werden, so ergibt sich hieraus die Verpflichtung zu einem Handeln, welches das gesteckte Ziel der Erhaltung der Anpassungsfähigkeit auch tatsächlich erreichbar macht.

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Genetic Differences between „Tolerant" and „Sensitive" Beeches (Fagus sylvatica L.) in an Environmentally Stressed Adult Forest Stand

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Summary

In a severely damaged natural forest stand in the higher-elevation Bavarian Forest, adult beech trees were selected with either no apparent damage symptoms ("tolerant") or irreversible injury ("sensitive"), each group comprising 44 trees. The genotyping of these trees at 14 polymorphic enzyme gene loci reveals the following:

Significant deviations between the genetic structures of both groups are obtained with respect to single loci. The "tolerant" group contains one-third more different alleles

and genotypes. The "tolerant" individuals have a 15% higher degree of heterozygosity than the "sensitives" (0.314 vs. 0.274). The multilocus genic diversity in the "tolerant" group exceeds that in the "sensitive" group by 138%.

Classical genic viability selection in favour of single loci is not indicated, but rather a complex reaction with respect to the majority of the studied gene loci. This is interpreted as being a response to the complexity of the actual stress situation. The obtained results allow the conclusion that under the given environmental conditions, the adaptability and thus the survival ability of a population is favoured by a high genetic diversity on the population level and presumably also by a high degree of heterozygosity on the individual level.

Key words: Air pollution, viability, heterozygosity, genetic diversity, adaptation, forest stand, *Fagus sylvatica* L.

Zusammenfassung

In einem stark umweltbelasteten Waldbestand der Hochlagen des Bayerischen Waldes wurden Buchen ausgewählt, die entweder keine erkennbaren Schadsymptome zeigten ("tolerant") oder irreversible geschädigt waren ("sensitiv"). Jede dieser beiden Gruppen umfaßt 44 Bäume. Die Bestimmung der Genotypen dieser Bäume an 14 polymorphen Genloci erbrachte folgendes: Zwischen den genetischen Strukturen beider Gruppen bestehen an einzelnen Genloci signifikante Unterschiede. Die "tolerante" Gruppe enthält ein Drittel mehr Allele und Genotypen. Die "toleranten" Individuen haben einen 15% höheren Heterozygotiegrad als die "sensitiven". Die genische Multilocus-Diversität in der "toleranten" Gruppe übersteigt die der "sensitiven" Gruppe um 138%.

Statt klassisch genischer Viabilitätsselektion an einzelnen Genloci zeigt sich eine komplexe Reaktion unter Beteiligung der meisten der untersuchten Genorte. Dies wird als Reaktion auf die Komplexität der gegebenen Streßsituation interpretiert. Die Ergebnisse legen die Schlußfolgerung nahe, daß die Anpassungs- und damit die Überlebensfähigkeit unter den gegebenen Umweltbedingungen durch eine große genetische Diversität auf der Ebene der Population und voraussichtlich auch durch einen hohen Heterozygotiegrad auf der Ebene des Individuums begünstigt wird.

Introduction

Effects due to air pollution have become a dominant factor in the environmental stress on forest ecosystems in Central and Eastern Europe. Recent inventories in the Federal Republic of Germany clearly indicate that approximately one-half of the total forest area is affected to varying extents by foliar and/or root injury due to air pollution. Damage is especially severe in the mountainous regions, which mostly are less exposed to local emissions of toxic agents but suffer from long distance transport of air pollutants. The most severe damage caused by this new type of stress factor is evident primarily in coniferous species, such as *Picea abies*, but also increasingly in the deciduous European beech (*Fagus sylvatica* L.), especially in the Bavarian Forest region.

In *Fagus sylvatica* as well as in many other species, the phenotypic response of individual trees to a given stress situation varies substantially: In both natural environments and in stress experiments under controlled conditions, certain individuals can be observed which still appear fully viable whereas at the same time others are irreversibly damaged and will die. This phenomenon may be explained for the present as a consequence of genotypic variation among the respective individuals. Due to a lack of related studies on Fagus species, this assumption could not have been proven earlier. However, the results of various studies on other tree species clearly indicate a genotype-dependent variation in the reaction of trees to air pollution and single stress components, respectively (e.g. Dochinger and Seliskar 1965, Rohmeder und v. Schönborn 1965, Houston and Stairs 1973, Scholz and Knabe 1976, Karnoski 1977, Karnoski and Houston 1979, Scholz *et al.* 1979, Kriebel and Leben 1981, Tzschacksch 1981). Biochemical studies on the reaction of forest trees to stress by air pollutants were recently surveyed by Mejnartowicz (1984). Applying enzyme gene markers, an indication of selection due to air pollution was found by Mejnartowicz (1983) in Scots pine stand and in fumigation experiments with sulfur dioxide by Scholz and Bergmann (1984) in Norway spruce clones.

