

## GENETIC VARIATION OF BEECH (*FAGUS SYLVATICA* L.) PROVENANCES IN AN INTERNATIONAL BEECH PROVENANCE TRIAL

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### ABSTRACT

Using isoenzyme-gene markers, genetic investigations were carried out on 16 beech provenances included in an international beech provenance trial. The goal was to check whether the genetic structure and variation of the material included in the field trials was representative of the respective provenance region. Provenances of *Fagus sylvatica* from Central Europe as well as from the edges of the natural distribution range were included in the study. Most provenances had patterns of genetic variation which were representative of the respective provenance region. A few provenances however, had a unexpected genetic structure or a very low genetic diversity which differed considerably from the provenance region. For such provenances, it is recommended that the results of the field trials should be interpreted with caution before provenance recommendations are made. The necessity and the potential for using gene markers when establishing provenance trials or evaluating existing trials is discussed.

**Key words:** *Fagus sylvatica*, beech, provenances, isoenzyme analysis, genetic variation

### INTRODUCTION

Beech – *Fagus sylvatica* L. – is the most common broadleaved tree species in Central Europe. Beech grows on a wide variety of sites from the lower elevation up to the higher elevation of the Alps. It is found as a dominant species as well as a subordinate species in mixture with conifers. As far as possible beech is often regenerated naturally. In order to establish more natural, site adapted forests (away from pure coniferous forests) beech is increasingly planted on these conversion sites. Beech is planted under existing coniferous forests to increase stand stability and to change species composition to include more broadleaves. This is especially the case in regions of forest decline. The choice of the correct, best adapted but also genetically variable (great adaptive potential) provenance is important for the stability of the future forests.

Information on the growth and development of the different provenances on various sites can be obtained from provenance trials. In order to understand how provenances react under different environments one must understand the genetic component we are dealing with. The provenances included in such trials must be representative of the provenance region in their genetic composition. This is not always the case as was shown by investigations on a European silver fir provenance trial (HUSSENDÖRFER & KONNERT 1997).

Beech provenance trials have been established in several countries in Europe, as for example in France

(eg. TEISSIER DU CROS 1993), Poland (RZEZNIK 1993) and Spain (PUERTAS TRICAS 1993).

During a workshop on beech in Ahrensburg in 1993 it was decided to establish a European-wide provenance trial, where all regions where beech occurs should be represented by a sufficiently high number of provenance samples (MUHS & VON WÜHLISCH 1993). The project was coordinated by the BFH in Grosshansdorf, Germany. The first field test sites were established in 1997. A total of 59 provenances are included in the different field trials, which are located in 16 European countries (VON WÜHLISCH *et al.* 1998).

Considerable phenotypic data was collected in many of these trials (eg. VON WÜHLISCH *et al.* 1993, MUHS 1985, TEISSIER DU CROS *et al.* 1988, THOMASIUS & GÄRTNER 1985); however, it is not known whether any information on the genetic structure of the individual provenances included in the provenance trial was obtained.

Through investigations on several provenances from the International Beech Provenance Trial established in 1997 we wanted to see whether the expected genetic structure for the respective provenance regions is maintained in the respective population in the provenance trial and what the extent of genetic variation in that population is.

### MATERIAL AND METHODS

The 16 beech provenances from the international

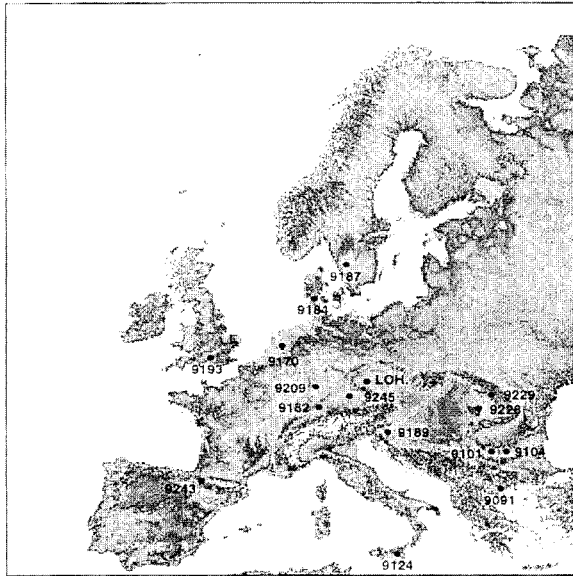


Figure 1. Distribution of investigated provenances.

provenance trial included in the genetic study are given in Table 1, the distribution of provenances is illustrated in Figure 1.

