SPATIAL GENETIC DIFFERENTIATION AMONG POPULATIONS OF EUROPEAN BEECH (*FAGUS SYLVATICA* L.) IN WESTERN GERMANY AS IDENTIFIED BY GEOSTATISTICAL ANALYSIS

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ABSTRACT

The spatial genetic differentiation among European beech stands in western Germany was analysed by a new method. The genetic structure at 8 enzyme gene loci of 100 sampled populations was used as data base. The data represent authors' own results and published data from 8 different studies. For 10 geographic distance classes [h] from 0 to 500 km, the average genetic distance $\hat{d}(h_k)$ between the populations for each single gene locus, a gene-pool distance $\hat{d}(h_k)$ and the semivariances $\hat{\gamma}(h_k)$ of genetic diversity υ_{gam} were computed. Significant deviation from random spatial genetic structure was tested by permutation analysis. In many cases (*Lap–B, Mdh–B, Mdh–C* and *6Pgdh–C*) the mean genetic distance $\hat{d}(h_k)$ between stands with spatial distance up to 200 km was significantly smaller and the genetic distance between stands with geographic distances of 200 and 400 km was significantly greater than expected for random spatial genetic structure. Similar tendencies were found for the gene-pool distance and the semivariances $\hat{\gamma}(h_k)$ of diversity. Kriging, as a method for spatial interpolation, was used to draw synthetic maps of the spatial patterns of allelic frequencies and genetic diversity. The influence of postglacial recolonisation and regeneration with foreign seed material on the spatial genetic patterns are discussed.

Key words: *Fagus sylvatica*, spatial patterns, genetic differentiation, genetic distograms, kriging, permutation test, genetic diversity

INTRODUCTION

Plant European beech is a widespread, hermaphroditic and wind pollinated tree species. Like many other tree species (HAMRICK *et al.* 1992) beech reveals a high level of genetic variation at allozyme gene loci (MÜLLER–STARCK & ZIEHE 1991). The intra-population components of genetic variation in beech populations are quite high in comparison to the inter-population components (PAULE *et al.* 1995, LEONARDI & MENOZZI 1995, TRÖBER 1995, HATTEMER & ZIEHE 1996, TUROK 1996). Despite low differentiation among populations, geographic trends at enzyme gene loci were observed. In an extensive study, including almost 500 stands, COMPS *et al.* (1990) found significant associations of climate and allelic diversity for two peroxidase loci. In this study the inter-population component of the diversity was highest in the Mediterranean region. At the enzyme loci *Got–B, Mdh–B* and *Skdh–A*, PAULE *et al.* (1995) found some alleles, specific for one or several adjacent regions in Southeast Europe. Within 21 Italian populations of beech, LEONARDI & MENOZZI (1995) observed allelic frequencies related to latitude and longitude.

In Germany the genetic inventories in beech populations were aimed at on three different topics:

- analysis of the impact of air pollutants on the genetic structure (*e.g.* MÜLLER-STARCK 1993)
- conservation of gene resources at regional level (*e.g.* KONNERT 1995, TRÖBER 1995, TUROK 1996)
- population genetic studies on the mating system and viability selection by comparison of different ontogenetic stages (*e.g.* GREGORIUS *et al.* 1986, GREGORIUS & DEGEN 1994, MÜLLER-STARCK 1996)

Regarding the low levels of genetic differentiation in beech (TRÖBER 1995, PAULE *et al.* 1995, HATTEMER & ZIEHE 1996, TUROK 1996) new sensitive methods for detecting spatial genetic patterns are necessary. For developing such methods, in this study published and unpublished data as well as published data from other authors on allele frequencies were brought together and analysed for the genetic differentiation among beech populations at a higher spatial scale. Data from invento

ries in western Germany with common nomenclature for loci and alleles and available allele frequencies were used as prerequisites for joint evaluation as an example.

MATERIAL

The analysis is based on published and own data on allele frequencies at 8 enzyme gene loci of 100 sampled stands. Table 1 shows the references, number of analysed stands, total number of individuals and ontogenetic stage of the sampled individuals.