The present study is part of a concept which includes the genotyping of adult trees under long-term environmental stress primarily due to air pollution and of stressed seedling populations from defined genetic material. The purpose of the first category of experiments is to contrast groups of apparently non-affected trees with groups of heavily affected trees in the same stand, while the second category should contrast the initial population with the survivors in field experiments and under controlled stress conditions. This paper deals with the first category by attempting to characterize genetic differences between "tolerant" and "sensitive" trees of *Fagus sylvatica* in an adult forest stand in the Bavarian Forest region.

Material and Methods

Studied population and site

The studied forest stand originates from natural regeneration and consists of the species *Picea abies*, *Fagus sylvatica* and *Abies alba* in the percentages 53, 30 and 17%, respectively, over the full area of 25 hectares. In the experimental area of approx. 3.5 hectares, the proportion of *Fagus sylvatica* amounts to over 60%. The ages of the adult trees range between 125 and approx. 160 years and of the natural regeneration between 1 and approx. 20 years. The stand is situated in the Bavaria Forest National Park, district 21, compartment 2 at an elevation of 810—830 m above sea level. The soils originate from the glacial epoch with mesotrophic or better nutrition level and have a sufficient water supply (precipitation measures approx. 1000 mm per year).

Symptoms and causes of damage

A rapid increase in damage has been observed in beech stands since the mid 1970's. The predominant symtom in the adult trees is a changed branching habitus accompanied by a thinning in the crowns and subsequent dying of the upper crown sections, which usually results in the death of the whole tree within several years. The causes of damage must be expected to be very complex. There is no single prevailing stress factor, as is the case with the sulfur oxides in the north-eastern parts of Bavaria and adjacent parts of Czechoslovakia. It can be expected that the observed symptoms originate mainly from acidic fogs, although chlorophyll injury by photooxidation as well as effects due to ozone and to frost shocks may be involved; acidic stress from the soils is reported to act only as a marginal effect (Rehfuess, Lehrstuhl für Bodenkunde, Universität München, pers. comm.). Particularly on the experimental area, water stress cannot be assumed. The results of inventories by the Lehrstuhl für Forstbotanik, Universität

München, clearly indicate that damage by insects, fungi or other biotic effects is not a primary factor (SCHÜTT and SUMMERER, pers. comm.).

Selection of experimental trees

Within an area of 5 hectares, two groups of beech trees were selected which represent the extremes in the observable reactions of individual trees to the given experimental stress situation: Trees which appeared to be entirely unaffected before and during flushing in 1984 were designated as "tolerant"; trees with dying or dead crowns as "sensitive". About 35% of the standing beech trees belonged to one of these two categories, 60% carried intermediate characters and 5% were already dead. In many cases, pairs of neighbouring "tolerant" and "sensitive" trees were selected. The age and sociological class distributions of the two groups can be expected to be similar. The oldest trees are not included in either group. Special care was taken to choose trees in both groups which apparently were not handicapped by intra- or interspecific competition. The sample size for each group is 44 trees.

Genotyping

The multilocus genotype of each individual tree was determined simultaneously at 14 enzyme gene loci by applying the enzyme systems of acid phosphatase (ACP, EC 3.1.3.2.), glutamate oxalacetate transaminase (GOT, EC 2.6.1.1), isocitrate dehydrogenase (IDH, EC 1.1.1.42), leucine aminopeptidase (LAP, EC 3.4.11.1), malate dehydrogenase (MDH, EC 1.1.1.37), peroxidase (PER, EC 1.11.1.7), 6-phosphogluconate dehydrogenase (6PGDH, EC 1.1.1.44), shikimate dehydrogenase (SKDH, EC 1.1.1.25).

Buds from each tree were crushed together with water-insoluble polyvinylpyrrolidone in liquid nitrogen with an Ultra-Turrax apparatus (Jahnke und Kunkel, FRG, T 18/10, 18 N) and freeze-dried for permanent storage. This material was homogenized in a 0.08 M tris — 1.00 M HCl buffer pH 7.3 with the addition of 0.6 mg/ml bovine albumin and selected agents from RHODES (1977) (see MÜLLER-STARCK 1982). The enzymes were separated by means of horizontal starch zone-electrophoresis by applying the following buffer systems (gel buffer/electrode buffer): 0.05 M tris — 0.01 M citric acid pH 8.1/0.05 M LiOH-0,19 M boric acid pH 8.1 (LUNDKVIST 1979) for LAP and ACP; 0.07 M tris — 1.00 M HCl ph 8.7/0.06 M NaOH-0.30 M boric acid pH 8.2 for GOT; 0.07 M tris-0.01 M citric acid pH 8.7/0.06 M NaOH — 0.30 M boric acid pH 8.2 (POULIK 1957, modified by BERGMANN 1973) for PER; 0.038 M tris — 0.013 M citric acid pH 7.0/0.135 M tris — 0.045 M citric acid pH 7.0 (SHAW and PRASAD 1970, modified) for MDH, IDH, SKDH, 6PGDH. Gel-concentration 11—12% voltage distribution 15—30 V/cm, bridge distance 12—15 cm. Staining solutions originate with slight modifications BERGMANN 1973, 1974 and pres. comm., MÜLLER-STARCK unpublished) from BECKMANN *et al.* 1964 (LAP), HENDERSON 1965 (IDH), SCANDALIOS 1969 (ACP, MDH), BREWER 1970 (6PGDH), SHAW and PRASAD 1970 (PER), SICILIANO and SHAW 1976 (GOT), LINHART *et al.* 1981 (SKDH). To test whether or not the enzyme phenotypes in the gels in fact refer to the enzyme system under consideration, the respective enzyme substrate was omitted in one gel slice and the resulting phenotypes compared with those in the second slice. In the case of MDH, IDH and 6PGDH substrates, unspecific enzyme phenotypes are apparent in one zone in each zymogram ("nothing dehydrogenases", SHAW and KOEN 1964). For the present, this zone is excluded from further interpretation.

