Genetic Studies on Leaf Retention in *Quercus robur*

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Abstract

Whereas the autumn abscission of withered leaves in deciduous trees has been the subject of several previous studies, it remains an open question whether it is caused mainly by environmental of by genetic factors. Based on isoenzyme analysis the level of genetic variation and genetic (genotypic as well as allelic) structure in 1 leaf-retaining and 1 leaf-abscising oak stand have been estimated. Both subpopulations were compared on this basis and significant differences have been found for the gene loci under study. Thus, the present study provides some evidence for a genetic basis of the phenomenon of leaf retention.

Key words: Quercus, leaf retention, genetics, isoenzymes, differentiation.

FDC: 165.5; 161.4; 176.1 *Quercus robur.*

Résumé

La chute des feuilles des arbres en automne est un phénomène qui a déjà dans le passé fait l'objet de nombreuses études. Cependant, actuellement on ignore toujours si ce phénomène est causé par des facteurs génétiques ou par des facteurs environmentaux. Par des analyses d'isoenzymes, nous avons pu éstimé le faux de variation génétique et la structure génétique (génotypique aussi bien qu'allélique) à la fois dans une feuille caduque et dans une feuille retenue de chêne. La comparison des deux souspopulations par cette méthode a permis de mettre en evidence des différences significatives pour les locus du gène examiné. Cette étude soumét donc des éléments en faveur d'une cause génétique du phénomène de la retenue des feuilles.

Mots-clés: Quercus, retenue des feuilles, génétique, isoenzymes, différentiation.

Introduction

In the last several decades, the autumn shedding of withered leaves in deciduous trees has been the subject of several morphological and physiological studies (e.g. CHANDLER, 1925; ADDICOTT and STOCKING LYNCH, 1955; ADDICOTT, 1982; KOZLOWSKI, 1973). The retention of leaves observable in different genera, such as beech (*Fagus*) or oak (*Quercus*) has been interpreted to be a "juvenile trait" (SCHAFFALITZKY DE MUCKADELL, 1956). One physiological correlate of leaf retention was assumed to be a lower absisic acid content of the leaves and, as a consequence, differences in the regulation of leaf water status (RINNE *et al*., 1992). However, whereas a number of previous studies imply that leaf abscission is triggered mostly by environmental conditions, studies of ADICOTT (1982) provide evidence that the phenomenon of leaf retention does not strictly depend on age nor on site factors or weather conditions. These observations led us to the hypothesis of a genetic disposition for the phenomenon of leaf retention. To contribute to this question, the objectives of the present study are to record the genetic structures and to estimate the level of genetic variation in one leaf-retaining and one leaf-abscising oak stand under the same site conditions. Both stands are compared with respect to the hypothesis of genetic differences. Moreover, the present study is the first to focus on adult oak stands and thus it supplements the genetic inventory of European oak populations initiated by MÜLLER-STARCK and ZIEHE (1991), KREMER *et al*. (1991), HERZOG (1993), HERZOG and MÜLLER-STARCK (1993), as well as MÜLLER-STARCK *et al.* (1993).

Material und Methods

Two neighbouring stands of pedunculate oak (*Quercus robur* LINNÉ) were studied. They are situated in compartments (85 A and D) of Forstbetriebsbezirk Röttgen, Staatliches Forstamt Kottenforst, Wuchsgebiet Niederrheinische Bucht, Wuchsbezirk Ville, State of Nordrhein-Westfalen, Germany. The climatic, edaphic and light conditions are the same for both stands. One stand (compartment 85 A) originated from the planting of trees ca. 1.5 m in height in a 5 m by 5 m pattern at the beginning of this century. The other stand (compartment 85 D) was sown at the same time, using ca. 150,000 acorns per ha. The seed sources are unknown and may be different for the 2 stands. Abscission was recorded in autumn 1991 and 1992. For both years, nearly all trees (more than 90%) of the 85 A stand showed normal shedding of senescent leaves from the respective year, whereas more than 80% of the trees of the other stand exhibited the phenomenon of leaf retention until the end of the following vegetation period.

