The Impact of Air Pollution on the Genetic Structure of Norway Spruce*)

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Summary

In order to investigate the impact of air pollution on the genetic structure of a relatively sensitive forest tree species, heavily damaged (subsets S) and relatively healthy tree groups (subsets T) of Norway pruce (Picea abies) were compared with respect to their genetic structures determined at nine polymorphic enzyme gene loci. The subsets originated from both clone collections fumigated with single pollutants (SO_2, HF, O_3) and forest tree stands located at polluted sites in the Harz mountains.

The comparisons showed that remarkable genetic differences between the subsets S and T occur at four enzyme loci, whereby for two loci relationships between biochemical or physiological functions of the enzyme and the degree of plant damage may exist. Differences in allele and genotype frequencies at three enzyme loci between the subsets S and T were relatively consistent when the Harz stands were compared with the clone collection fumigated with SO_2 and O_3, the presumed main components of air pollution in the Harz mountains. Comparisons of the genetic diversity revealed that for the fumigated clone collection the subsets S generally possess higher values than the subsets T, whereas for the Harz stands the subsets T exhibit by far higher values. Based on these data the consequences for Norway spruce populations were discussed.

Key words: Air pollution, fumigation, genetic structure, genetic diversity, enzyme gene loci, Norway spruce.

Zusammenfassung

Zur Untersuchung der Auswirkung von Luftverunreinigungen auf die genetische Struktur einer relativ empfindlichen Waldbaumart wurden stark geschädigte und nicht-geschädigte Baumgruppen der Fichte *(Picea abies)* bzgl. ihrer genetischen Strukturen an 9 Enzym-Genloci verglichen. Derartige anhand von visueller Bonitur ausgewählte Baumgruppen wurden sowohl nach kontrollierten Begasungsversuchen mit den Schadgasen SO_2, HF und O_3 als auch in zwei stark geschädigten Fichtenbeständen des Oberharzes gebildet.

Deutliche genetische Unterschiede zwischen den beiden Baumgruppen fanden sich bei 4 Enzym-Genloci, wobei in 2 Fällen Beziehungen zu biochemischen oder physiologischen Funktionen der Enzyme möglich erscheinen. Gewisse Ähnlichkeiten in den Allel- und Genotyphäufigkeitsunterschieden zwischen den Baumgruppen fanden sich bei dem mit SO_2 oder O_3 begasten Klonkollektiv und den Fichtenbeständen im Harz. Vergleiche der genetischen Diversität, die mit Hilfe dreier Diversitätsmaße bestimmt wurde, ließen erkennen, daß die infolge von kontrollierter Begasung geschädigten Baumgruppen höhere Werte aufweisen als die nicht-geschädigten Baumgruppen, daß aber in den Harzbeständen genau umgekehrte Verhältnisse beobachtet wurden. Die hieraus sich ergebenden Konsequenzen für Fichtenpopulationen wurden diskutiert.

Introduction

There is now great concern that air pollution (and its conversion products) can alter the genetic structure of forest tree populations by processes which are assumed to have selective effects (Scholz 1984, 1986; Gregorius *et al.* 1985). Since this man-made environmental stress is neither temporally nor spatially limited in Central Europe, its consequences for the gene pool of European forest tree species may be dangerous in that certain genes are decreasing range-wide in their frequencies and will ultimately be lost. Such a genetic impoverishment leads, however, to a generally reduced adaptability of tree populations to natural stress factors in future generations (for review, see Gregorius *et al.* 1985).

In order to study the intensity and direction of genetic changes in Norway spruce (*Picea abies* (L.) Karst.) caused by air pollution, we investigated both clone collections fumigated with gaseous pollutants and tree samples in severely damaged forest stands. In both cases, the genetic structures of tolerant tree groups were compared with those of sensitive groups, using gene and genotype frequencies determined at nine polymorphic enzyme gene loci. Genetic differences between such kinds of tree groups are, of course, the primary prerequisite for subsequent selection processes (Bergmann and Scholz 1985), and were already found at single enzyme loci in Scots pine (Mejnartowicz 1983), Norway spruce (Scholz and Bergmann 1984) and beech (Müller-Starck 1985).