The genetic control of the applied enzyme systems was elucidated by studying the offspring from controlled crossings at the seed stage and, in a few cases, also at the juvenile tree stage. Since 1980, controlled self and cross pollinations were performed in the Göttingen area by using a total of 12 beech trees as female and 25 trees as male parents. The results of the genetic analyses of parent and offspring populations (viable seeds) and the description of the allelic variation at the monitored enzyme gene loci will be given separately (MÜLLER-STARCK, in preparation). From this study, 13 gene loci were employed here: ACP-A, B; GOT-A, B; IDH-A, B; LAP-A, B; MDH-B, C; PER-A; 6PGDH-A; SKDH-A. MDH-A has shown no variation to date. PER-B served as the 14th polymorphic locus but had to be studied in bud tissue since it is not active in seeds. In oder to justify utilization of the monitored gene loci also in bud tissue, the genotypes of the parental trees by identified controlled crossings were compared with the respective enzyme phenotypes in their bud tissues. From this it can be stated that the genotypes at the given 13 loci can also be determined from buds. In addition, young leaves from the offspring of five controlled cross pollinations with one female parent were studied which had been performed at HORSHOLM Arboretum, Denmark (NIELSEN and SCHAFFALITZKI DE MUCKADELL 1954). Buds from the same crossings were used by all investigations to data of the genetic control of enzyme systems in *Fagus sylvatica:* KIM (1979) for one ACP and one LAP gene locus, THIEBAUT *et al.* (1982) for one GOT locus and two PER loci. These loci correspond to ACP-A, LAP-A, GOT-A and PER-A, B in the present article.

Genetic parameters

The allelic and genotypic structures at each gene locus were determined for the "tolerant" and the "sensitive" group of trees and compared by the log likelihood ratio test (G-test) of heterogeneity in contingency tables (model II, k x 2 table, WEBER 1978, chap. 6.7.5; also ELANDT-JOHNSON 1971, chap. 13.10, for general concepts). The genetic distance (GREGORIUS 1974) between the two groups and the genetic diversity (GREGORIUS 1978) within each group were calculated for alleles and genotypes, and the degree of heterozygosity was determined. Computations were performed by means of the GSED program ("Genetic Structures from Electrophoretic Data", GILLET *et al.*, in preparation).

Results

Genetic structures

Deviations between the genotypic and/or the allelic frequencies within the "tolerant" and the "sensitive" groups are statistically significant in the case of the gene loci ACP-B, GOT-B, MDH-B and SKDH-A (see *Table 1).* The actual numbers of alleles and of genotypes differ substantially: The group of "tolerant" trees contains on the average one-third more alleles and genotypes than the "sensitive" group (a total of 44 vs. 33 alleles and of 61 vs. 46 genotypes at the 14 gene loci).

Marked deviations between the groups are indicated in the case of the SKDH-A locus (4 alleles in the "tolerant" group vs. 1 allele in the "sensitive" one) and to LAP-B and GOT-B (4 vs. 2 alleles). There is no allele which is represented in the "sensitive" group but not in the "tolerant". Only 2 genotypes fulfill this relationship, while 17 statisfy the reverse statement.

Table 1. — Comparison of the genetic structures at 14 enzyme gene loci and of the numbers of alleles and genotypes between the group of "tolerant" (TOL) and of "sensitive" (SEN) beech trees in an air-polluted adult forest stand.