One shoot per tree of the current year's growth was collected in January, 1992, by the crossbow method of WALDSCHMIDT (1992). A total of 191 twigs was sampled, 116 from the leaf-retaining and 75 from the shedding stand. They were stored during transport at temperatures between 4 °C and 10 °C for a maximum of 48 hours. Thereafter, the buds were removed and frozen in liquid nitrogen before storage at −80 °C.

Isoenzyme analysis followed HERZOG (1993). The buds were thawed and homogenized in a 0.08/0.02 mol/l TRIS/HCl buffer at pH 7.3. To inhibit phenols and tannins, 2% to 5% [w/v] polyvinylpyrrolidone, 10 mmol/l to 130 mmol/l mercaptoethanol, 3 mmol/l ethylenediaminetetraacetic acid (EDTA) as well as 3 mmol/l to 6 mmol/l dithiothreitol were added. The resulting slurry was absorbed onto filter paper wicks and loaded onto gel slabs. Horizontal starch gel electrophoresis was performed using a starch concentration of 11.5% [w/v]. The bridge distance was 12 cm with a voltage distribution of 20 V/cm to 30 V/cm.

Six isoenzyme systems (*Table 1*), representing 7 polymorphic gene loci, were identified as genetic markers by genetic analysis of complete families (MÜLLER-STARCK and HATTEMER, 1990; MÜLLER-STARCK *et al.,* in press; ZANETTO *et al.,* in press). They were studied using different electrode and gel buffer systems (*Table 1*) as described by HERZOG (1993). Solutions used for enzyme staining were modified following CHELIAK and PITEL (1984).

Results and Discussion

Genotypic structures of both stands are shown in *tables 2* and *3*. Allelic structures can be easily calculated from these

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Table 1. – Enzyme systems and buffers used in the present study.

Enzyme system and E.C. code	Electrode buffer and Gel buffer
Shikimate dehydrogenase E.C. 1.1.1.25	0.14/0.05 mol/l TRIS/citric acid, pH 6.5 0.04/0.014 mol/l TRIS/citric acid, pH 6.6
Isocitrate dehydrogenase E.C. 1.1.1.42	0.14/0.04 mol/l TRIS/citric acid, pH 7.8 0.04/0.011 mol/l TRIS/citric acid, pH 7.8
6-phosphogluconate dehydrogenase E.C. 1.1.1.44	0.14/0.04 mol/l TRIS/citric acid, pH 7.8 0.04/0.011 mol/l TRIS/citric acid, pH 7.8
Glutamate dehydrogenase E.C. 1.4.1.2	0.06/0.30 mol/l NaOH/boric acid, pH 8.0 0.07/0.02 mol/l TRIS/HCl, pH 8.7
Phosphoglucomutase E.C. 2.7.5.1	0.14/0.05 mol/l TRIS/citric acid, pH 6.5 0.04/0.014 mol/l TRIS/citric acid, pH 6.6
Phosphoglucose isomerase E.C. 5.3.1.9	0.05/0.19 mol/l LiOH/boric acid, pH 8.1 0.05/0.01 mol/l TRIS/citric acid, pH 8.1

data. They represent the first results of genetic studies on adult oak stands in Europe. Deviations from HARDY-WEINBERG proportions were observed at several loci. In detail, the leaf-retaining stand shows significant deviations for the gene loci *PGM-A, 6-PGD-B*, and *SKDH-A*, whereas the leaf-abscising stand shows such deviations for *GDH-A, PGM-A*, and *SKDH-A* (*Tables 2* and *3*). Yet, among the loci showing deviations from HARDY-WEINBERG proportions in both stands, qualitative differences were observed in that *PGM-A* shows a relative surplus of homozygotes in one case and lack in the other case. Moreover, in most cases the expected genotype frequencies are less than 5, which may erroneously suggest rejection of the hypothesis using the *G*-test. Only for 1 gene locus (*IDH-A*) were all expected frequencies sufficient. In this case, the ob-

Table 2. – Genotypic structures of the leaf-retaining subpopulation, corresponding HARDY-WEINBERG structures and G-test of homogeneity between observed and expected structures.