Number of analysed individuals sum up to 19410. Sample size per stand varied from 24 to 2285 individuals (average = 194 individuals). In some stands, data from more than one ontogenetic stage were available. From these stands allele frequencies of all analysed ontogenetic stages were averaged. Only data representative for the whole genetic structure of the stand were included in our spatial analysis. This is assumed for random sampling of adult trees or random sampling of seeds from at least 20 mother trees and also for regular sampling according to a grid whereas data of pairwise sampling were excluded.

Figure 1 shows the geographic position and the sample size of the analysed stands.

METHODS

Genetic inventories

The own genetic investigations and the inventories of the already published data were carried out by means of horizontal starch gel electrophoresis. Five enzyme systems which code for 8 gene loci were included in the analysis (table 2). The methods and nomenclature follow MÜLLER-STARCK & STARKE (1993). Mendelian inheritance of the gene loci were proved by KIM (1979), MERZEAU *et al.* (1989) and MÜLLER-STARCK & STARKE (1993).

Spatial data analysis

In a first step the allele frequencies and information about the sampled stand and sampling strategy were integrated into a data base. In some cases the nomenclature of the alleles had to be adjusted. This data base was linked to the Geographic Information System (ArcView® GIS Version 3.0 from ESRI). For the majority of the stands their geographic position was drawn from published maps. This procedure may account for an error of ± 10 km regarding positioning of the stands.

Table 1. References for the data, number of analysed stands, total number of individuals and ontogenetic stage

Reference	No. of stands	No. of individuals	Adult trees	Seeds	Seedlings, young trees
DEGEN & SCHOLZ (unpublished data)	7	200			X
DEGEN 1992, FROMM 1992, GREGORIUS & DEGEN 1994	3	590	X	X	X
DEGEN 1996	5	1200	X	X	
KONNERT 1995	20	2015	X		
LÖCHELT & FRANKE 1995	8	320	X		
MÜLLER-STARCK 1993	7	1294		X	
R. MÜLLER-STARCK 1996	3	4866	X	X	
TABEL & MAURER 1992, STARKE *et al.* 1995	22	6367	X		X
TUROK 1996	25	2558		X	

Table 2. Surveyed enzyme systems and gene loci scored

Enzyme system	E.C. Ref. No.	Gene loci
Glutamate oxalacetat transaminase	2.6.1.1	*Got–B*
Isocitrate dehydrogenase	1.1.1.42	*Idh–A*
Leucine aminopetidase	3.4.11.1	*Lap–A*
Malate dehydrogenase	1.1.1.37	*Mdh–B, –C*
6-Phoshogluconate dehydrogenase	1.1.1.44	*6Pgdh–A, –B, –C*