Material and Methods

For the fumigation experiments, about 120 clones propagated from young trees were used, representing various half-sib families from maternal trees in Slovakia. This clonal material (6 ramets per tree) was fumigated with SO_2, HF or O_3 in open top chambers for three or four weeks until the phenotypic variation in damage ranged from "not visibly injured" to "total necrosis of needles or died back, compared to not fumigated ramets as a control (a detailed description of these experiments is given by Scholz *et al.*, in prep.). For genetic comparisons in each of the three fumigation experiments, 28—40 most tolerant clones were combined to a subset T and most sensitive clones to a subset S.

Field stands of Norway spruce were chosen in two regions of the Harz mountains (Sonnenberg, Bruchberg) with higher deposition of air pollutants (Hartmann *et al.*, 1986). In these forest stands, 25 pairs of closely adjacent trees

*) dedicated to Prof. W. Langner on the occasion of his 80th birthday.

Table 1. -- Enzyme systems and enzyme coding gene loci analysed in the clone collections and forest stands.

Enzyme systems	Enzyme coding gene loci	Polymorphic gene loci
Leucine aminopeptidase	LAP-A, LAP-B	LAP-B
Glutamate oxaloacetate transaminase	GOT-A, GOT-B, (GOT-C)	GOT-B
Glutamate dehydrogenase	GDH-A	
Malate dehydrogenase	MDH-A, MDH-B, MDH-C, MDH-D	MDH-C
Isocitrate dehydrogenase	IDH-A, IDH-B	IDH-A
Glucose-6-phosphate dehydrogenase	G-6-PDH-A	G-6-PDH-A
NADH dehydrogenase	NDH-A	NDH-A
Glutathione reductase	GRD-A	GRD-A
Phosphoglucomutase	PGM-A, PGM-B	PGM-B
Phosphoenolpyruvate carboxylase	PEPCA-A	PEPCA-A

were chosen, of which one tree appeared to be relatively healthy and the other severely injured. For each stand, the healthy trees were combined to a subset T and the injured trees to a subset S.

For isozyme analysis, meristem tissue of dormant buds collected from non-fumigated ortets or from green twigs of the trees in the forest stands was extracted, and these extracts were then subjected to horizontal starch gel zone-electrophoresis. After electrophoretic separation, the gels were stained for various enzyme systems, the genetic control of which was already known for Norway spruce. Details of the electrophoretic procedures, staining recipes and formal genetic analysis were described by LUNDKVIST 1979; POULSEN *et al.* 1983; CHELIAK and PITEL 1984, BERGMANN, in prep.).

The enzyme systems used in this study are listed in *Table 1* together with the gene loci coding for the isozymes of each system and the gene loci found to be polymorphic in the plant material investigated. Most of these enzyme systems were selected because of their biochemical role in metabolic processes related to resistance mechanisms in plants or their particular sensitivity to pollutant metabolites as mentioned in the literature (GRILL and ESTERBAUER 1973, 1981; JÄGER and KLEIN 1980; RABE and KREEB 1980; MEJNARTOWICZ 1984).

Results and Discussion

Differences in genetic structure

Of the 18 gene loci coding for the isozyme patterns of 10 enzyme systems, nine were polymorphic in at least one collection of plants studied (*Table 1*). The numbers of alleles detected at these loci differed from one to four (LAP-B), whereby in most cases one and the same allele predominates in the clone collection and the forest stands. In addition, the frequencies of many genotypes in the clone collection are similar to those in the forest stands of the Harz mountains. Thus, as was to be expected from the postglacial reimmigration pattern, the clone collection derived from maternal trees located in Slovakia and the Harz stands seem to originate from the same gene pool, since both localities belong to the so-called Hercynic-Carpathian range of Norway spruce.

