Different Genetic Structures of Two Morphological Types of Scots Pine (Pinus sylvestris L.)

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Summary

The management of Scots pine forests in the North-eastern German lowland distinguishes two morphological types, the so called A-type with a narrow crown and finer branches, which can perform timber of a high quality, and the so called B-type with a wide crown and thicker branches.

In the present work first results of a genetic analysis with isozyme markers of these two morphological types selected from three provenances are shown. We found a higher level of heterozygosity based on a higher number of rare alleles in the A-type group compared with the B-type group.

The silvicultural thinning practice which favours the A-type trees by removing the B-type trees is discussed with regard to the genetic aspect.

Key words: *Pinus sylvestris*, morphology, genetics, isozyme markers, thinning.

FDC: 165.3; 165.51; 165.62; 242; 174.7 *Pinus sylvestris*.

Introduction

At least since selective thinning has been introduced by Schädelin (1936) phenotypic traits of forest trees have become decisive when marking trees during silvicultural and tending measures. In pine management Olberg (1950) was the one who built up on those findings and reported on his rich experience in the book "Die Durchforstung der Kiefer"[1]), giving clear thinning guidelines to attain the production target of this tree species. Qualitative traits, which most probably have a genetic origin, played an always larger part. These reflections have been developed by Erteld and Kräuter (1957) and were finally the background of Kräuter's "relative tree classification" (1965) of pine into the so called A-type and B-type, which he characterizes according to morphological traits (*Table 1*).

Lockow (1992) describes these types A and B as follows: "Whereas type A shows a close connection between crown length and crown width, relatively short and thin branches, large branch angles in the lower part of the stem and a concentric crown structure, type B is characterized by a low crown ratio, relatively long and thick branches, small branch angles in the lower part of the stem and a mostly irregular, partly one-sided crown. Yardstick for long/short and small/large are the average traits of the same tree stratum." (page 170).

After a comprehensive data compilation on original plots established by Kräuter (1965) the same author concludes that types A and B can be characterized in a simple but clear way by means of the crown ratio, the branch thickness and the crown width.

The morphological traits of Scots pine were described by Velling and Tigerstedt (1984) in a similar way. Trees

[1]) "Pine Thinning".

Table 1. — Definition of A-type and B-type (Kräuter): Tree classification of Scots pine according to morphological traits.

Morphological traits	A-type	B-type
crown ratio (crown lenght/crown width)	high	low
crown structure	around the stem stable	partly lateral flat
branch thickness in the lower part of the stem	low	large
branch lenght	short	long
branch angle in the lower part of the stem	large	small
stem taper	full boled	conical
height growth as young tree	moderate	fast
diameter of same height class*)	generally lower than in B	generally higher than in A

*) Only in young stands.

with desired characteristics (analogous to our A-type) are called "ideotype" by Pulkinen et al. (1989).

In provenance trial plots at the thicket stage the crown ratio was sufficient to characterize both types since it is the prevailing trait of trees which are still quite green and it consists in height and length of the most outstretched branches (Kohlstock and Schneck, 1991). In doubtful cases the branch thickness could be used as an additional trait. The Eberswalde silvicultural and yield department has worked a lot in this field (Erteld, 1955 and 1958; Erteld and Kräuter, 1957; Wagenknecht and Henkel, 1962; Flöhr and Kohlstock, 1981 and 1982; Dittmar, 1991; Lockow, 1992) and deepened knowledge of the subject.

Advances in the field of forest genetics gave always more importance to the genetic aspect and raised the question whether genetic differences can be demonstrated through isozyme marker analyses between the phenotypically different A and B-types.

Material and Methods

Plant Material

90 sample trees of type A and 95 sample trees of type B (number of trees per provenance in *Table 2*) from the provenances Rostock, Kolpin and Suprasl (Poland) were selected out of a 17-yr-old trial with 72 pine progenies from Central and Eastern Europe (*Pinus sylvestris* L.)

Table 2. — Mean **diameter and height values of** 3 Scots pine provenances divided **into A type and B-type, significant** difference between A-type and **B-type with** $p = 0.10$ (*) and $p = 0.001$ (***).