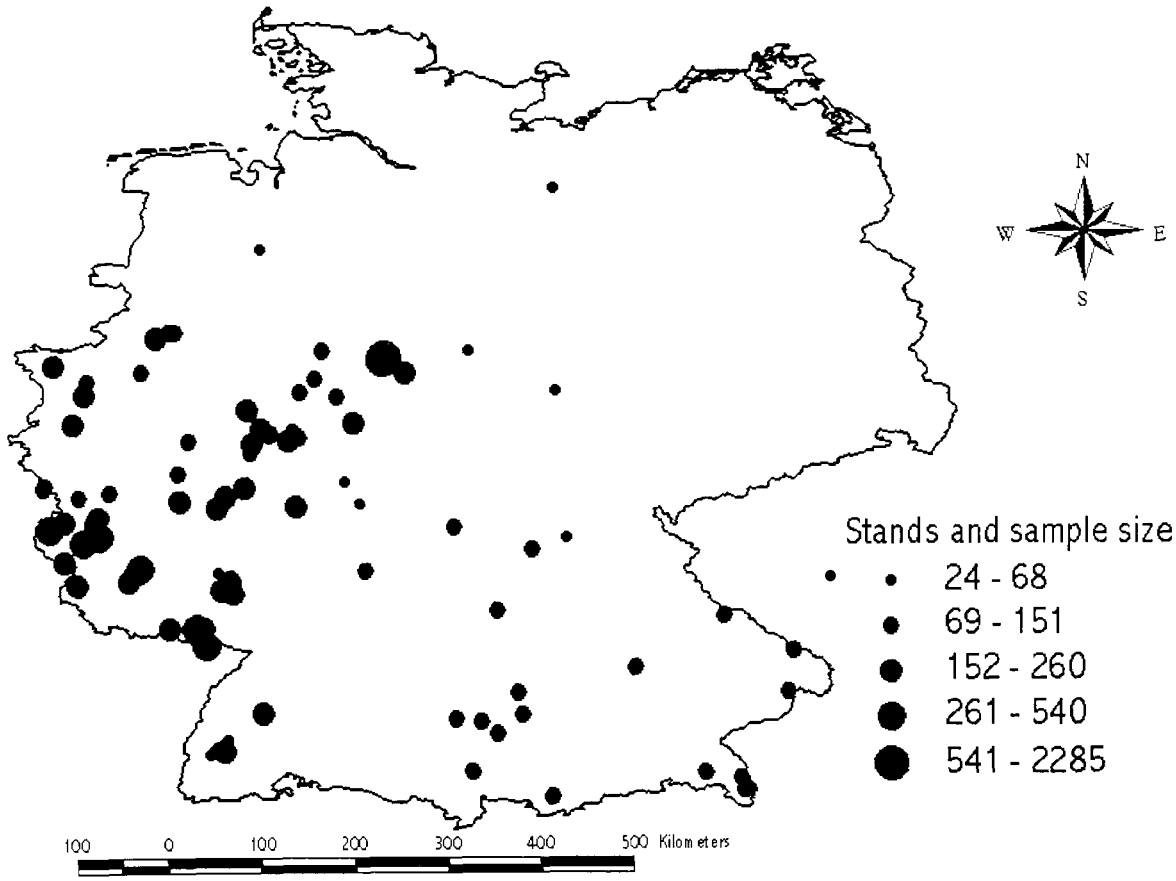

Figure 1. Position and sample size of 100 analyzed European beech stands (for source of data, see table 1)

Construction of experimental variogram and genetic distogram

The construction of experimental variograms is a common method in geostatistics to describe and analyse the spatial pattern of a given variable (WACKERNAGEL 1995). Consider the case of n measurements $z(\boldsymbol{x}_1)$, $z(\boldsymbol{x}_2)$,.....$z(\boldsymbol{x}_n)$. The bold letter x stands for the array of coordinates of the point where these measurements are taken. Plot the squared differences,

$$½\ [z(x_i) - z(\acute{x}_i)]^2$$

against the separation distance $\|x_i - x_j\|$ for all measured pairs. In the common method of plotting the experimental variogram, the axis of separation distance is divided into consecutive intervals. The k-th interval $[h_k^l, h_k^u]$ is which contains N_k pairs of measurements $[z(x_i), z(x_j)]$. Then, compute the semivariance:

$$\hat{\gamma}(h_k) = \frac{1}{2N_k}\sum_{i=1}^{N_k}[z(x_i) - z(\acute{x}_i)]^2$$

where index i refers to each pair of measurement $z(x_i)$ and $z(x'_i)$ for which

$$h_k^l \le \|x_i - \acute{x}_i\| < h_k^u$$

Next the points $[h_k, \hat{\gamma}(h_k)]$ are connected to form the experimental variogram (KITANIDIS 1997). In general $\hat{\gamma}(h_k)$ represents an average dissimilarity of all pairs in a given distance interval.

In the present study, semivariances $[\hat{\gamma}(h_k)]$ were calculated for genetic variability of each population. The genetic variability was computed as hypothetical gametic diversity υ_{gam} (GREGORIUS 1978):

$$V_{gam} = \prod_{i=1}^{L} v(l)$$

$$v(l) = (\sum_{i=1}^{n} p_{il}^2)^{-1}$$

where: l = locus, and p_l = frequency vector of all alleles of locus l.

In analogy to the experimental variograms we calculated genetic distograms where the dissimilarity of each pair of measurement $z(x_i)$ and $z(x'_i)$ was calculated by use of genetic distance measure (GREGORIUS 1974):

$$\hat{d}(h_k) = \frac{1}{N_k} \sum_{i=1}^{N_{k-1}} \sum_{j=i+1}^{N_k} d_{ij}$$

where d_{ij} represents the genetic distance between the allele frequencies of population i and j

The values $\hat{d}(h_k)$ represent the average genetic distance of all pairs of population in the k^{th} spatial interval $[h_k^l, h_k^u]$.