To a large part provenances from the edge of the natural distribution range were selected, since the genetic variation of beech in Central Europe has been intensively investigated (e.g. COMPS *et al.* 1991a, LEONARDI & MENOZZI 1995, LARSEN 1996, TUROK 1996, TUROK *et al.* 1998, KONNERT 1995, KONNERT *et al.* 2000, TRÖBER 1995, COMPS *et al.* 2001 etc.) and found to have little variation at many enzyme-gene-loci. The provenance Ebrach was chosen because data was

available on the genetic variation of the seed, the natural regeneration and the old trees from the seed collection stand (KONNERT, unpublished).

For the study we investigated seedlings from the 16 populations before they were distributed to the field test sites for planting. For 15 provenances the seedlings were raised in the BFH nursery in Grosshansdorf. For the provenance „Lohmen“ the sample material was provided by the Saxonian Forest Institute in Graupa. How many trees were sampled for the respective provenance collection was not known. The initiators of the provenance trial where we carried out our investigations have no information on the number of trees sampled for the respective provenance collection. Since beech nuts are generally collected by laying out nets, it is difficult to identify the specific number of sample trees.

For determining the genetic structure isoenzyme gene markers were used. 150 individuals per provenance were analyzed at fifteen gene loci by utilizing four electrode and gel buffer systems (Table 2). The technical procedure and the genetic interpretation of zymogrames followed MÜLLER-STARCK & STARKE (1993). On the basis of allele frequencies, the genetic diversity was quantified using the parameters  $n_e$  = effective number of alleles per locus, (CROW & KIMURA 1970),  $v_{gam}$  = hypothetical gametic multilocus diversity (GREGORIUS 1978),  $\delta_i$  = genetic differentiation and  $H_o$  = observed level of heterozygosity. The pairwise genetic distance, a measure of differentiation among populations, was calculated according to GREGORIUS (1974). Differences between frequencies of genetic types were tested statistically by using the  $\chi^2$ -test and

Table 1. Investigated provenances from the International Beech Provenance trial

| Prov. nr. | Country | Name            | Longitude | Latitude | Elevation (m) |
|-----------|---------|-----------------|-----------|----------|---------------|
| 9091      | GR      | Chalkidiki      | *         | *        | *             |
| 9101      | BG      | Maglij          | 25° 21'   | 42° 38'  | 1100          |
| 9104      | BG      | Buynovtzi       | 25° 53'   | 42° 56'  | 800           |
| 9124      | I       | Nave            | 14° 58'   | 37° 48'  | 1600          |
| 9170      | NL      | Aarnink         | 6° 44'    | 51° 56'  | 45            |
| 9182      | D       | Urach           | 9° 27'    | 48° 28'  | 760           |
| 9184      | DK      | Grasten, F.413  | 9° 35'    | 54° 55'  | 45            |
| 9187      | S       | Gullmarsberg    | 11° 39'   | 58° 22'  | 25            |
| 9189      | SLO     | Postojna Javor  | 14° 21'   | 45° 44'  | 1040          |
| 9193      | GB      | BE 95 (4010)    | 1° 9'     | 50° 55'  | 50            |
| 9209      | D       | Graf von W.     | 8° 47'    | 51° 31'  | 375           |
| 9228      | RO      | Bihor-Izbuc     | 22° 09'   | 46° 36'  | 640           |
| 9229      | RO      | Maramures-Baia  | 24° 00'   | 47° 33'  | 800           |
| 9243      | F       | 19-Pyreness Or. | 2° 19'    | 42° 55'  | 670           |
| 9245      | D       | Ebrach          | 10° 30'   | 49° 51'  | 406           |
| LOH       | D       | Lohmen          | 14° 04'   | 49° 58'  | 290           |