Provenance	Number of trees		Diameter (cm)		Height (m)	
	A-type	B-type	A-type	B-type	A-type	B-type
Kolpin	27	31	9,94 ***	14,73	8,26	8,57
Rostock	31	31	9,45 ***	14,06	8,46 *	8,89
Suprasl	32	32	9,73 ***	13,40	8,67	8,78
all	90	95	9,70 ***	14,05	8,48 *	8,75

Table 3. — Enzyme systems used for genetic analysis.

Enzyme	Nomenclature number	References
SKDH	E.C. 1.1.1.25	LINHARDT et al. (1981)
6PGDH	E.C. 1.1.1.43	SZMIDT, A. E. & YAZDANI, R. (1984)
FDH	E.C. 1.2.1.2	HERTEL, H. (unpubl.)
GDH	E.C. 1.4.1.2	RUDIN, D. (1977)
AAT	E.C. 2.6.1.1	MÜLLER-STARCK, G. (1982)
LAP	E.C. 3.4.11.1	RUDIN, D., EKBERG (1978)

according to the criteria of crown ratio, branch thickness and crown width. Diameter at breast height and tree height were measured.

Enzyme electrophoresis and detection

The buds have been homogenized in a 0.1 M Tris borate buffer of pH 7.4 (according to LUNDKVIST, 1974) into which Polyclar AT had been added. Lateral buds were used as far as possible because they had clearer zymogram patterns. After centrifugation of the homogenates the soluble proteins of the supernatant were separated through polyacrylamide gel electrophoresis (alkaline standard system according to MAURER, 1968; 7.5 % gel of pH 8.9). The gels were stained for six enzyme systems (*Table 3*) shikimate-dehydrogenase (SKDH), 6-phosphogluconate dehydrogenase (6PGDH), glutamate dehydrogenase (GDH), formiate dehydrogenase (FDH), leucine aminopeptidase (LAP) and aspartate aminotransferase (AAT). Staining solutions have been modified according to YEH and O'MALLEY (1980) and VALLEJOS (1983). Formiate dehydrogenase was stained in 50 ml of 0.1 M Tris-HCI buffer (pH 8.0) containing 400 mg Na-formiate, 10 mg Nicotinamide-adenine-dinucleotide (NAD), 10 mg Thiazolyl blue (MTT) and 5 mg Phenazine methosulfate (PMS).

A total of 9 polymorphic enzyme loci were available for the analyses. When describing the genotypes of single loci, both alleles present have been separated by an oblique. The loci SKDH-B and 6PGDH-B have not been considered, since enzyme activities are often not sufficient to distinguish clearly the banding patterns.

Calculations

The G-test (likelihood quotient) has been used to compare frequencies. The classes have been grouped in such a way that all classes with values ≥ 5 were occupied.

The comparison of mean values has been done with the T-test for all samples with an approximately normal distribution. When no normal distribution was available the mean values have been compared using the non-parametric U-test of KRUSKAL and WALLIS. The level of significance have been indicated with $p=0.10$ (*), $p=0.05$ (**) $P=0.01$ (***).

The genetic distance, the gene pool diversity and the multilocus diversity have been measured according to GREGORIUS (1978).

Results

Comparison of the provenances analysed

The genetic structure of the material tested and selected from 3 provenances is first described shortly. The alleles

Table 4. — Allele frequencies at 9 polymorphic isozyme loci in 3 Scots pine provenances (A-types and B-types together), the R_m-value is the relative moving distance in relation to the most frequent allele of the respective locus.

Gene locus	Allele	R_m	Kolpin	Rostock	Suprasl
SKDH-A	1	108	-	-	.016
	2	106	-	.016	.023
	3	100	.776	.857	.820
	4	94	.224	.103	.125
	5	90	-	-	.008
	6	82	-	.024	.008
6PGDH-A	1	115	.009	-	-
	2	100	.759	.778	.789
	3	90	.224	.222	.211
	4	82	.009	-	-
FDH	1	136	.009	.008	-
	2	118	.086	.071	.125
	3	100	.879	.905	.875
	4	83	.026	.016	-
GDH	2	120	.379	.413	.367
	3	100	.621	.587	.633
AAT-A	1	112	-	.016	.008
	2	100	.948	.976	.992
	3	90	.052	.008	-
AAT-B	1	135	.017	.008	-
	2	125	.017	.024	.039
	3	120	.095	.032	.039
	4	117	.328	.325	.375
	5	100	.534	.611	.539
	6	83	.009	-	.008
AAT-C	2	138	.328	.310	.333
	4	100	.672	.690	.667
LAP-A	3	100	.991	.984	.969
	4	93	.009	.016	.031
LAP-B	1	109	-	.016	-
	2	105	.034	.040	.023
	3	100	.940	.905	.891
	4	95	-	-	.016
	5	93	.026	.040	.070