Gene locus	Genetic structures G-Test of homogeneity +) Alleles	Genotypes	Number of diff. alleles TOL	SEN	Number of diff.genotypes TOL	SEN	Frequencies (in parentheses) of unique alleles and genot. Alleles present only in TOL	SEN	Genotypes present only in TOL	SEN
ACP-A	2.59	5.63	4	3	6	6	A_1(1)	-	A_1A_2(1)	A_3A_3(3)
ACP-B	7.49*	6.10	3	2	4	2	B_2(5)	-	B_2B_2(1); B_2B_3(3)	-
GOT-A	1.98	2.04	2	2	2	2	-	-	-	-
GOT-B	11.07*	12.45*	4	2	5	3	B_1(2); B_4(5)	-	B_1B_2(2); B_3B_4(5)	-
IDH-A	2.88	3.45	2	2	3	3	-	-	-	-
IDH-B	6.43	7.59	4	4	6	5	-	-	B_1B_4(1)	-
LAP-A	5.89	8.59	4	3	8	6	A_1(3)	-	A_1A_1; A_1A_3(1)	-
LAP-B	7.23	7.32	4	2	5	3	B_2(2); B_4(3)	-	B_2B_3(2); B_3B_4(3)	-
MDH-B	7.52*	4.87	3	2	3	2	B_4(4)	-	B_4B_4(2)	
MDH-C	2.36	2.44	2	2	3	3	-	-	-	-
PER-A	0.03	4.98	2	2	3	3	-	-	-	-
PER-B	3.46	11.19	4	4	7	5	-	-	B_2B_2(1); B_2B_4, B_4B_4(2)	B_1B_4(1)
6PGDH-A	0.00	0.00	2	2	2	2	-	-	-	-
SKDH -A	9.99*	10.31*	4	1	4	1	A_2; A_4(1); A_5(5)	-	A_2A_3; A_3A_4(1); A_3A_5 (5)	-

The obtained values may be affected by the fact that in the available sample of 44 trees per group, many alleles are represented only in small frequencies. As can be seen in *Table 1,* the largest frequency of an allele present only in the "tolerant" group is 5 out of 88 (= 5.7%) and of a genotype with this property 5 out of 44 (= 11.4%). A comparison of the actual number of genotypes with the number possible for the given alleles (n = (n + 1)/2 with n = number of alleles) results in a quite high representation in both samples: 76.7% of the theoretically possible number is realized in the "sensitive" group and 62.9% in the "tolerant" one.

The 11 different unique alleles in the „tolerant" group appear primarily in heterozygotes: Among the respective 13 different genotypes in *Table 1* only 3 are homozygotes (ACP-B_2B_2; LAP-A_1A_1; MDH-B_4B_4). However, comparing the obtained genotypic frequencies with the corresponding Hardy-Weinberg proportions, the resulting deviations cannot be interpreted to support the assumption of a heterozygote excess with respect to the unique alleles.

Viewing these results in their entirety, this ought to be interpreted as a clear indication of a tendency towards greater genetic variation within the "tolerant" group of trees as compared to the "sensitive" trees.

Genetic distance

The calculated distance measures the proportion of alleles (allelic distance) or genotypes (genotypic distance) by which two populations differ on a continuous scale of values between zero and 1. The genetic distances result in zero in the case of the genetic identity and in the value 1 if the two populations do not have any alleles or genotypes in common.

The obtained allelic distances (see *Table 2)* vary between zero and 0.13; the genotypic distances vary between zero and 0.20. Maximum distance values need not necessarily correspond to large G-values from the test of homogeneity in *Table 1,* because this test statistic is not a distance measure and is affected by the manner of occupany of single frequency classes. Comparatively large values for both the allelic and genotypic distances are indicated for the gene loci GOT-B, IDH-B, LAP-A and to a lesser degree, for IDH-A, MDH-C, PER-B, SKDH-A. Very small distances are evident for GOT-A, and genetic identity between the two groups is indicated in the case of the 6PGDH locus. In total the apparent genetic distances do not to reveal substantial differences between the groups.

Heterozygosity

The proportion of heterozygous genotypes at each of the 14 gene loci for both groups of trees is surveyed in *Table 2.* Within the "tolerant" trees, the single locus values vary between 0.09 and 0.68, within the "sensitives" between zero and 0.48, The GOT-B locus has the largest proportions of heterozygotes in both groups. The opposite holds for GOT-A and MDH-B within the "tolerant" trees and for GOT-A and SKDH-A within the "sensitives". The deviations between the proportions of heterozygotes in the "tolerant" and the "sensitive" group are statistically significant only in the cases where the heterozygosity is greater in the "tolerant" group (PER-A and SKDH-A; 2 x 2 contingency table, $0.05 > P \geqslant 0.001$).