\* no information provided

**Table 2.** Enzyme systems assayed, scored loci and separation method.

| Enzyme system (abbrev.), EC nomenclature no. | Investigated gene loci                 | Separation system employed |
|--|--|----------------------------|
| Aconitase (ACO), 4.2.1.1                     | <i>Aco-A</i> , <i>-B</i>               | TRIS-Citrate pH = 7.5      |
| Aspartate aminotransferase (AAT), 2.6.1.1    | <i>Aat-B</i>                           | Ashton                     |
| Leucinaminopeptidase (LAP), 3.4.11.1         | <i>Lap-A</i>                           | Ashton                     |
| Isocitrate dehydrogenase (IDH), 1.1.1.42     | <i>Idh-A</i>                           | TRIS-Citrate pH = 7.5      |
| Malate dehydrogenase (MDH), 1.1.1.37         | <i>Mdh-A</i> , <i>-B</i> , <i>-C</i>   | TRIS-Citrate pH = 7.0      |
| 6-Phosphogluconatedehydr. (6PGDH), 1.1.1.44  | <i>6Pgdh-A</i> , <i>-B</i> , <i>-C</i> | TRIS-Citrate pH = 7.5      |
| Menadione reductase (MNR), 1.6.99.2          | <i>Mnr-A</i>                           | Poulik                     |
| Phosphoglucose isomerase (PGI), 5.3.1.9      | <i>Pgi-B</i>                           | Poulik                     |
| Phosphoglucomutase (PGM), 2.7.5.1            | <i>Pgm-A</i>                           | Poulik                     |
| Shikimate dehydrogenase (SKDH), 1.1.1.25     | <i>Skdh-A</i>                          | TRIS-Citrate pH = 7.0      |

the log likelihood ratio test (G-test) of homogeneity in contingency tables.

On the matrix of the calculated distances, a cluster analysis (average linkage procedure) was performed using the SAS- program.

## RESULTS

### Genetic differentiation

Allele frequencies for the 16 provenances and the 15 investigated gene loci are listed in Table 3. All gene loci are polymorphic in at least one of the populations. However, there are great differences between some populations in the allele frequencies as well as in the occurrence of rare alleles. For example, the provenance 9193 – BE95 from England differs significantly from all the other provenances at the gene locus *Aco-B*. With a frequency of 60 %, allele *B<sub>2</sub>* has significantly higher values than in all the other investigated provenances. At this gene locus the range of allele frequencies is unexpectedly high. The frequency of the allele *B<sub>2</sub>* ranges from 8 % for the provenance 9170 – Aarnink from the Netherlands to the above mentioned 60 % for the English provenance.

The English provenance stands out in other gene loci as well. The allele *Mnr-A<sub>2</sub>* in this provenance reaches a frequency of only 78.7 % whereas all of the other provenances have frequencies of *Mnr-A<sub>2</sub>* greater than 90 %. Further gene loci where the English provenance stands out are *Mdh-C* (*C<sub>1</sub>* with 45 % has the highest frequency), *6-Pgdh-B* (*B<sub>1</sub>* with 47 % also has the highest value) and *Aat-B*, where the allele *B<sub>2</sub>* has a frequency of 65.7 %, which is only comparable with the provenance 9228 – Bihor from the Romanian West Carpathians (called Apuseni Mountains).

The provenance 9228 – Bihor also has several other distinctive features: At the gene locus *Aat-B* the variant *B<sub>2</sub>* is most frequent, as for the English provenance

mentioned above. At the gene locus *Lap-A* a clear minor-polymorphism can be observed, with the allele *Lap-A<sub>2</sub>* having a frequency of 73 % whereas all other provenances investigated have two alleles of equal frequency. The provenance 9228 is the only provenance which has 4 alleles at the *Mnr-A* gene locus, while at the same time it is the only provenance showing no variation at the *Aco-A* and *Pgi-B* loci.

The Romanian provenance 9229 – Maramures (Romanian East Carpathians called Carpatii Orientali) differs considerably from the provenance 9228 – Bihor in the frequency of various alleles at several gene loci, as well as in the occurrence of rare alleles. At the gene loci *Aco-A* and *Pgi-B* where the provenance 9228 – Bihor shows no variation, the provenance 9229 – Maramures has 3 alleles respectively. For *Mdh-C* the frequency of the allele *C<sub>1</sub>* is 8 % for provenance 9228 – Bihor and 28 % for the provenance 9229 – Maramures.