The construction of genetic distograms has two advantages. First they describe spatial patterns for more than one variable simultaneously (not only the frequency of one allele) and second it applies established concepts of genetic distances to measure dissimilarities.

The average genetic distance $\hat{d}(h_k)$ for each single gene locus and the semivariance $\hat{\gamma}(h_k)$ of diversity υ_{gam} were computed for 10 distance classes [h] from 0 to 500 km (width of each class = 50 km). Since not all 8 gene loci have been analysed in all 100 sampled stands, the number of stands included in the calculations varied from 41 to 95. In 76 stands the allele frequencies were investigated at the same 5 gene loci (*6Pgdh–A, Got–B, Lap–A, Mdh–B* and *Mdh–C*). Therefore in addition to the single locus measures a 'gene pool' distance was calculated as a mean distance over these 5 loci.

In case of positive spatial autocorrelation the estimates $\hat{d}(h_k)$ and $\hat{\gamma}(h_k)$ increase with increasing geographic distance between the populations. A permutation procedure (resampling without replacement) was applied to test significant deviation from spatial random distribution of $\hat{d}(h_k)$ and $\hat{\gamma}(h_k)$ (NOREEN 1989; WEIR 1996). Each permutation consisted of a random redistribution of allele frequencies or diversity υ_{gam} over the spatial coordinates of the sampled stands (for the unit of redistribution see VAN DONGAN 1995). For each of the 10 spatial distance classes h_k, observed $\hat{d}(h_k)$ and $\hat{\gamma}(h_k)$ values were compared with the distribution obtained after 1000 permutations. A 95 % confidence interval for the parameters has been constructed as the interval from the 26th to the 975th ordered permutation estimates.

Kriging

Kriging is an advanced interpolation procedure that generates an estimated surface from a scattered set of points with z values. This method is frequently used in geostatistical analysis (WACKERNAGEL 1995; KITANDIS 1997) and has already been applied to model the spatial pattern of genetic structures in forest trees (LE CORRE *et al.* 1998). By use of kriging it is possible to predict values at unsampled locations and to generate maps. Kriging is based on the regionalized variable theory which assumes that the spatial variation in the phenomenon represented by the z values is statistically homogeneous throughout the surface; that is, the same pattern of variation can be observed at all locations on the surface.

The kriging procedure consists of three steps:

1. The spatial variation is quantified by the semivariogram (see calculation of $\hat{\gamma}(h_k)$). The semivariogram is estimated by the sample semivariogram which is computed from the input point data set.

2. The semivariogram is modelled by fitting a theoretical function (*e.g.* exponential, spherical or circular function) to the sample semivariogram. The semivariogram is then fited to the variance points.

3. By use of this optimised function the estimates for the *z*-values of each point of a grid are computed as a linear combination of the observed values taken within a given search neighbourhood. The estimates are both unbiased (the mean of estimation errors equals zero) and optimal (the estimation variance is minimised).

As examples kriging was performed to model the spatial distribution of the frequency of allele $Mdh\text{–}B_6$ and the spatial distribution of the diversity υ_{gam}. In correspondence to (LE CORRE *et al.* 1998) the experimental variogram were adjusted to the exponential model:

$$\gamma(h) = c_o + c(1 - \exp(\frac{-h}{r}))$$

$$h>0$$

$$\gamma(0) = 0$$

The search neighbourhoods were variably including the 12 nearest observed points (moving neighbourhoods). This number is suggested by current research (WACKERNAGEL 1995). Kriging was performed on a irregular grid. For each grid cell with size of 0.1° East and 0.1° North a *z*-value was modelled.

RESULTS

Table 3 contains the computed $\hat{d}(h_k)$ values in 10 geographic distance classes h for 8 gene loci and the respective $\hat{d}(h_k)$ values for gene pool distances calculated from 5 loci (*6Pgdh–A, Got–B, Lap–A, Mdh–B* and *Mdh–C*). The last column represents the semivariance $\hat{\gamma}(h_k)$ of the hypothetical gametic diversity υ_{gam} of 5 loci (*Mdh–B, Idh–A, Lap–A, Got–B, 6Pgdh–A*). Figure 2 shows the genetic distograms of *Idh–B* and *Mdh–B* as examples.