Table 5. — Comparison of the frequencies of genotypes and alleles between the A-type group and the B-type group of Scots pine (G-test).

Provenance	Gene locus	Genotype	Frequency		Level of significance	
			A-type	B-type	Alleles/Genotypes	
all	SKDH-A	3/3	55	70		
		3/4	22	22	*	**
		remaining	13	3		
all	FDH	2/3	23	10		
		3/3	64	80	**	*
		remaining	3	5		
Kolpin	6PGDH-A	2/2	10	23		
		2/3	14	7	***	***
		remaining	3	1		
Suprasl	6PGDH-A	2/2	26	17		
		2/3	6	9	**	***
		3/3	0	6		
Suprasl	LAP-B	3/3	21	29	**	**
		remaining	11	3		

Table 6. — Level of heterozygosity and diversity of A-type and B-type trees of 3 Scots pine provenances.

	Type	Kolpin	Rostock	Suprasl	all
H_o	A	0,34	0,32	0,31	0,32
	B	0,30	0,28	0,26	0,28
H_e	A	0,32	0,28	0,31	0,31
	B	0,27	0,26	0,26	0,27
Gene pool	A	1,47	1,40	1,44	1,44
diversity	B	1,37	1,36	1,36	1,37
Multilocus	A	45,6	26,5	35,9	36,1
diversity	B	24,1	19,8	22,9	22,4

Table 7. — Comparison of the mean level of heterozygosity and of the portion assigned to major polymorphism and to minor polymorphism between A-type and B-type Scots pine trees.

Level of heterozygosity	A-type (n=90)	B-type (n=95)	Comparison of mean values / level of significance	
H_o (total)	0,32	0,28	T-test	0,025 **
H_o (major polym.)	0,232	0,228	T-test/U-test	n. s.
H_o (minor polym.)	0,088	0,052	U-test	0,05 **

Table 8. — Mean values of diameter and height of A-type and B-type Scots pine trees with low or high individual number of heterozygous loci (in brackets: number of trees).

Trait	Type	Low heterozygosity 0 - 2 loci	High heterozygosity 3 - 7 loci
Diameter	A	9,23 (34)	9,99 (56) ***
(cm)	B	13,92 (50)	14,20 (45)
	all	12,02 (84)	11,87 (101)
Height	A	8,57 (34)	8,42 (56)
(m)	B	8,72 (50)	8,79 (45)
	all	8,66 (84)	8,58 (101)

present and their frequencies at 9 polymorphic enzyme loci (*Table 4*) show a great similarity between the provenances of the common alleles (no significant differences) but differences however in the presence or absence of some rare alleles. This has however no influence on the genetic multiplicity of the material tested, which shows only little difference with a number of alleles per locus of A/L = 3.0 for the provenances Kolpin and Suprasl and A/L = 3.3 for the provenance Rostock.

The mean genetic distances, considering all loci, amount to d_0=0.043 between the provenances Kolpin and Rostock, to d_0=0.044 between Kolpin and Suprasl and to d_0=0.038 between Rostock and Suprasl. These distance are on the whole very low and do not indicate, at least not for the enzyme loci analysed, large genetic differences between the Polish provenance on the one hand and both Central European provenances on the other.

Significant differences between the provenances are observed only when comparing the mean diameter of the B-types (*Table 4*, p=0.025**). The comparison of the mean diameters of the A-types and the height measured did not show any significant differences between the provenances.

For the comparison of the genetic structure of both growth types we considered single loci as well as mean values of all loci analysed.