The average degree of heterozygosity based on the 14 gene loci is 0.314 for the "tolerant" trees and 0.274 for the "sensitives". Recall that this degree is identical to the arithmetic mean taken over the proportions of heterozygotes found in each of the loci (Gregorius 1977, 1978). The obtained differences between the degrees of heterozygosity of the two groups is 0.040, which means a surplus in favour of the "tolerant" trees of 15%. This surplus confirms the tendency observed for the single locus comparison. However, a possibly more appropriate method of comparing multilocus-heterozygosities between the two groups consists in determining the number of loci for which the "tolerants" show higher heterozygosities than the "sensitives' and vice versa. It turns out that for the 14 loci studied, a surplus of heterozygotes in the "tolerants" is obtained for 8 loci, whereas the opposite holds for 3 loci. This is further support for the previous findings. Yet all these measurements are subject to the criticism that they do not distinguish beween "pure" heterozygosity and heterozygosity introduced merely by effects of gene frequencies. This can be avoid by applying a standardization of heterozygosity by forming a ratio with the maximum heterozygosity, which can be realized for the given gene frequencies (Gregorius 1978). This measure results in a surplus of heterozygotes in the "tolerants" for 7 loci, whereas the opposite holds for 5 loci. The general tendency apparent in the

empirical data is confirmed, however to a lesser degree. This can be attributed to the sample sizes which are probably to small for the last mentioned analysis. Anyway, the normalized heterozygosity allow for an independent study of heterozygosity and genetic diversity.

Genetic diversity

In order to quantify the genetic heterogeneity within the "tolerant" and the "sensiive" groups of trees, the genetic diversities were calculated with respect to the allelic and to the genotypic frequencies (allelic and genotypic diversities, see *Table 2).* Diversities equal to zero are obtained in the cases of fixation to one allele or the presence of only one genotype. Values greater than zero are proportional to the respective allelic or genotypic variation. For example, a diversity value of n indicates that the actual population is equivalent to an ideal population with n + 1 uniformly distributed alleles or genotypes, respectively. Obviously, the genotypic diversities can not be smaller than the allelic ones.

In the "tolerant" group the allelic diversities range between 0.09 and 1.63 and the genotypic diversities between 0.20 and 3.02. The corresponding values in the "sensitive" group vary between zero and 1.81 or 4.29, respectively. The LAP-A locus shows remarkably high diversities in both groups, while GOT-A and SKDH-A along with ACP-B, MDH-B and 6PGDH-A reflect the opposite tendency, Fixation to one allele and one genotype is evident for SKHD-A in the "sensitive" group. The single locus comparison between the "tolerant" and the "sensitive" groups favours the first group but does not seem to reveal unequivocal results: The majority of the studied gene loci indicate greater genetic diversities in the "tolerant" group, but the deviations within these loci appear to be small, with only a few exceptions such as IDH-B. Average diversities per gene locus cannot function as a criterion for discrimination because an averaging is not suitable in the case of widely differing frequency distributions.

To allow for more clear interpretations, the 14 allelic diversities were used to calculate the respective multilocus diversities (Gregorius 1978). The obtained values are 553.07 for the "tolerant" and 232.73 for the "sensitive" group. Each value is equal to the number of genetically different gametic types which can be produced by the respective group in the case of the studied 14 loci. Thus a substantial superiority in the genetic diversity of the "tolerant" group as compared to the "sensitive" one is revealed by using the multilocus information potential. The resulting surplus in favour of the "tolerant" group amounts to 138%.

Discussion

Effects of air pollution are complex and are only one part of a manifold system of environmental stress. To study long-term effects on the genetic structures of a forest tree population in vivo, an experimental situation was chosen with especially severe symptoms caused by such environmental stress, the prevailing component of which is air pollution: Other stress factors such as biotic effects, water stress or lacking nutrient media should act only as marginal events. Nevertheless, the environmental complexity to which this type of field experiment is subject cannot be expected to favour the determination of distinct selective effects in he classical allelic sense as could be he case with the exposure of test populations to controlled single stress factors.

An essential requirement for the monotoring of genetic selection is fulfilled: The applied enzyme markers have so far been proven by genetic analysis of full sib offspring to be bunder genetic control and thus environmentally independent. A modification of enzyme phenotypes due to air pollutants, as for instance with respect to glutamate dehydrogenase in the case of pea seedlings after sulfur dioxide fumigation (Pahlich 1972), could not explicitly be tested but is highly improbable: All observed enzyme phenotypes in the "sensitive" trees were known from previous genetic analysis. The chance that pollution acts so specifically that the charge of enzyme subunits is altered exactly from the expression of one allele to that of another is extremely small. Furthermore, the greater enzymatic variation was obtained in the "tolerant" and not in the "sensitive" group.

The observed genetic structures of the "tolerant" and the "sensitive" groups are distinguishable by quantitative methods. The number of different alleles and genotypes is suprisingly high among the "tolerants" as compared to the "sensitives". The genetic distances show some diffe-

Table 2. — Genetic distances, frequency of heterozygous genotypes and genetic diversities at 14 enzyme gene loci for the group of "tolerant" (TOL) and of "sensitive" (SEN) beech trees in an air-polluted adult forest stand.

