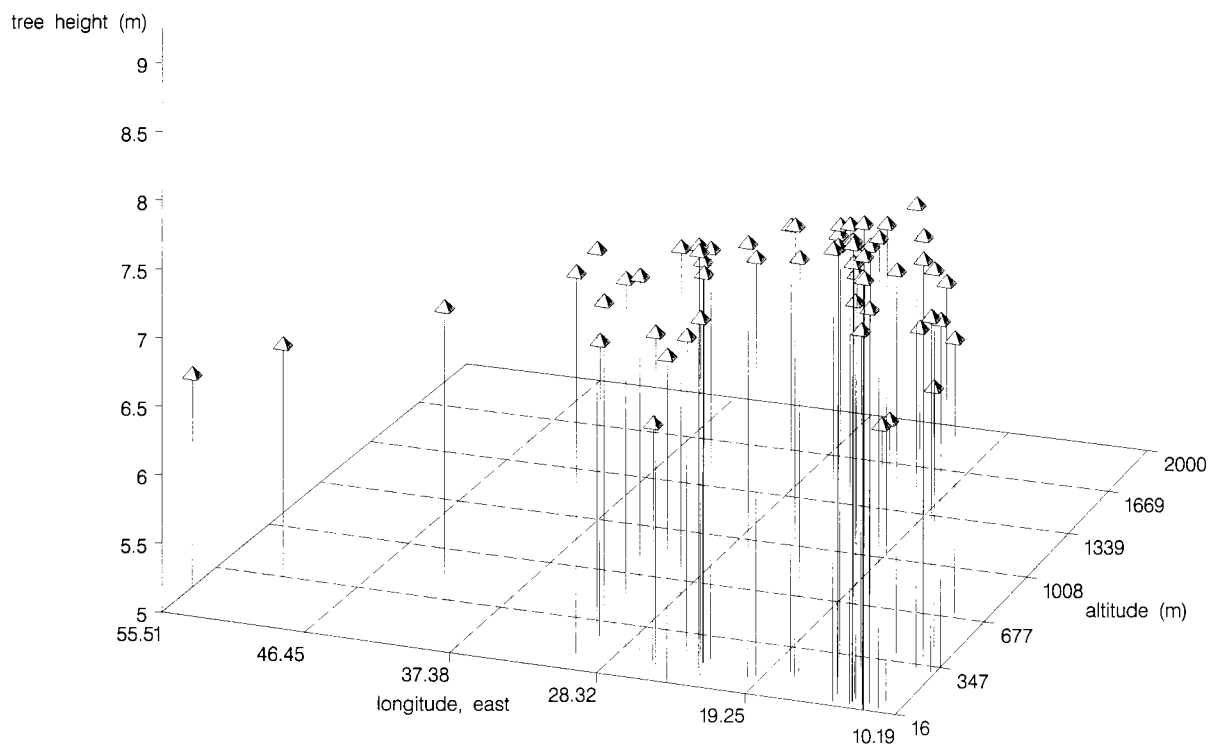


Figure 1. Mean tree height at age of 20 years in relation to longitude and altitude of places of origin.