	Genotype	Genotype frequencies		$\hat{G}$
		observed	Hardy-Weinberg-Structure	
GDH-A	00	0	0.002	17.607**
	01	0	0.263	
	02	0	0.112	
	03	1	0.621	
	11	11	8.019	
	12	9	6.836	
	13	30	37.862	
	22	5	1.457	
	23	7	16.138	
	33	53	44.690	
PGM-A	22	44	42.847	27.405***
	23	18	18.233	
	24	32	35.250	
	25	3	1.823	
	33	6	1.940	
	34	0	7.500	
	35	0	0.388	
	44	13	7.250	
	45	0	0.750	
	55	0	0.019	
IDH-A	22	8	6.284	0.766 n.s.
	23	38	41.431	
	33	70	68.284	
PGI-B	11	0	0.009	17.166 n.s.
	12	2	0.043	
	13	0	1.845	
	14	0	0.078	
	15	0	0.017	
	22	0	0.054	
	23	3	4.612	
	24	0	0.194	
	25	0	0.043	
	33	100	98.698	
	34	9	8.302	
	35	2	1.845	
	44	0	0.175	
	45	0	0.078	
	55	0	0.009	
6-PGD-A	33	112	112.034	0.070 n.s.
	34	4	3.931	
	44	0	0.034	
6-PGD-B	22	1	0.216	1.857 n.s.
	23	8	9.526	
	25	0	0.043	
	33	106	105.261	
	35	1	0.953	
	55	0	0.002	
SKDH-A	22	2	0.106	16.678***
	23	3	6.668	
	24	0	0.121	
	33	108	105.261	
	34	2	3.810	
	44	1	0.034	

served frequencies are in good accordance with HARDY-WEINBERG proportions. This means that the cases of apparent deviation from HARDY-WEINBERG proportions should not be overestimated. However, providing the deviations were truly significant, they may suggest an influence of selection or of the mating system, but the present data base does not allow further conclusions in this context. The data have been analyzed with respect to parameters of variation within and differentiation between stands.

Variation within subpopulations and heterozygosity

One commonly used parameter to describe genotypic structures of individuals and populations is the degree of heterozygosity (*Table 4*). Its estimation relies on genotypic rather than on allelic frequencies. However, the "actual degree of heterozygosity" (H_A) depends on the actual allele frequencies. Thus, it seems to be appropriate to calculate instead the "conditional degree of heterozygosity", which relates the actual amount of heterozygosity to the potential maximum under the given allele frequencies. Details are described by GREGORIUS (1978) and GREGORIUS *et al.* (1986). Previous studies on the 2 most common oak species of central Europe, *Quercus petraea* and *Quercus robur*, show very similar results with respect to their heterozygosities. Thus, the average heterozygosity at the species level estimated to be H_A = 21.3% for *Quercus robur* and between 21.9% and 22.9% for *Quercus petraea*. Conditional heterozygosities were found to be H_C = 56.6% in *Quercus robur* and H_C = 56.7% in *Quercus petraea* (MÜLLER-STARCK and ZIEHE, 1991; HERZOG and MÜLLER-STARCK, 1993; MÜLLER-STARCK *et al.*, 1993).

The present study revealed an average (arithmetic mean) actual heterozygosity of H_A = 25.3% over both subpopulations,

Table 3. – Genotypic structures of the leaf-abscising subpopulation, corresponding HARDY-WEINBERG structures and G-test of homogeneity between observed and eypected sturctures.

	Genotype	Genotype frequencies		$\hat{G}$
		observed	Hardy-Weinberg-Structure	
GDH-A	11	4	3.413	5.145 n.s.
	12	10	6.400	
	13	14	18.773	
	22	1	3.000	
	23	18	17.600	
	33	28	25.313	
PGM-A	22	18	19.253	8.282*
	23	2	4.053	
	24	38	33.440	
	33	2	0.213	
	34	2	3.520	
	44	13	14.520	
IDH-A	22	13	12.403	0.081 n.s.
	23	35	36.193	
	33	27	26.403	
PGI-B	11	0	0.003	1.075 n.s.
	12	0	0.007	
	13	1	0.913	
	14	0	0.073	
	22	0	0.003	
	23	1	0.913	
	24	0	0.073	
	33	63	62.563	
	34	9	10.047	
	44	1	0.403	
6-PGD-A	22	0	0.013	1.670 n.s.
	23	2	1.853	
	24	0	0.120	
	33	65	64.403	
	34	7	8.340	
	44	1	0.270	
6-PGD-B	11	0	0.003	10.294*
	12	0	0.073	
	13	1	0.920	
	22	3	0.403	
	23	5	10.120	
	33	66	63.480	
SKDH-A	22	0	0.213	29.284***
	23	3	7.147	
	24	5	0.427	
	33	65	59.853	
	34	1	7.147	
	44	1	0.213	