Gene locus	Genetic distances between TOL and SEN		Heterozygosity +)		Genetic diversities Allelic ++)		Genotypic	
	Allelic	Genotypic	TOL	SEN	TOL	SEN	TOL	SEN
ACP-A	0.07	0.07	0.39	0.36	0.72	0.89	1.37	1.67
ACP-B	0.06	0.09	0.14	0.11	0.20	0.12	0.39	0.25
GOT-A	0.03	0.07	0.09	0.02	0.09	0.02	0.20	0.05
GOT-B	0.13	0.20	0.68	0.48	1.22	0.74	1.81	1.28
IDH-A	0.11	0.11	0.34	0.34	0.79	0.51	1.55	1.02
IDH-B	0.10	0.20	0.39	0.21	0.71	0.35	1.70	0.71
LAP-A	0.11	0.20	0.34	0.46	1.63	1.81	3.02	4.29
LAP-B	0.06	0.11	0.41	0.36	0.59	0.48	1.40	0.96
MDH-B	0.06	0.11	0.09	0.21	0.20	0.23	0.32	0.48
MDH-C	0.10	0.16	0.34	0.46	0.51	0.77	1.02	1.37
PER-A	0.01	0.20	0.39	0.18	0.74	0.71	1.43	1.22
PER-B	0.09	0.18	0.39	0.39	0.82	0.54	1.82	1.37
6PGDH-A	0.00	0.00	0.25	0.25	0.28	0.28	0.60	0.60
SKDH -A	0.08	0.16	0.16	0.00	0.18	0.00	0.39	0.00

+) Degree of heterozygosity: 0.314 for TOL, 0.274 for SEN

++) Multilocus diversity: 553 for TOL, 233 for SEN

rences, but none of the single locus values is so large as to support the hypothesis of the involvement of classical form of allele-specific viability selection.

High degrees of heterozygosity were observed in the studied trees. One monomorphic zone in the MDH system (MDH-A) is not included in the given values, but even if it is, the degrees of heterozygosity remains high. This fact may be interpreted to be a response to the general environmental stress to which long lived and non migrating organisms such as forest trees are generally exposed. The "tolerant" group shows larger values than the "sensitive" group: The difference amounts to two-thirds of the estimated total degree of heterozygosity in other plant or vertebrate species (0.056 and 0.060 respectively, see e. g. AYALA and KIGER 1980) but is to small to allow general conclusions. For the present, the actual surplus in favour of the "tolerant" trees may be interpreted to support the hypothesis that increasing heterozygosity is one of the factors in ensuring a greater adaptability of these trees, which has enabled this subpopulation to survive the existing environmental stress until now.

The most marked differences between the "tolerant" and the "sensitive" group of trees appear in the multilocus genic (allelic) diversities. It turned out that the deviations at the single loci level accumulated in such a way that an excess of diversity occurred in favour of the "tolerant" group. To interprete such differences, it is useful to recall that reduced genetic diversities means reduced frequencies of those alleles which were already rare. This provides evidence for the hypothesis that at least the possession of some rare alleles at the set of loci studied may increase the chances for survival. Consequently, it appears that the management of forest tree populations should not reduce the genetic diversity at certain gene loci, because this could imply the risk of endangering survival under the given environmental stress. It shall be mentioned that it cannot be ruled out that one of the reasons that large areas of forest suffer especially severe damage due to environmental stress is a defiency of genetic diversity in the respective populations.

Viewing all obtained results, it is evident, that the observed differences between the groups are not restricted to single loci but rather affect all loci except GOT-A and 6PGDH-A to some extent, may be interpreted as follows: The complexity of stress by air pollution and other environmental factors results here in a correspondingly complex response of the affected genotypes. Thus the response to selective effects originating from single stress factors, i.e. specific environmental changes, the effects of which can be investigated under artificially controlled in vitro conditions, are complemented, compensated or modified in a complex system of interactions. For the given in vivo experiment conditions, it can be concluded that an increase in the adaptability and thus the survival abilities is favoured by a high genetic diversity on the population level and presumably also by a high degree of heterozygosity on the individual level.

If these results are representative, any strategy which attempts to counter threats of air pollution damage by means of mass propagation of few genotypes instead of favouring genetically diverse populations should remain ineffective. Beyond this, it is self-evident that efforts to stabilize adaptive abilities should augment but never replace efforts to reduce the environmental stress on forest ecosystems, especially the emission of air pollutants.