Table 3. The average genetic distance $\hat{d}(h_k)$ $\hat{d}(h_k)$ for 8 single gene loci (column 2–8), for gene pool distance (column 9) and semivariance $\hat{\gamma}(h_k)$ of the hypothetical gametic diversity υ_{gam} (column 11) calculated on the basis of 5 loci (*Mdh–B, Idh–A, Lap–A, Got–B, 6Pgdh–A*) between the stands in 10 geographic distance classes [h]; number of stands = N, * = exceeding the 95% confidence interval of 1000 permutations

Distance h [km]	$\hat{d}(h_k)$ Locus								$\hat{d}(h_k)$ Gene pool	$\hat{\gamma}(h_k)$ V_{gam}
	Got–B	*Idh–A*	*Lap–B*	*Mdh–B*	*Mdh–C*	*6Pgdh–A*	*6Pgdh–B*	*6Pgdh–C*		
0–50	0.0646	0.0757	0.1297*	0.0726*	0.0549	0.0448	0.0530*	0.0842	0.0708*	15.95
50–100	0.0662	0.0688*	0.1466	0.0630*	0.048*	0.0429	0.0648	0.0914	0.0739*	13.86
100–150	0.0730	0.0783	0.1555	0.0730*	0.0560	0.0435	0.0570	0.0893	0.0795	15.69
150–200	0.0698	0.0796	0.1583	0.0788*	0.0556	0.0450	0.0645	0.0970	0.0829	14.26*
200–250	0.0652	0.0766*	0.1681*	0.0805	0.0587	0.0479	0.0753	0.0999	0.0843	17.07
250–300	0.0713	0.0797	0.1736*	0.0982*	0.0679	0.0534	0.0726	0.0845	0.0930*	23.64
300–350	0.0684	0.0835	0.1576	0.1026*	0.0617	0.0453	0.0663	0.0908	0.0861	23.39
350–400	0.0715	0.0863	0.1567	0.0971*	0.0683	0.0517	0.0610*	0.0964	0.0867	26.45
400–450	0.0770	0.0984*	0.1641	0.1024*	0.0646	0.0594	0.0978*	0.1011	0.0882	27.70
450–500	0.0655	0.1038*	0.1451	0.0841	0.0699	0.0518	0.0678	0.1074	0.0847	29.44
N	80	95	87	95	92	95	48	41	76	80

Except gene loci *Got–B* and *6Pgdh–A* all loci showed genetic distances $\hat{d}(h_k)$ significantly different from the expected values of permutations. In these cases we reject the null hypothesis of random spatial genetic differentiation. Also for the gene pool distances (gene pool) and the semivariance $\hat{\gamma}(h_k)$ of the diversity υ_{gam} at least one value was significant. In general the genetic distances increase with increasing geographic distance (see also figure 2). The majority of significant values were observed in the lowest geographic distance classes from 0–200 km (*Idh–A, Lap–B, Mdh–B, Mdh–C, 6Pgdh–B*) and in the classes from 350–400 km (*Idh–A, Mdh–B, 6Pgdh–B*). In contrast, for *Got–B, Lap–B, Mdh–B, 6Pgdh–A, 6Pgdh–B* and for the gene-pool distances the values decreased in the highest distance class (450–500 km). Most significant values were found for *Mdh–B*. In general the differences of genetic distances between geographic distance classes were very small. For *Got–B* the values vary between 0.0646 and 0.0770. *Lap–A* had the greatest genetic distances. Only at this gene locus all values exceeded 0.10 (0.1297–0.1736). In the geographic distance classes 150–200 km the semivariance $\hat{\gamma}(h_k)$ of diversity υ_{gam} was significantly different from the expected values of permutations.