Table 4. – Gene pool variation within subpopulations (for details see text).

Gene pool variation measure	Leaf retaining subpopulation	Leaf abscising subpopulation
H_A	21.2%	29.3%
H_C	71.2%	64.9%
A_L	3.3	3.0
v	1.347	1.417
δ_T	0.259	0.322

i.e. H_A = 21.2% for the leaf-retaining subpopulation and H_A = 29.3% for the leaf-abscising one. Conditional heterozygosities are estimated to be H_C = 71.2% and H_C = 64.9% respectively, the average (arithmetic mean) over both subpopulations being H_C = 68.1% (*Table 3*). The actual heterozygosities lie near to the upper bounds of the spectrum given by previous authors for oak populations. The conditional heterozygosities found in the present study represent the highest values that have found for oaks to date. This phenomenon may be explained by the greater age of the populations investigated. As mentioned above, the present study relies on adult stands whereas all previous publications report data obtained from juvenile (mostly 3- to 5 year-old) populations. However, the age of the stand may explain the high level of heterozygosity in general, but not the remarkable differences between the populations. These differences will be discussed below.

The average number of alleles per gene locus (A_L) was found to be 3.3 for the leaf-retaining and 3.0 for the leaf-abscising subpopulation (*Table 4*). These values fit perfectly into the frame given by a study of MÜLLER-STARCK *et al.* (1993). The difference between the subpopulations is of the same magnitude as differences between populations found by MÜLLER-STARCK *et al.* (1993).

Diversity is measured using the gene pool diversity (v, GREGORIUS, 1978, 1987) and the total population differentiation (δ_T*, GREGORIUS, 1987; *Table 4*). Especially the calculation of v makes the data comparable to other studies. Whereas the present study revealed a total population differentiation of δ_T* = 0.259 in the sown leaf-retaining and δ_T* = 0.322 in the planted leaf-abscising stand, the gene pool diversity v was found to be 1.35 in the former and 1.47 in the latter stand (*Table 3*). MÜLLER-STARCK and ZIEHE (1991) as well as MÜLLER-STARCK *et al.* (1993) calculated gene pool diversities between v = 1.33 and v = 1.41 for *Quercus robur* and between v = 1.29 und v = 1.49 for *Quercus petraea*. HERZOG and MÜLLER-STARCK (1993) found v's between 1.26 and 1.47 for *Quercus petraea*. Thus, the present findings show a slightly higher gene pool diversity than the previously studied juvenile populations of pedunculate oak, and they fit into the framework given for european oak species in general. However, the values are high compared to the results of studies on other plant species. HAMRICK and GODT (1990) reanalyzed more than 600 studies and found an average "effective number of alleles" to be 1.24. This measure is to be compared to the obtained diversity v which indicates a relatively high diversity for oaks. This may result from the above mentioned spatial and temporal heterogeneity of the environments.

Differentiation between subpopulations

The genetic distances as well as the results of *G*-tests of homogeneity are shown in *table 5*. Three loci (*PGM-A, IDH-A* and *6-PGD-A*) show significant differences for both allelic and genotypic structures using the *G*-test. Moreover, 2 other loci (*GDH-A* and *SKDH-A*) show those differences only for genotypic structures. Especially for *PGM-A* and *IDH-A*, the genetic distances d_0 (GREGORIUS, 1974, 1984) clearly exceed those found for the other gene loci.