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Luftverunreinigung durch Industrieabgase. Ein Beitrag zur Züchtung einer relativ rauchresistenten Fichtensorte. Forstwiss. Centralblatt **84**, 1—13 (1965). — Scandolious, J. G.: Genetic control of multiple molecular forms of enzymes in plants: A review. Biochem. Gen. **3**, 37—79 (1969). — Scholz, F. and Knabe, W.: Investigations on buffering capacity in spruce clones of different resistance to air pollution. XVI IUFRO World Congress, Oslo, Norway, S 209 04, 1—6 (1976). — Scholz, F., Timman, T. and Krusche, D.: Untersuchungen zur Variation der Resistenz gegen HF-Begasung bei *Picea abies*-Familien. In: Bericht der X Fachtagung der IUFRO-Fachgruppe S 2 09 — Luftverunreinigung. Ljubljana 1978. Mitteilungen des Institutes für Forst- und Holzwirtschaft, Ljubljana, 244—258 (1979). — Scholz, F. and Bergmann, F.: Selection pressure by air pollution as studied by isozyme-gene-systems in Norway spruce exposed to sulphur-dioxide. Silvae Genetica **33**, 238—241 (1984). — Shaw, C. R. and Prasad, R.: Starch gel electrophoresis of enzymes — a compilation of recipes. Biochem. Gen. **4**, 297—320 (1970). — Shaw, C. R. and Koen, A. L.: On the identity of "nothing dehydrogenase". Journ. Histochem. and Cytochem. **13**, 431—433 (1964). — Siciliano, M. J. and Shaw, C. R.: Separation and visualization of enzymes on gels. In: Smith i (ed.) Chromatographic and electrophoretic techniques. Vol. 2, Heinemann, London, 185—208 (1976). — Thiebaut, B., Lumaret, R. and Vernet, P.: The bud enzymes of beech (*Fagus sylvatica* L.) Genetic distinction and analysis of polymorphism in several French populations. Silvae Genetica **31**, 51—60 (1982). — Tzschacksch, O.: Stand der Perspektiven der forstlichen Rauchresistenzzüchtung in der DDR. Beiträge f. d. Forstwirtschaft **15**, 134—137 (1981). — Weber, E.: Mathematische Grundlagen der Genetik. VEB Gustav Fischer, Jena, GDR (1978).

Buchbesprechungen

Handbuch der Nadelgehölze. Von Dr. h. c. Gerd Krüssmann. 2., neubearbeitete Auflage unter Mitwirkung von Hans-Dieter Warda. 1983. 396 S. mit 785 teils ganzseitigen Abb., davon 457 auf 128 Schwarzweißtafeln und 97 auf 32 Farbtafelseiten. Verlag Paul Parey, Berlin und Hamburg. Ganzleinen DM 290,—. (ISBN 3-489-62622-2).

Das „Handbuch der Nadelgehölze" wurde nach seinem Erscheinen im Jahre 1972 schnell zum Standardwerk. Jetzt liegt die 2. Auflage vor, deren Bearbeitung G. Krüssmann selbst leider nicht mehr zu Ende führen konnte. Nach seinem Tod im Juni 1980 hat die Fertigstellung H.-D. Warda, Technischer Leiter des Botanischen Gartens Hamburg, übernommen. Die Gesamtkonzeption des Werkes blieb erhalten. Neu aufgenommen wurden über 300 Arten und Sorten, so daß das Handbuch jetzt 607 botanische Arten und 2075 Formen und Cultivare enthält. Das sind nahezu alle in der Welt existierenden Arten und kultivierten Gartenformen. Außer den eigentlichen *Coniferae* werden Ginkgo und von den *Gnetales* die Familie der *Ephedraceae* ausführlich behandelt. Neu sind die Winterhärtezonen-Karten für Gehölze in Mitteleuropa, die von W. Heinze und D. Schreiber auf der Grundlage der USDA Hardiness Zone Map entwickelt wurden. Bei der Beschreibung der Arten wird die Winterhärte entsprechend dieser Zoneneinteilung durch Symbole gekennzeichnet. Einer systematischen Übersicht über die rezenten Gymnospermen sowie einer kurzen Charakterisierung der behandelten Familien und Gattungen folgt im Hauptteil des Buches die alphabetische Aufzählung der Gattungen, Arten und Cultivare. Die Beschreibungen beschränken sich auf wesentliche Merkmale und Eigenschaften, geben Hinweise auf Abbildungen in anderen Werken, nennen die Heimat und schließen häufig mit Anmerkungen über Standortansprüche und Verwendungsmöglichkeit der Baumart oder Sorte. Hervorzuheben ist die ausgezeichnete Illustration des Buches. Sehr viele Arten und Sorten kann man aufgrund der Zeichnungen im Text oder der fotografischen Abbildungen auf Tafeln leichter identifizieren. Gegenüber der 1. Auflage wurden einige Fotos zusätzlich eingefügt oder ausgetauscht und vor allem die Zahl der Farbaufnahmen beträchtlich erhöht. Das Werk schließt mit einer Erklärung botanischer Ausdrücke, einem kurzen Bestimmungsschlüssel für Nadelgehölzgattungen (von F. H. Meyer), sowie Verzeichnissen ungültiger Pflanzennamen, deutscher Pflanzennamen und wichtiger Sammlungen. — Insgesamt ist ein umfassendes Handbuch der Nadelgehölze entstanden, das die reichen Kenntnisse des Autors widerspiegelt und zusammen mit dem dreibändigen „ Handbuch der Laubgehölze" unentbehrlich ist für alle, die beruflich oder aus Liebhaberei mit Gehölzen zu tun haben.