Connection between growth type and structure at single loci

The frequency distributions of the genotypes and alleles of the A or B-types of the provenances are homogenous for 8 of the 9 gene loci analysed (with the exception of 6PGDH-A), this allows a grouping of all A-types of the 3 provenances or respectively of all B-types of the same gene loci, and a better statistical support. Besides the differences between the enzyme loci 6PGDH-A and LAP-B of some provenances there are also significant differences between the loci FDH and SKDH-A of the A and B-types of the whole material tested (*Table 5*). In most cases the heterozygous genotypes occur more often in the A-type group and the homozygous genotypes more often in the B-type group. This is also true for the majority of the remaining enzyme loci which did not show significant differences.

Connection between growth type and genetic parameters including all loci analysed

The level of heterozygosity, H_0 and H_e, as well as the gene pool diversity and multilocus diversity describe a higher genetic variation in the A-type group than in the B-type group (*Table 6*) for all 3 provenances analysed, without exception.

The difference between both morphological types is most obvious in the hypothetical gametic diversity, which represents the potency to form genetically different gametes (Gregorius, 1978). The average differences of the A-types amounts to 1.6 times the multilocus diversity of the B-types.

The mean level of heterozygosity H_0 is by 14 % higher in the A-type group than in the B-type group (*Table 6*). This mean value however contains loci with a minor polymorphic structure (AAT-A, LAP-A), loci with a major polymorphic structure (GDH, AAT-C) and mixed forms (e.g. AAT-B), which can contribute with a different intensity to the whole level of heterozygosity of a tree. When this level of heterozygosity is distributed between the portion coming from minor polymorphism (established by the presence of an allele with a frequency ≤ 0.1 at a heterozygous locus) and the portion coming from major polymorphism (all other heterozygotes), both morphological types still differ only through the minor polymorphisms (*Table 7*). The higher level of heterozygosity of the A-types is due to a more frequent occurrence of rare alleles in this group.

Connection between growth production and genetic parameters

Both morphological types described differ significantly through the diameters measured, whereas the trees of type B show only a tendency to have a larger height (*Table 2*). There was no correlation between the data on height and diameter compiled for each tree as well within both groups (A-types: regression coefficient r = 0.08, B-types: r=0.10) as on the whole (r=0.15).

The B-type group with a high mean diameter has a low mean level of heterozygosity compared to the A-types (*Table 6*). If the trees are however assigned within a growth type to a group with a low heterozygosity (0 to 2 heterozygous loci per tree) and to a group with a high

heterozygosity (3 to 7 heterozygous loci, whereas 6 and 7 heterozygous loci occur only once in the A-type group) the A-type trees with a higher level of heterozygosity also have a significantly larger diameter (*Table 8*).

Discussion

The generally higher fitness attributed to the B-types, expressed by a radial growth above average and a correspondingly large crown form, and leading to an overdominance in the stand, is not connected with a higher genetic variation in our study, as it could be assumed when considering the frequently described and discussed positive connection between heterozygosity and fitness (Overdominance model of SMOUSE, 1986).

There are numerous examples of such a connection between higher heterozygosity of forest trees on the one hand and fitness expressed by a higher resistance to pollutants on the other (e.g. *Fagus sylvatica:* MÜLLER-STARCK, 1985; *Pinus sylvestris:* GEBUREK et al., 1987; Picea abies: BERGMANN and SCHOLZ, 1987; 1989; *Fagus sylvatica:* HERTEL and ZANDER, 1991). Trees grouped according to the degree of damage were compared in these studies. No connection has been observed however when comparing the degree of damage and heterozygosity of provenances (*Picea abies:* FRANKE and KONNERT, 1990).

When correlating growth characteristics with heterozygosity it has often not been possible to demonstrate a correlation in seedling trials (e.g. *Pseudotsuga menziesii:* EL-KASSABY, 1982) or only under special conditions of cultivation (e.g. *Pinus banksiana:* GOVINDARAJU and DANCIK, 1986, 1987). In older trees this correlation has not been possible either or only partly (*Pinus ponderosa:* LINHART and MITTON, 1985; *Pseudotsuga menziesii*: BONGARTEN et al., 1985; *Pinus rigida*: LEDIG et al., 1983; BUSH et al., 1987; *Pinus attenuata:* STRAUSS, 1986). These contradictory findings could have their origin not only in the number and selection of the isozyme markers analysed (minor and major polymorphisms) but also in the type of phenotypes put in connection with genotypes like traits of vegetative growth, resistance or success of propagation which should express fitness. The method of evaluation of the data differs just as well, which can occur through an assignment of the material in two or more groups and a comparison of the mean values or of the linear or other correlations with or without weighting of the classes.