In respect to the occurrence of rare alleles it becomes apparent that this is the case for a number of provenances from the southern distribution range of beech. For example we found the following rare alleles:

*Mnr-A<sub>1</sub>* only in the provenances:

|                   |          |
|-------------------|----------|
| 9091 – Chalkidiki | Greece   |
| 9104 – Buynovtzi  | Bulgaria |
| 9124 – Nave       | Italy    |
| 9228 – Bihor      | Romania  |
| 9229 – Maramures  | Romania  |

*Mdh-A<sub>2</sub>* only in the provenances:

|                       |          |
|-----------------------|----------|
| 9091 – Chalkidiki     | Greece   |
| 9101 – Maglij         | Bulgaria |
| 9104 – Buynovtzi      | Bulgaria |
| 9189 – Postojna Javor | Slovenia |

*Pgi-B<sub>1</sub>* only in the provenances:

|                   |          |
|-------------------|----------|
| 9091 – Chalkidiki | Greece   |
| 9101 – Maglij     | Bulgaria |
| 9104 – Buynovtzi  | Bulgaria |
| 9124 – Nave       | Italy    |

Table 3. Allele frequencies in 16 provenances included in the beech provenance trial.

| Locus           | Allele                | Provenance / country |         |         |        |         |        |         |        |
|-----------------|-----------------------|----------------------|---------|---------|--------|---------|--------|---------|--------|
|                 |                       | 9091 GR              | 9101 BG | 9104 BG | 9124 I | 9170 NL | 9182 D | 9184 DK | 9187 S |
| <i>Aco-A</i>    | <i>A</i> <sub>1</sub> | -                    | -       | -       | -      | -       | -      | -       | -      |
|                 | <i>A</i> <sub>2</sub> | 0.933                | 0.901   | 0.863   | 0.870  | 0.890   | 0.993  | 0.993   | 0.983  |
|                 | <i>A</i> <sub>3</sub> | 0.067                | 0.099   | 0.137   | 0.130  | 0.110   | 0.007  | 0.007   | 0.017  |
| <i>Aco-B</i>    | <i>B</i> <sub>2</sub> | 0.440                | 0.266   | 0.310   | 0.457  | 0.082   | 0.167  | 0.120   | 0.090  |
|                 | <i>B</i> <sub>3</sub> | 0.560                | 0.655   | 0.667   | 0.543  | 0.915   | 0.824  | 0.880   | 0.910  |
|                 | <i>B</i> <sub>4</sub> | -                    | 0.079   | 0.023   | -      | 0.003   | 0.010  | -       | -      |
| <i>Aat-B</i>    | <i>B</i> <sub>2</sub> | 0.110                | 0.161   | 0.263   | 0.340  | 0.401   | 0.291  | 0.103   | 0.450  |
|                 | <i>B</i> <sub>3</sub> | 0.857                | 0.839   | 0.737   | 0.660  | 0.599   | 0.709  | 0.897   | 0.550  |
|                 | <i>B</i> <sub>4</sub> | 0.033                | -       | -       | -      | -       | -      | -       | -      |
| <i>Idh-A</i>    | <i>A</i> <sub>2</sub> | 0.140                | 0.184   | 0.177   | 0.317  | 0.240   | 0.232  | 0.117   | 0.123  |
|                 | <i>A</i> <sub>3</sub> | 0.860                | 0.803   | 0.820   | 0.646  | 0.760   | 0.765  | 0.853   | 0.877  |
|                 | <i>A</i> <sub>4</sub> | -                    | 0.003   | 0.003   | 0.037  | -       | 0.003  | 0.030   | -      |
| <i>Lap-A</i>    | <i>A</i> <sub>1</sub> | 0.020                | 0.020   | 0.023   | -      | 0.010   | 0.070  | -       | -      |
|                 | <i>A</i> <sub>2</sub> | 0.434                | 0.530   | 0.477   | 0.437  | 0.185   | 0.304  | 0.516   | 0.437  |
|                 | <i>A</i> <sub>3</sub> | 0.393                | 0.378   | 0.363   | 0.436  | 0.521   | 0.399  | 0.297   | 0.400  |