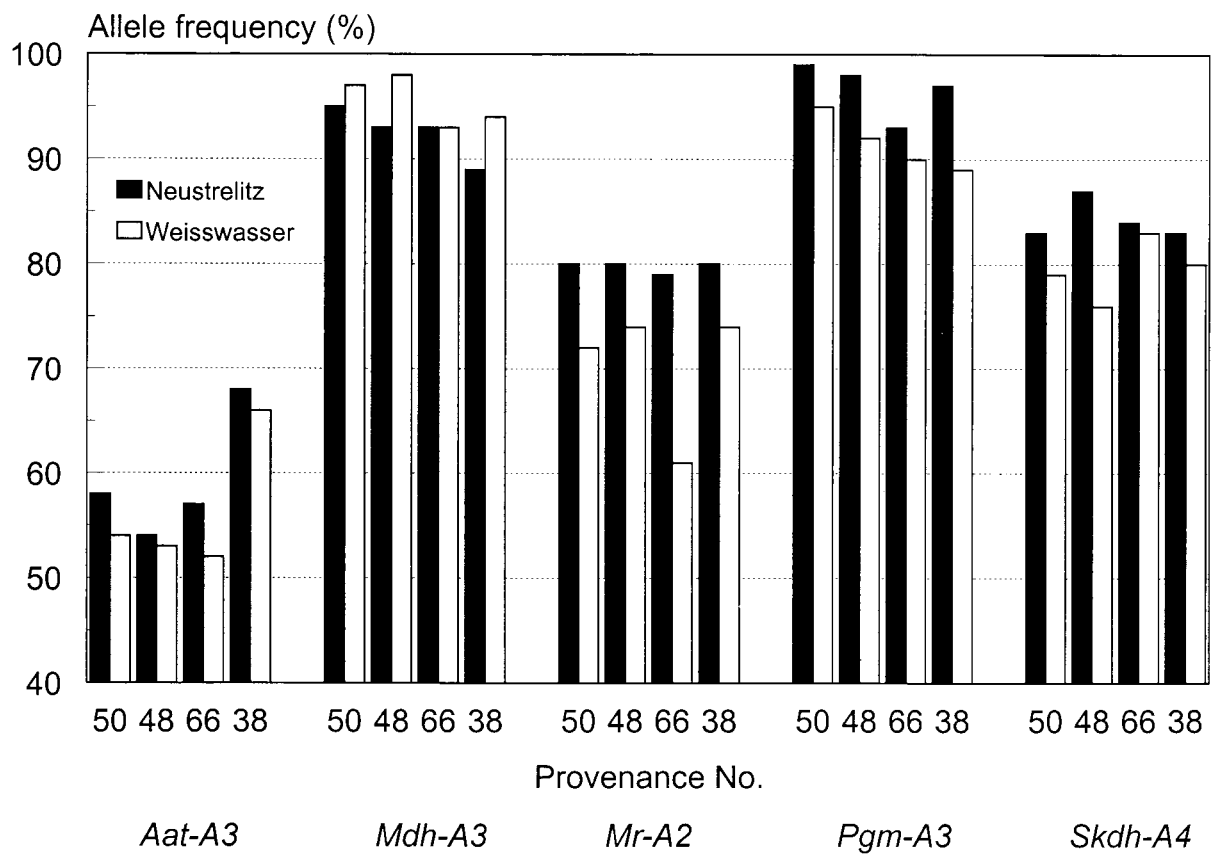


Figure 2. Shift of frequencies of common alleles of 5 isozyme loci for 4 eastern provenances.

ic distances  $\delta$  between populations without a hierarchical order. The subdivision by experimental sites resulted in a subpopulation differentiation of  $\delta = 0.017$ , and the subdivision by seed lots resulted in  $\delta = 0.041$ . The differentiation by seed lots was 2.4-times as high as that by environmental conditions.

The third possibility to estimate the portion of influence of seed origin and influence of environmental conditions on the genetic structure is the graphical visualization. The principal component analysis allowed the presentation of a part of the multilocus variation of the tested populations. In order to reduce the number of variables and to eliminate random effects, only alleles with mean frequencies above 0.02 were included into the principal component analysis. Each point in the plot of the first two components (first axis 18.7% and second axis 13.1% of the total variation) represents one of the 24 populations (Figure 3). The points for each of the two experimental sites are randomly distributed whereas a grouping is rather possible for the seed lots.