In our study the homozygous genotypes seem to have the advantage when considering the whole material, which remind of a negative impact of rare alleles (e.g. *Pseudotsuga menziesii*: BONGARTEN et al., 1985; *Pinus radiata:* STRAUSS and LIBBY, 1987; *Fagus sylvatica:* ZIEHE, 1990; *Picea abies*: VON WÜHLISCH and KRUSCHE, 1991; *Picea abies:* HERTEL, unpublished). The consideration of the morphological types gave the following succession, ordered according to the falling mean diameter: B-types with a higher heterozygosity, B-types with a lower heterozygosity, A-types with a higher heterozygosity and A-types with a lower heterozygosity.

The assignment of a tree to a morphological type rather determined the diameter growth than the genetic variation described through isozyme markers. It is obviously a superposition of several effects which allows no simple formal explanation. Whether there are connections and which ones between gene markers and growth besides the morphological types considered, has to be cleared by further analyses, which do not include only trees selected according to specific phenotypes but also samples representing the whole population.

The results presented here temporarily give no direct reason to fear that the silvicultural method of selective thinning applied up to now in the pine stands of the northeastern German lowland has led to a substantial narrowing of the genetic base and therefore to a reduction of the potency of adaptation to future environmental conditions (KOHLSTOCK and HERTEL, 1992; KOHLSTOCK, 1993).

Our silvicultural interest in genetic analyses is focused on pine provenances which are sufficiently adapted to the conditions of Central Europe with periods of drought during the vegetation time and alternate periods of frost or no frost in the wintertime. It is however imaginable that the morphological and genetic structures of the populations on the western limit of the natural range of this species are not to be generalized. When examining furthermore the connection between growth production, growth form and genotype one should not only include more trees from the provenances analysed up to now and a large number of markers, but also additional plant material as well from Central Europe as form Eastern Europe. The comparison of older and younger stands lets us expect interesting results just as well.

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Genetic Structure of Marginally Located Pinus nigra var pallasiana Populations in Central Turkey

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Summary

To determine the genetic structure of marginally located populations of *Pinus nigra* var *pallasiana*, seedlings of open pollinated families from 7 populations were raised in Kizilcahamam nursery near Ankara for 2 years. Seed weight (SW) and cone weight (CW) for families, number of cotyledon per seedling (COT), timing of bud set in 1990 (BS90) and in 1991 (BS91), bud burst timing of seedlings in 1991 (BB91), height growth in 1991 (HT90) and final height growth in 1991 (HT91) and final diameter growth of seedlings (DM91) were recorded. Among the traits studied, the component of genetic variation attributed to regions (ranging from 0% to 5.7% of the total variation) and populations (ranging from 0% to 9%) made up very small portion of the total genetic variation while variation among the families within population was very high (ranging from 11.5% to 91.5%). The estimated family heritabilities were moderately high for the most of the traits, ranging from 0.28 for BB91 to 0.98 for SW. Correlations between seedling traits and topographic variables were not significant, suggesting that effects of aspect, slope and altitude on genetic differentiation of population are minor. In general, phenotypic and genetic correlations between seedling traits were generally the same sign and magnitude, however, genetic correlations between height growth and bud set timing were strongly negative (—0.54).

It was concluded that the marginal populations of Anatolian black pine maintain a large within population genetic variation in order to be able to adapt to the mosaics of micro-environments that exists in these locations. The implications of the findings in the study in terms of tree improvement and genetic adaptation mechanisms in the species are discussed in detail.

Key words: Pinus nigra var *pallasiana,* genetic variation, family heritability, marginal populations, genetic correlations, genetic adaptation.

FDC: 165.3; 165.5; 174.7 *Pinus nigra;* (560).

Introduction

European black pine (*Pinus nigra*) has a natural distribution in southern Europe, extending from Spain to Tur-

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