|                 | <i>A</i> <sub>4</sub> | 0.153                | 0.072   | 0.137   | 0.127  | 0.284   | 0.291  | 0.187   | 0.163  |
| <i>Mnr-A</i>    | <i>A</i> <sub>1</sub> | 0.013                | 0.013   | 0.030   | 0.023  | -       | -      | -       | -      |
|                 | <i>A</i> <sub>2</sub> | 0.974                | 0.931   | 0.903   | 0.977  | 0.983   | 0.928  | 0.937   | 0.970  |
|                 | <i>A</i> <sub>3</sub> | -                    | -       | -       | -      | 0.003   | 0.003  | -       | -      |
|                 | <i>A</i> <sub>4</sub> | 0.013                | 0.056   | 0.067   | -      | 0.014   | 0.069  | 0.063   | 0.030  |
| <i>Mdh-A</i>    | <i>A</i> <sub>1</sub> | -                    | 0.003   | -       | -      | -       | -      | -       | -      |
|                 | <i>A</i> <sub>2</sub> | 0.043                | 0.030   | 0.063   | -      | -       | -      | -       | -      |
|                 | <i>A</i> <sub>3</sub> | 0.957                | 0.967   | 0.937   | 1.000  | 1.000   | 1.000  | 1.000   | 1.000  |
| <i>Mdh-B</i>    | <i>B</i> <sub>1</sub> | 0.037                | 0.049   | 0.050   | 0.043  | 0.024   | 0.013  | 0.167   | 0.087  |
|                 | <i>B</i> <sub>2</sub> | -                    | -       | 0.010   | -      | 0.031   | 0.029  | 0.003   | -      |
|                 | <i>B</i> <sub>3</sub> | 0.933                | 0.826   | 0.827   | 0.957  | 0.921   | 0.905  | 0.807   | 0.876  |
|                 | <i>B</i> <sub>4</sub> | 0.027                | 0.105   | 0.113   | -      | 0.024   | 0.052  | 0.023   | 0.037  |
|                 | <i>B</i> <sub>5</sub> | -                    | 0.020   | -       | -      | -       | -      | -       | -      |
| <i>Mdh-C</i>    | <i>C</i> <sub>1</sub> | 0.037                | 0.306   | 0.113   | -      | 0.377   | 0.363  | 0.373   | 0.313  |
|                 | <i>C</i> <sub>2</sub> | 0.963                | 0.694   | 0.887   | 1.000  | 0.623   | 0.637  | 0.627   | 0.687  |
| <i>Pgi-B</i>    | <i>B</i> <sub>1</sub> | 0.063                | 0.010   | 0.093   | 0.003  | -       | -      | -       | -      |
|                 | <i>B</i> <sub>2</sub> | 0.934                | 0.987   | 0.897   | 0.987  | 0.997   | 0.997  | 0.953   | 0.997  |
|                 | <i>B</i> <sub>3</sub> | 0.003                | 0.003   | 0.010   | 0.010  | 0.003   | 0.003  | 0.047   | 0.003  |
| <i>Pgm-A</i>    | <i>A</i> <sub>2</sub> | 0.133                | 0.115   | 0.210   | -      | 0.356   | 0.441  | 0.420   | 0.497  |
|                 | <i>A</i> <sub>3</sub> | 0.867                | 0.882   | 0.790   | 0.967  | 0.644   | 0.559  | 0.580   | 0.503  |
|                 | <i>A</i> <sub>4</sub> | -                    | 0.003   | -       | 0.033  | -       | -      | -       | -      |
| <i>6-Pgdh-A</i> | <i>A</i> <sub>2</sub> | 0.927                | 0.961   | 0.883   | 0.997  | 0.921   | 0.954  | 0.940   | 0.821  |
|                 | <i>A</i> <sub>3</sub> | -                    | 0.010   | 0.050   | -      | -       | -      | -       | -      |
|                 | <i>A</i> <sub>4</sub> | 0.073                | 0.030   | 0.067   | 0.003  | 0.079   | 0.046  | 0.060   | 0.179  |
| <i>6-Pgdh-B</i> | <i>B</i> <sub>1</sub> | 0.050                | 0.049   | 0.057   | 0.037  | 0.038   | 0.154  | 0.107   | 0.323  |
|                 | <i>B</i> <sub>2</sub> | 0.950                | 0.951   | 0.943   | 0.963  | 0.962   | 0.846  | 0.893   | 0.677  |

Table 3. Allele frequencies in 16 provenances included in the beech provenance trial (continued).