Figures 3 and 4 represent kriged maps of the spatial distribution of *Mdh–B*$_6$ allele frequencies and the spatial distribution of diversity υ_{gam} in beech populations, respectively. These examples were selected because of the strong significant deviation from

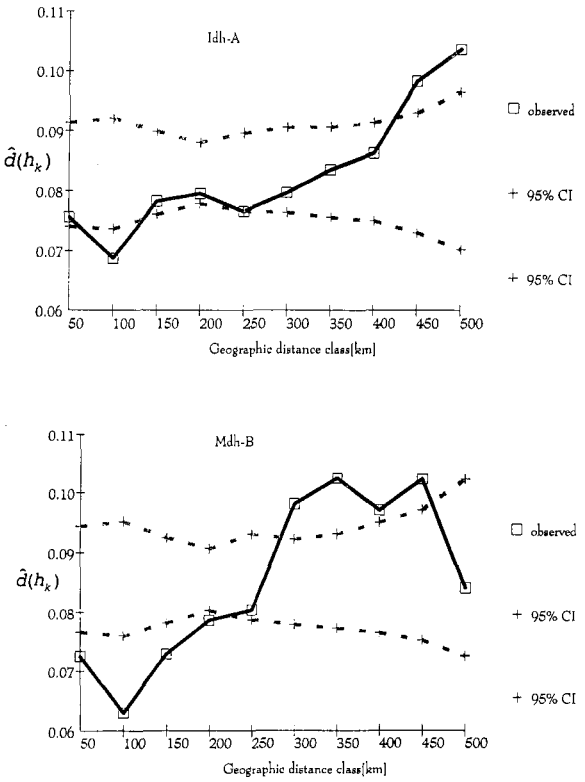

Figure 2. Genetic distogram of genetic distances $\hat{d}(h_k)$ in 10 geographic distance classes (0–500 km) for the gene loci *Idh–A* and *Mdh–B*, 95% confidence intervals of $\hat{d}(h_k)$ (95% CI) were computed by means of 1000 permutations over subpopulations with redistributed geo-coordinates.