Remarkable differences in allele and/or genotype frequencies between the subsets S and T of the fumigated clone collection and/or the Harz stands were found for four enzyme loci (*Table 2*). Among these gene loci, however, the genetic differences between the subsets were found to be heterogeneous with respect to the genotype classes involved. For the G-6-PDH-A locus, all genotypes carrying the allele A_1 (A_1A_1 and A_1A_2) are more frequent in subsets S (except for the O_3-collection) which, accordingly, is reflected in the allele frequency differences between the subsets. As the genotype differences are statistically significant in several cases, a direct involvement of this enzyme-gene-system in tolerance mechanisms is imaginable, especially since G-6-PDH is the key enzyme of the pentose phosphate cycle, which is postulated to become very im-

Table 2. — Frequencies of genotypes and of the common allele (in brackets) for four enzyme gene loci estimated in subsets S and T of the clone collections and the forest stands. Asterisks indicate significant differences (G-test) at the 5 percent level or the values approach the 5 percent level.

	Norway spruce material	N	GOT-B B_1B_2	B_2B_2	B_2B_3	B_3B_3	(B_2)	G-6-PDH-A A_1A_1	A_1A_2	A_2A_2	(A_2)	PEPCA-A A_1A_1	A_1A_2	A_2A_2	(A_1)	GRD-A A_1A_2	A_1A_3	A_2A_2	A_2A_3	A_3A_3	(A_2)
Clone collections	SO_2 fumigation																				
	subset S	31	0.10	0.42	0.26	0.22	0.60	0.03	0.26	0.71	0.84	0.78	0.19	0.03	0.87	0.03	0.03	0.65	0.23	0.06	0.77
	subset T	30	-	0.43	o.47	0.10 *)	0.67	-	0.07	0.93 *)	0.97	0.83	0.17	-	0.92	0.03	-	0.50	0.40	0.07	0.71
	HF fumigation																				
	subset S	40	-	0.58	0.25	0.17 *)	0.70	0.03	0.22	0.75 *)	0.86	0.72	0.25	0.03	0.85	0.07	0.03	0.58	0.27	0.05	0.75
	subset T	35	0.09	0.34	0.40	0.17	0.58	-	0.06	0.94	0.97	0.74	0.26	-	0.87	0.03	-	0.68	0.29	-	0.84
	O_3 fumigation																				
	subset S	28	0.07	0.57	0.25	0.11	0.73	-	0.14	0.86	0.93	0.75	0.25	-	0.87	0.14	-	0.64	0.18	0.04	0.80
	subset T	28	-	0.50	0.32	0.18	0.66	-	0.22	0.78	0.89	0.89	0.11	-	0.95	0.04	-	0.53	0.36	0.07 *)	0.73
Forest stands	Sonnenberg (Harz)																				
	subset S	25	-	0.44	0.40	0.16	0.64	-	0.20	0.80	0.90	0.80	0.20	-	0.90	0.04	0.04	0.84	0.08	-	0.90
	subset T	25	0.04	0.32	0.52	0.12	0.60	-	0.08	0.92	0.96	0.68	0.32	-	0.84	0.16	-	0.64	0.20	-	0.82
	Bruchberg (Harz)																				
	subset S	25	0.04	0.28	0.32	0.36	0.46	-	0.32	0.68	0.84	0.72	0.24	0.04	0.84	-	-	0.72	0.20	0.08	0.82
	subset T	25	-	0.20	0.56	0.24	0.48	-	0.20	0.80	0.90	0.68	0.32	-	0.84	0.04	-	0.60	0.36	-	0.80
	Combined Harz stands																				
	subset S	50	0.02	0.36	0.36	0.26	0.55	-	0.26	0.74	0.87	0.76	0.22	0.02	0.87	0.02	0.02	0.78	0.14	0.04	0.86
	subset T	50	0.02	0.26	0.54	0.18	0.54	-	0.14	0.86	0.93	0.68	0.32	-	0.84	0.10	-	0.62	0.28	- *)	0.81

portant in plant metabolism under stressful environmental conditions (see SCHOLZ and BERGMANN 1984).