| Locus           | Allele                | Provenance / country |         |        |         |         |        |        |       |
|-----------------|-----------------------|----------------------|---------|--------|---------|---------|--------|--------|-------|
|                 |                       | 9189 SLO             | 9193 GB | 9209 D | 9228 RO | 9229 RO | 9243 F | 9245 D | LOH D |
| <i>Aco-A</i>    | <i>A</i> <sub>1</sub> | 0.013                | -       | -      | -       | 0.003   | -      | -      | -     |
|                 | <i>A</i> <sub>2</sub> | 0.937                | 0.957   | 0.963  | 1.000   | 0.976   | 0.919  | 0.983  | 0.980 |
|                 | <i>A</i> <sub>3</sub> | 0.050                | 0.043   | 0.037  | -       | 0.020   | 0.081  | 0.017  | 0.020 |
| <i>Aco-B</i>    | <i>B</i> <sub>2</sub> | 0.173                | 0.600   | 0.220  | 0.087   | 0.243   | 0.174  | 0.190  | 0.169 |
|                 | <i>B</i> <sub>3</sub> | 0.827                | 0.397   | 0.770  | 0.890   | 0.747   | 0.813  | 0.807  | 0.831 |
|                 | <i>B</i> <sub>4</sub> | -                    | 0.003   | 0.010  | 0.023   | 0.010   | 0.013  | 0.003  | -     |
| <i>Aat-B</i>    | <i>B</i> <sub>2</sub> | 0.320                | 0.657   | 0.373  | 0.687   | 0.297   | 0.302  | 0.357  | 0.225 |
|                 | <i>B</i> <sub>3</sub> | 0.680                | 0.343   | 0.627  | 0.313   | 0.679   | 0.698  | 0.643  | 0.772 |
|                 | <i>B</i> <sub>4</sub> | -                    | -       | -      | -       | 0.024   | -      | -      | 0.003 |
| <i>Idh-A</i>    | <i>A</i> <sub>2</sub> | 0.263                | 0.123   | 0.320  | 0.083   | 0.291   | 0.117  | 0.243  | 0.174 |
|                 | <i>A</i> <sub>3</sub> | 0.730                | 0.874   | 0.677  | 0.917   | 0.706   | 0.873  | 0.754  | 0.826 |
|                 | <i>A</i> <sub>4</sub> | 0.007                | 0.003   | 0.003  | -       | 0.003   | 0.010  | 0.003  | -     |
| <i>Lap-A</i>    | <i>A</i> <sub>1</sub> | 0.027                | -       | 0.010  | 0.003   | 0.027   | 0.094  | 0.003  | 0.048 |
|                 | <i>A</i> <sub>2</sub> | 0.307                | 0.260   | 0.407  | 0.731   | 0.402   | 0.228  | 0.350  | 0.497 |
|                 | <i>A</i> <sub>3</sub> | 0.489                | 0.570   | 0.373  | 0.183   | 0.389   | 0.426  | 0.413  | 0.287 |
|                 | <i>A</i> <sub>4</sub> | 0.177                | 0.170   | 0.210  | 0.083   | 0.182   | 0.252  | 0.207  | 0.162 |
| <i>Mnr-A</i>    | <i>A</i> <sub>1</sub> | -                    | -       | -      | 0.010   | 0.027   | -      | -      | 0.014 |
|                 | <i>A</i> <sub>2</sub> | 0.910                | 0.787   | 0.993  | 0.963   | 0.905   | 0.970  | 0.927  | 0.907 |
|                 | <i>A</i> <sub>3</sub> | 0.053                | -       | -      | 0.010   | 0.007   | -      | -      | 0.003 |
|                 | <i>A</i> <sub>4</sub> | 0.037                | 0.213   | 0.007  | 0.017   | 0.061   | 0.030  | 0.073  | 0.076 |
| <i>Mdh-A</i>    | <i>A</i> <sub>1</sub> | -                    | -       | -      | -       | -       | -      | -      | -     |
|                 | <i>A</i> <sub>2</sub> | 0.007                | -       | -      | -       | -       | -      | -      | -     |
|                 | <i>A</i> <sub>3</sub> | 0.993                | 1.00    | 1.000  | 1.000   | 1.000   | 1.000  | 1.000  | 1.000 |