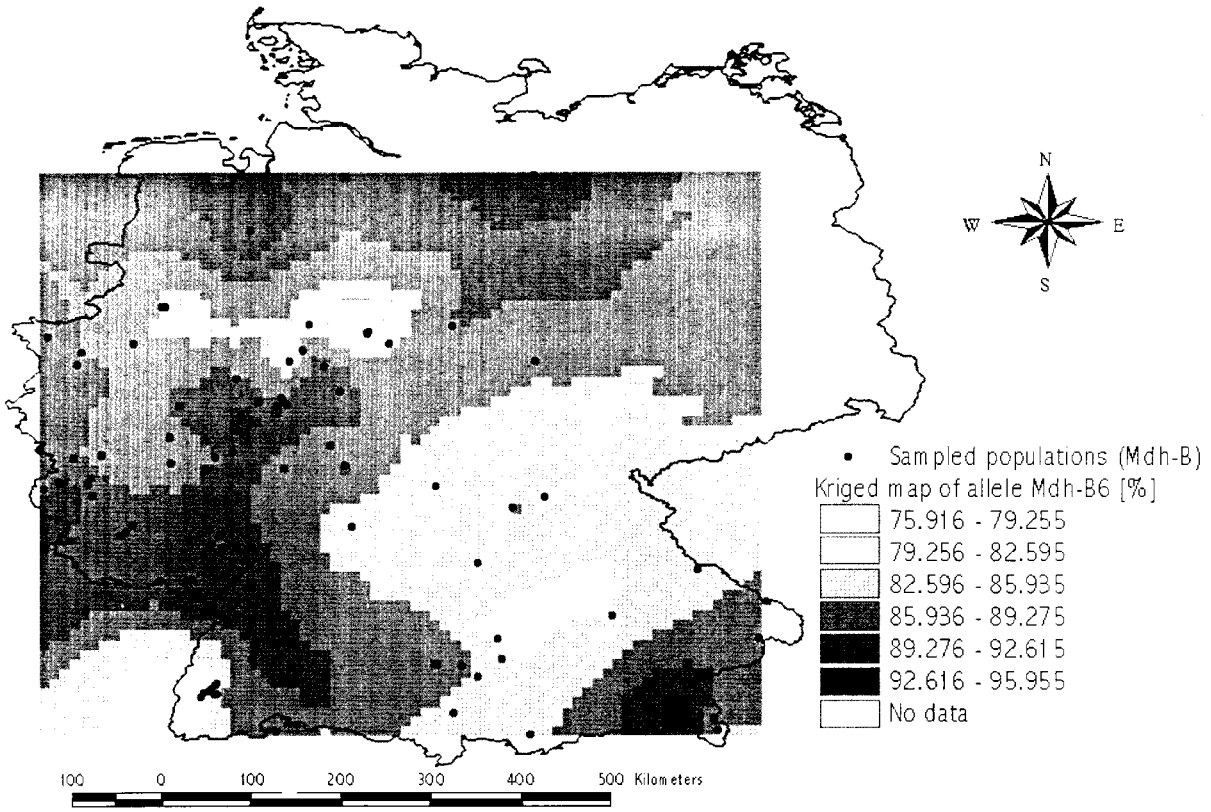

Figure 3. Kriged map of allele frequencies of *Mdh–B*$_6$ and position of the sampled stands (for source of data, see table 1). The reliability of the map increases with the density of sampled stands.

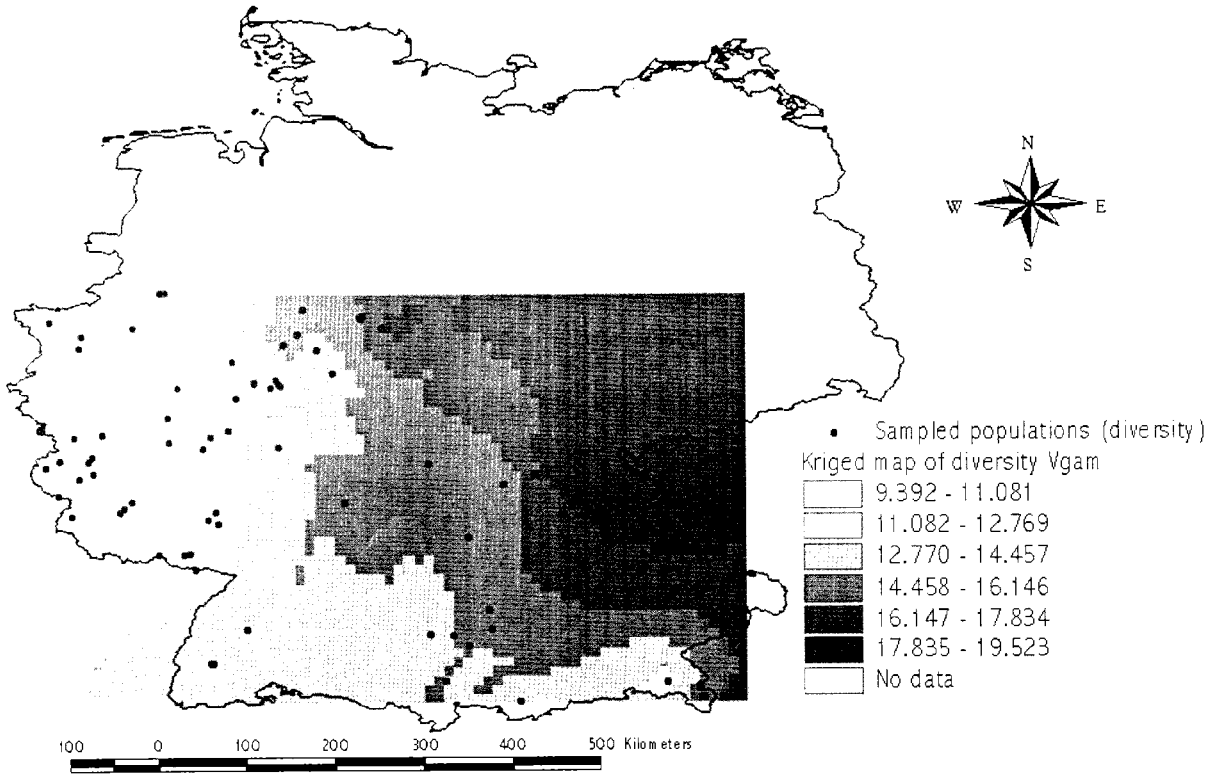

Figure 4. Kriged map of diversity υ_{gam} and position of the sampled stands (for source of data, see table 1). The reliability of the map increases with the density of sampled stands.

random spatial structure for *Mdh–B* (see table 3) and the aggregated character of υ_{gam}. The modelled distribution of *Mdh–B*$_6$ showed three regional areas with relatively low frequencies and two closed areas in the West and North with relative high frequencies of *Mdh–B*$_6$ (figure 3). In figure 4, the region of southern Westfalia shows a low level of diversity υ_{gam}. In contrast, beech populations in the south-east of Germany (Bavaria) exhibited a higher level of diversity υ_{gam}. In both maps patches of higher scale (80–200 km) and also patches of local scale (10–80 km) were observed.