The differences at the three other loci are mainly concerned with particular heterozygous genotypes, such as GOT-B_2B_3 being more frequent in all T-subsets (*Table 2*). The polymorphism at this enzyme locus represents the so-called classical type (major polymorphism = two predominant alleles with similar frequencies) in all spruce populations as yet studied, so that a balanced selection regime may be assumed to maintain this polymorphism (LEWONTIN 1985). Therefore, it is reasonable to suppose that the heterozygote GOT-B_2B_3 is better adapted to environmental heterogeneity, since it has more isozyme variants than the homozygotes. Similarly, GRD-A_2A_3 is more frequent in all subsets T compared to the respective subset S. The greatest and significant differences between the subsets S and T were observed for the O_3-fumigated collection, which corresponds well with the biochemical function of this enzyme, since it converts oxydated glutathione (GSSG) to reduced glutathione (GSH), a protective peptide against radicals and other oxydation metabolites (e.g. released from O_3). For the gene locus PEPCA-A, the heterozygote A_1A_2 was found more frequently in the subsets T of both Harz stands, but appears with higher frequency in the subset S of the O_3-fumigated clones (*Table 2*).

Only minor genetic differences between the subsets were found for the other enzyme loci, indicating no involvement of their genotypes in the extent of pollution tolerance/sensitivity. Regarding differences in allele frequencies, it should be mentioned that rare alleles predominate more often in the subset S (19 comparisons) than in the subset T (8 comparisons). The allele C_3 at the locus MDH-C, for instance, generally occurs more frequently in the S-subsets due to the higher frequency of genotypes C_2C_3 and/or C_3C_3.

In the Harz mountains, SO_2 and O_3 are reported to be the main pollution components responsible for the forest decline (HARTMANN *et al* 1986). Therefore, it is interesting to test whether the genetic differences between the T- and S-subsets of the spruce stands from the polluted sites coincide with those of the clone collection fumigated in controlled experiments. For this comparison, the data of both Harz stands were combined, since they are exposed to a similar pollution regime (*Table 2*). For GOT-B_2B_3, the difference between the subsets S and T of the Harz stand is particularly reflected by the SO_2-fumigated clone collection, but the data of tthe HF and O_3 collections are also in accordance. Similarly, the frequencies of A_1A_2 and A_2A_2 at the G-6-PDH-A locus observed for the Harz subsets coincide well with those of the SO_2 and HF subsets. There is also a correspondence of frequencies of the GRD-A_2A_2 and -A_2A_3 genotypes, when the Harz subsets are compared with the SO_2- and O_3-fumigated subsets. Therefore, it can be stated that the most pronounced agreement appears between the Harz data and those of the clone collections fumigated with SO_2 and O_3, which are assumed to represent the main detrimental pollution components (*Table 2*).

Table 3. — Values of genetic variation for the subsets S and T estimated by three diversity (variation) measures.

	Norway spruce material	Alleles/Locus	Gene pool diversity	Observed Heterozygosity mean	range
Clone collections	SO_2 fumigation				
	subset S	2.25	1.35	0.24 (0.25)	0.06-0.48
	subset T	2.37	1.25	0.23 (0.26)	0.03-0.53
	HF fumigation				
	subset S	2.37	1.31	0.23 (0.22)	0.03-0.45
	subset T	2.37	1.23	0.22 (0.26)	0.03-0.57
	O_3 fumigation				
	subset S	2.50	1.28	0.20 (0.21)	0.04-0.40
	subset T	2.25	1.27	0.19 (0.21)	0.09-0.42
Forest stands	Sonnenberg				
	subset S	2.11	1.25	0.20 (0.21)	0 -0.48
	subset T	2.44	1.30	0.26 (0.31)	0.04-0.56
	Bruchberg				
	subset S	2.22	1.31	0.24 (0.25)	0 -0.44
	subset T	2.33	1.34	0.31 (0.35)	0.04-0.60

Differences in genetic diversity

Apart from differences in allele frequencies, considerable differences in the overall genetic diversity between the subsets S and T should be of great importance, if there is pollution-affected reproduction in the respective forest stands. Therefore, several diversity (variation) parameters were calculated, including the average number of alleles per locus, the gene pool diversity (harmonic mean over loci of the effective number of alleles, $v = \frac{1}{\Sigma p_i^2}$, see GREGORIUS 1987) and the average degree of observed heterozygosity. The resulting data based on gene and genotype frequencies of all of the nine polymorphic enzyme loci are compiled in *Table 3*.