Table 5. – Genetic distances and results of the tests of homogeneity between the leaf-abscising and leaf-retaining subpopulations.

Gene locus	Genetic distance d_o	$\hat{G}$ (allele frequencies)	$\hat{G}$ (genotype frequencies)
GDH-A	0.088	6.780 n.s.	17.684**
PGM-A	0.190	20.273***	26.640***
IDH-A	0.147	12.929***	12.197***
PGI-B	0.035	5.514 n.s.	8.967 n.s.
6-PGD-A	0.056	8.806*	8.749*
6-PGD-B	0.037	4.445 n.s.	5.036 n.s.
SKDH-A	0.059	5.226 n.s.	11.975*

Gene pool subpopulation differentiation D_j and δ (GREGORIUS and ROBERDS, 1986) as well as the genetic distance d_0 were calculated to be 0.091. This means that the adult stands of pedunculate oak are more differentiated than the juvenile populations previously studied by MÜLLER-STARCK and ZIEHE (1991, δ = 0.055) as well as HERZOG and MÜLLER-STARCK (1993; δ = 0.061). This is not surprising insofar as we could assume provenance differences and/or different collection procedures of the original seed material between the subpopulations under study. However, it has to be kept in mind that the site conditions and silvicultural treatment and thus selection factors have been the same for more than 70 years for both stands.

Evidence for a genetic basis of leaf retention

The observed genetic differences may not necessarily be directly responsible for the differing leaf-abscising behaviour or water content. However, what we can conclude is that 2 stands show an evident difference in the autumn leaf abscission that is not explainable by different site conditions, especially soil or microclimate.

The stands are genetically differentiated as could be shown using biochemical gene markers. The reasons for this differentiation remain to be discussed. At first sight, provenance differences may be responsible, as they result in different selection regimes at different original sites. However, the genetic differentiation in the adult stands under study may also be due to genetic drift resulting from the procedure or the time of cropping the seed material or even due to selection and/or genetic drift dependent on the mode of establishing the stands.

If there is genetic variation for leaf abscission in the species *Quercus robur*, the genes coding for retention are expected to be relatively rare. Thus we should expect less genetic variation in a population mainly consisting of leaf-retaining trees. Considering the relevant parameter δ_T*, we find support for this hypothesis. On the other hand, the average numbers of alleles per gene locus does not correspond to this hypothesis at first sight. However, the leaf-retaining stand shows a higher proportion of rare alleles. Its higher conditional heterozygosity may also be caused by higher proportion of rare alleles. For future studies, it may be helpful to study leaf-retaining trees within the leaf-abscising population separately and *vice versa*. However, summarizing the results of the present study, we can find good evidence for the hypothesis that phenomenon of leaf retention has a genetic rather than an environmental basis.

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An Attempt to Infer on the Origin of a Beech (*Fagus sylvatica* L.) Stand in Rheinland-Pfalz (Germany)

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Summary

Information on whether a stand represents a part of an autochthonous population is important for control of the seed trade and for the declaration of gene resources.

The genetic structure of a planted beech stand of questionable origin with an outstanding high proportion of forked trees, was compared with those of stands of the same region in western Germany that were either known or supposed to be autochthonous. Genetic structures were estimated for 11 enzyme gene loci. Comparisons were performed by determining genetic distances and applying measures of genetic differentiation. The degree of differentiation of beech populations at enzyme gene loci is generally low, which causes additional difficulties. Nevertheless, it may be concluded that the plants used to establish the stand in question could hardly have been raised from seed collected from a stand in the alleged part of the natural distribution range.

Key words: Faglls sylvatica L., enzyme gene loci, regional genetic differentiation, planted and autochthonous stands, seed trade.

FDC: 165.3; 165.5; 176.1 *Fagus sylvatica*; (430).

Zusammenfassung

Die Kenntnis der Zugehörigkeit eines Bestandes zu einer autochthonen Population ist sowohl für die Kontrolle des Vertriebs von Vermehrungsgut als auch die Ausweisung von Genressourcen bedeutsam.

Die genetische Struktur eines Buchenpflanzbestandes fraglichen Ursprungs mit außergewöhnlichem hohen Anteil

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