DISCUSSION

For interpretation of the results the influence of the sample size has to be considered. Low sample size might lead to underestimated genetic multiplicity (GREGORIUS 1980). For estimating such effects the correlation between diversity υ_{gam} (table 3) and sample size (figure 1) was computed. The correlation coefficient is low (0.03). Hence, influence of sample size can be neglected.

In this data analysis, allele frequencies of 9 different studies (table 1) were integrated. As these 9 studies were not initialised as part of an integrated genetic inventory the analysed stands were not equally distributed over Germany (figure 1). Especially stands in east Germany were not included because of missing allele frequencies in the published data. Sampling strategy, sample size and partly the analysed ontogenetic stages were not uniform. Genetic differences between different ontogenetic stages of the same stand can be on the same level as genetic differences between the same stage of different stands (GREGORIUS & DEGEN 1994). Therefore comparisons between samples of different stages may be problematic. Altogether the heterogeneity of data lead to an unsystematical bias. Therefore parts of existing spatial pattern may be underestimated or undetected.

In many cases the genetic distance $\hat{d}(h_k)$ between stands with spatial distance up to 200 km was significantly smaller than expected by permutations (see *Idh–A, Lap–B, Mdh–B, Mdh–C* and *6Pdgh–B* in table 3). On the other side greater genetic distances than expected were observed for geographic distances of 200 and 400 km between stands (*Lap–B, Mdh–B, 6Pgdh –B*). Similar tendencies were found for the gene-pool distances (see 'gene-pool' in table 3). Different processes and factors can cause genetic similarity between neighboured stands. One possible reason is descent from the same glacial refugia. For beech, PAULE (1995) found some evidence for this explanation. For other tree species such as silver fir (*Abies alba)* clinal variation in allele frequencies was explained by postglacial recolonisation (KONNERT & BERGMANN 1995). Also the spatial distribution of *Mdh–B*$_6$ frequency (figure 3) could be explained by recolonisation from a refugium in France. Moreover, LEONARDI & MENOZZI (1995) explained spatial genetic patterns of Italian beech populations with postglacial recolinisation from different refugia.

Stands in a geographic distance from 150 to 200 km had lower dissimilarities in their diversity υ_{gam} (table 3) than expected by permutations. The map in figure 4 exhibits the spatial distribution of diversity in beech populations. South Westfalia is a striking region in the map. It represents one of the most important industrial centres since the fifteenth century. In former times the ironworks needed immense amounts of wood. During this period the high beech forests were changed into coppice forests. This coppice forests were mainly covered by birch and oak. The size of the beech populations decreased drastically (HASEL 1985, page 159 ff.; SEIBERT 1966). After logging only few adult trees remained for reproduction. Simulation studies (DEGEN *et al.* 1996) show that such situations can cause genetic erosion in the next generation. Further studies in other coppice forests should be performed to prove the hypothesis of negative influence of coppicing on the level of diversity.

There were two categories of genetic patterns, patches on a higher (200 km diameter) and patches on a smaller (< 80 km) scale. This is visualised by the same shaded patches in figure 3 and 4. Large scale pattern can be the result of postglacial recolonisation and local differences can be the result of artificial regeneration with foreign seed material. Also LE CORRE *et al.* 1998 found within their geostatictical analysis of genetic structures of oaks different scales of spatial pattern. They explained the stationary patterns with effective isolation by distance among populations. Genetic drift after deforestation or different spatial adaptation can also explain local patterns. Genetic drift is caused by a strong reduction of population size due to deforestation or natural catastrophes such as fire or storm. For example LLAMAS and BRAUN (in ZIEGENHAGEN *et al.* 1995) explained the low genetic variation of silver fir in Saxonia as the result of air pollutants and silvicultural discrimination of this species. Examples of local adaptation at enzyme gene loci have been reported by BERGMANN & GREGORIUS (1993) for silver fir and BERGMANN (1978) for Norway spruce.

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