B. R. Stephan

Handbuch für Pilzfreunde. In 6 Bänden. Begründet von E. Michael, neubearbeitet von B. Hennig, weitergeführt und herausgegeben von H. Kreisel, Greifswald. Band 4: Blätterpilze - Dunkelblättler. Herausgegeben und bearbeitet von H. Kreisel. Mit Beiträgen von H. Dörfelt und G. Ritter. 3., bearb. Aufl. 1985. G. Fischer Verlag, Stuttgart. 488 S., mit farb. Abb. von über 300 Pilzarten auf 146 Taf., sowie 28 einfarb. Abb. Gzl. DM 58,—. ISBN 3-437-30463-1 (Lizenzausgabe).

Von diesem bekannten sechsbändigen Pilzhandbuch liegt jetzt der 4. Band in einer Neuauflage vor. Im Hauptteil des Buches werden auf 146 Farbtafeln über 300 dunkelsporige Blätterpilze *(Basidiomycetes)* dargestellt. Gegenüber der vorigen Auflage wurden die ausführlichen Artbeschreibungen überarbeitet, einige Farbabbildungen umgestaltet und die Nomenklatur auf einen gegenwärtig gültigen Stand gebracht. — Im allgemeinen Teil finden sich auf etwa 100 Seiten Beiträge zur Ökologie der Großpilze, zur geographischen Verbreitung und zur Pilzsoziologie. Sie enthalten viele wichtige, auch forstlich interessante Angaben über holzbewohnende Saprophyten, über Parasiten sowie zur Morphologie, Physiologie und zur floristisch-ökologischen Bedeutung der Mykorrhiza. Diese Abschnitte fassen das Wichtigste zusammen und sind daher zur schnellen Orientierung gut geeignet. Hervorzuheben ist hier insbesondere der gute Überblick über die Pilzgesellschaften und ihre Beziehungen zu Waldgesellschaften. — Im systematischen Teil (etwa 60 S.) werden Bestimmungsübersichten über die artenreichsten Gattungen und Familien der dunkelsporigen Basidiomyceten gegeben. — Auch der vorliegende Band des umfassenden Bestimmungs- und Nachschlagewerkes für die mitteleuropäische Pilzflora kann nachdrücklich allen an den Großpilzen Interessierten empfohlen werden.

B. R. Stephan

Biologie in Zahlen. Eine Datensammlung in Tabellen mit über 9000 Einzelwerten. Von Prof. Dr. Rainer Flindt, Ludwigsburg. Gustav Fischer Verlag, Stuttgart, New York. 1985. XIV + 280 S.Kart. DM 39,—. (ISBN 3-437-30466-6).

Oft sucht man Antworten zu folgenden Fragen: Zahl der Pflanzen- und Tierarten, höchster oder ältester Baum, Geschwindigkeit bestimmter Tierarten, Zahl der Blätter einer Buche und ihre Leistung, oder ähnliche Themen. Oft ist eine befriedigende Antwort erst nach langem Suchen zu finden, und oft sind entsprechende Fachbücher oder Nachschlagewerke gerade nicht zur Hand. Hier füllt die vorliegende Datensammlung eine Lücke. In über 300 zum Teil umfangreichen Tabellen sind mehr als 9000 Einzelangaben aus den Gebieten Zoologie, Botanik, Mikrobiologie und Humanbiologie zusammengestellt. Neben mehr allgemeinen Angaben lassen sich auch spezielle Daten aus dem zellulären, physiologischen, entwicklungsbiologischen oder genetischen Bereich finden. Bei den Tieren und Pflanzen liegt das Schwergewicht auf den in Mitteleuropa beheimateten Arten. Forstpflanzenrelevante Daten werden in zahlreichen Tabellen aufgeführt zu Stichworten wie Umtriebszeit, Höhe, maximale Durchmesser, Alter, Holzmerkmale, Chromosomenzahlen u. a. Natürlich müssen bei der Aufzählung von Einzelwerten Hinweise auf die Variationsbreite unberücksichtigt bleiben, so daß manches sehr allgemein bleibt. Dennoch bietet das Buch eine Fülle interessanter und wichtiger Informationen; beim Nachschlagen liest man sich schnell fest. Dem biologisch Interessierten erleichtert dieses nützliche Nachschlagewerk auf jeden Fall die oft umständliche Suche und bietet ihm eine gute Möglichkeit, wichtige Sachverhalte und Beziehungen vergleichend kennenzulernen.

B. R. Stephan

Conifers: morphology and variability. By M. Vidaković, Yugoslav Academy of Science and Arts, and Liber University Publisher. Publ. Zagreb, 1982. 710 p. (in Croatian)

Prof. Vidaković has taught dendrology and forest genetics at the Faculty of Forestry, University of Zagreb for more than 25 years. He is well known to the world community for his outstanding achievements in the sciences of tree morphology and genetics. This rare, but very desired combination of the author's expertise has