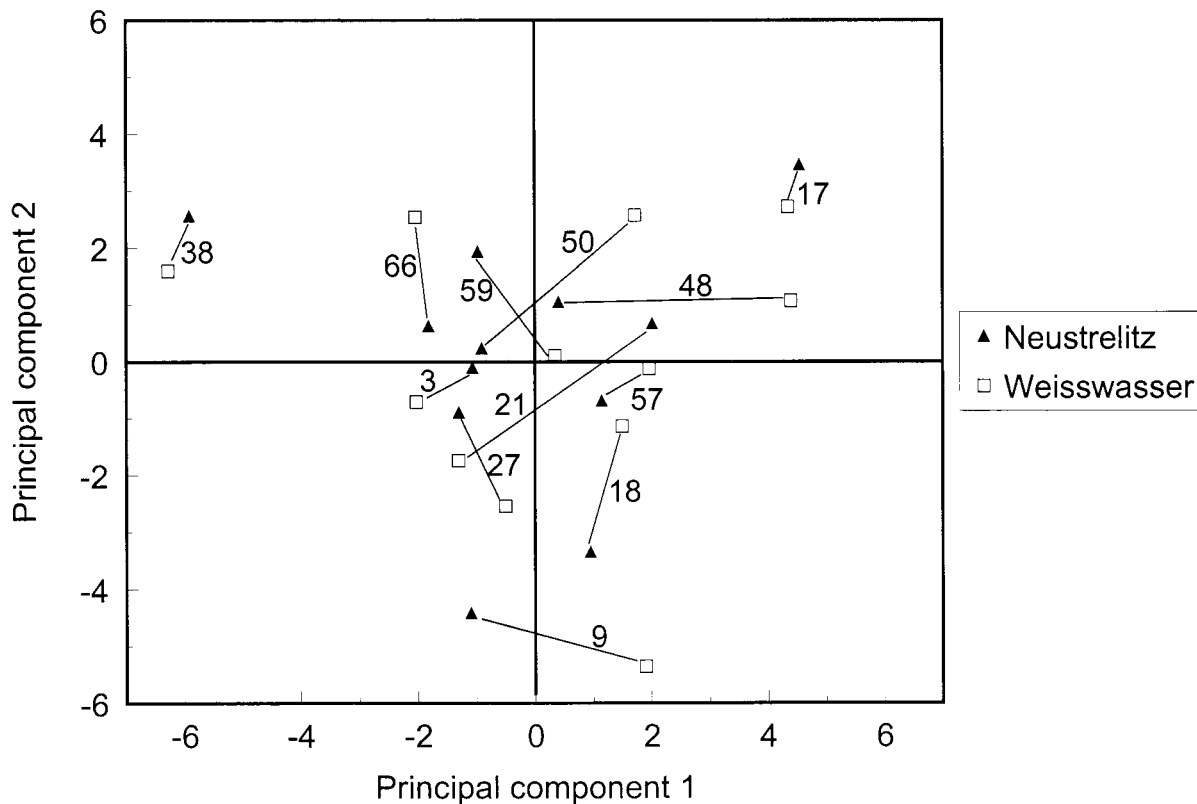
**DISCUSSION**

The genetic structure of Scots pine based on isozyme markers is known for its poor geographical differentia-

tion in comparison to other European tree species (PRUS-GŁOWACKI & BERNHARD 1994, PRUS-GŁOWACKI & STEPHAN 1994, GONCHARENKO *et al.* 1994). There exist, by contrast, large differences between provenances for growth and quality traits as shown in many provenance trials (for a review see GIERTYCH 1991, GIERTYCH & OLEKSYN 1992). Also in this investigation large variation between the tested provenances were detected for growth traits. These results are in accordance with the findings of other investigations of this trial series (KOHLSTOCK & SCHNECK 1992, KOHLSTOCK *et al.* 1996).

The lower survival rates of all provenances at the site 'Neustrelitz' with the more unfavorable conditions are not only a random loss of trees but also indicated a selection process. The absence of significant provenance by site interactions for all traits indicates that at both sites selection processes worked in the same way. Also the values for average genetic parameters support this assumption.

In contrast to the results for growth traits and survival the differentiation of the provenances based on isozyme markers was low. The component of genetic variation between 24 populations according to NEI  $[(1-H_c/H_T) * 100\%]$  equals to 2.2% of total variation. The subpopulation differentiation between the popula-



**Figure 3.** Principal component analysis based on frequencies of 40 alleles of 18 polymorphic loci (mean frequency > 0.02). For explanation of provenance numbers see Table 2.

tions according to GREGORIUS equals to  $\delta = 4.8 \%$ . These results indicated that more than 95 % of the genetic variation are within populations independent from the mode of calculation. Both methods based on average values of 18 polymorphic loci.

The multivariate computation of isozyme data by principal component analysis can represent the multilocus similarities of populations. Most provenances are very similar each to another, with the exception of the outstanding populations Angasjak (38), Colbitz (17), and Oranienburg (9). A weak differentiation by the geographic origin of populations was visible by the concentration of the most eastern provenances (Angasjak 38 and Voronezh 66) in the top left-hand corner of figure 3. Thus, the multilocus structure was more affected by the structure of seed lot than by environmental conditions at the two sites.

Of course, the genetic structure of seed material varied not only with the region of origin, but it was also overlaid by the structure of the random selected mother trees. Nevertheless, the observed differences at several single loci between the experimental sites based on identical seed lots.

The general accepted way for genetic inventories is to collect material from the original places. PRUS-GŁOWACKI & STEPHAN (1994) reported on 23 populations (app. 30 individuals per population and 7 polymorphic isozyme loci) and GONCHARENKO *et al.* (1994) reported on 18 populations (app. 30 individuals and 20 loci) of Scots pine in comprehensive parts of its natural range. Other publications described genetic structures on the basis of material from only one provenance trial site (PRUS-GŁOWACKI *et al.* 1993: 18 populations, 30 individuals and 8 loci, PRUS-GŁOWACKI & BERNHARD 1994: 13 populations, 12 to 30 individuals and 8 loci).

Up to now, no attempt was made to estimate the effect of site conditions in case of the use of material from provenance trials. The presented data show that it seems to be possible to use provenance trials for genetic inventories if the collection of material at the original places is impossible. But the interpretation at the level of single loci effects must be careful. More reliable results can be expected if more than one location of provenance trials are included in the investigations.

The preliminary data point out that the choice of provenance for stand establishment is very important in spite of the evident plasticity of the initial plant material. Further investigations with additional experimental plots in the provenance trial will provide data about the influence of forest management.

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