There are generally higher values for each of the three variation parameters in the subsets S of the clone collection fumigated with single pollutants, while in contrast, by far higher values are measured in the subsets T of the Harz stands. In particular, the mean heterozygosity is greater in the subsets T than in the subsets S of the spruce stands in the Harz mountains, resulting from those gene loci that exhibit heterozygote advantage.

While in controlled fumigation experiments using even-aged clone material, phenotypic differences in the degree of individual damage are assumed to be mainly caused by genetic differences in sensitivity to the respective pollutant (SCHOLZ *et al.* 1979), the phenotypic differences observed in air polluted field stands may be dependent on both different environmental modifications and genetic differences in resistance to a multiplicity of adverse environmental factors. Yet, it is remarkable that there are corresponding genetic differences between S- and T-subsets of the clone collection and the Harz stands, even though the selection of tree pairs will have reduced the modifying effects. Such correspondence between spruce clones and stands refers to the allele and genotype frequencies at the G-6-PDH-A locus and to the frequencies of specific heterozygotes at the loci GOT-B and GRD-A, respectively. On the other hand, there are deviations with respect to the genetic variation values measured (*Table 3*). In general, higher values for each of the three variation parameters calculated were found in subsets S of the fumigated clone material and on the contrary, in subsets T of the tree stands in the Harz mountains. These results agree well with the hypothesis that trees with a high individual diversity (heterozygosity) are better adapted to a temporally heterogeneous environment, whereas trees with a lower individual diversity are assumed to be better adapted to only one environmental stress factor, such as one specific pollutant (GREGORIUS *et al.* 1985).

Results from other tree species in polluted areas, such as Scots pine (MEJNARTOWICZ 1983, GEBUREK *et al.* 1987) and beech (MÜLLER-STARCK 1985), also support this hypothesis in that the tolerant subsets of the respective investigation ge-

nerally revealed a higher genetic variation (diversity and/or heterozygosity). On the other hand, no relationship between aluminium sensitivity and genetic diversity was obtained in studies where the Al-sensitivity of Norway spruce was tested under controlled hydroculture conditions (GEBUREK *et al.* 1986).

Finally these results, although limited to one montane region, demonstrate that genetic changes shall occur in Norway spruce if the sensitive trees (e.g. subsets S) dy prior to reproduction or if the reproduction rate of sensitive trees is decreasing (SCHOLZ 1986). Even though the tolerant trees exhibit a generally higher genetic diversity, particular alleles at some loci (e.g. G-6-PDH-A_1, MDH-C_3) and many rare alleles will decrease in frequency and may ultimately be lost. This is true even if the genetic causes for tolerance/sensitivity are associated with other gene loci closely linked to the enzyme loci analysed in this study (hitch-hiking effect).

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Clonal Mixtures, Juvenile-Mature Correlations and Necessary number of Clones*)

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Summary

In all fields of forest tree breeding and, therefore, in clonal forestry too, an utilization of juvenile-mature correlations with regard to an improvement of early testing must be of special interest. Both ages ('juvenile' and 'mature') are related with eachother. This relation has been described quantitatively by r_E (= juvenile-mature correlation based upon the means of the single clones) and r_M (= juvenile-mature correlation based upon the means of mixtures of different clones). If we have $r_M > r_E$ an improvement of the efficiency of early testing may be realized by using mixtures instead of single clones.

In this paper an explicit expression for r_M has been derived, which depends on 7 parameters: $r_M = r_M$ (n, b, b*, t, h^2, $(h^*)^2$, r_E) with n = number of clones in the clonal mixture, h^2 and $(h^*)^2$ = heritability at juvenile and mature age respectively, b and b* = exponents from FAIRFIELD-SMITH's empirical law for variances at juvenile and mature ages respectively, t = exponent from FAIRFIELD-SMITH's empirical law for the covariance between juvenile and mature ages. Numerical results obtained by using this r_M-function are given and discussed.

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