| <i>Mdh-B</i>    | <i>B</i> <sub>1</sub> | 0.007                | 0.013   | 0.010  | 0.067   | 0.092   | 0.117  | 0.073  | 0.211 |
|                 | <i>B</i> <sub>2</sub> | 0.007                | 0.007   | 0.003  | 0.003   | -       | 0.017  | 0.013  | -     |
|                 | <i>B</i> <sub>3</sub> | 0.913                | 0.877   | 0.817  | 0.833   | 0.824   | 0.809  | 0.817  | 0.747 |
|                 | <i>B</i> <sub>4</sub> | 0.073                | 0.103   | 0.170  | 0.097   | 0.084   | 0.057  | 0.097  | 0.042 |
|                 | <i>B</i> <sub>5</sub> | -                    | -       | -      | -       | -       | -      | -      | -     |
| <i>Mdh-C</i>    | <i>C</i> <sub>1</sub> | 0.333                | 0.450   | 0.270  | 0.093   | 0.284   | 0.376  | 0.237  | 0.233 |
|                 | <i>C</i> <sub>2</sub> | 0.667                | 0.550   | 0.723  | 0.907   | 0.716   | 0.624  | 0.763  | 0.767 |
| <i>Pgi-B</i>    | <i>B</i> <sub>1</sub> | -                    | -       | -      | -       | 0.003   | -      | -      | -     |
|                 | <i>B</i> <sub>2</sub> | 0.987                | 0.997   | 0.987  | 1.000   | 0.994   | 0.990  | 0.953  | 0.989 |
|                 | <i>B</i> <sub>3</sub> | 0.013                | 0.003   | 0.013  | -       | 0.003   | 0.010  | 0.047  | 0.011 |
| <i>Pgm-A</i>    | <i>A</i> <sub>2</sub> | 0.310                | 0.276   | 0.430  | 0.247   | 0.291   | 0.107  | 0.307  | 0.326 |
|                 | <i>A</i> <sub>3</sub> | 0.690                | 0.727   | 0.570  | 0.753   | 0.709   | 0.893  | 0.693  | 0.674 |
|                 | <i>A</i> <sub>4</sub> | -                    | -       | -      | -       | -       | -      | -      | -     |
| <i>6-Pgdh-A</i> | <i>A</i> <sub>2</sub> | 0.967                | 0.950   | 0.770  | 0.727   | 0.855   | 0.883  | 0.887  | 0.913 |
|                 | <i>A</i> <sub>3</sub> | -                    | -       | -      | -       | 0.003   | -      | -      | -     |
|                 | <i>A</i> <sub>4</sub> | 0.033                | 0.050   | 0.230  | 0.273   | 0.112   | 0.117  | 0.113  | 0.087 |
| <i>6-Pgdh-B</i> | <i>B</i> <sub>1</sub> | 0.120                | 0.470   | 0.160  | 0.043   | 0.125   | 0.044  | 0.100  | 0.031 |
|                 | <i>B</i> <sub>2</sub> | 0.880                | 0.530   | 0.840  | 0.957   | 0.875   | 0.965  | 0.900  | 0.969 |

Table 3. Allele frequencies in 16 provenances included in the beech provenance trial (continued).

| Locus           | Allele                | Provenance / country |         |         |         |         |        |         |        |
|-----------------|-----------------------|----------------------|---------|---------|---------|---------|--------|---------|--------|
|                 |                       | 9091 GR              | 9101 BG | 9104 BG | 9124 I  | 9170 NL | 9182 D | 9184 DK | 9187 S |
| <i>6-Pgdh-C</i> | <i>C</i> <sub>1</sub> | 0.806                | 0.773   | 0.940   | 0.920   | 0.504   | 0.820  | 0.787   | 0.847  |
|                 | <i>C</i> <sub>2</sub> | 0.007                | 0.007   | -       | 0.023   | 0.010   | 0.003  | -       | -      |
|                 | <i>C</i> <sub>3</sub> | 0.067                | 0.062   | 0.007   | 0.037   | 0.086   | 0.010  | -       | -      |
|                 | <i>C</i> <sub>4</sub> | 0.090                | 0.132   | 0.040   | 0.020   | 0.369   | 0.072  | 0.130   | 0.123  |
|                 | <i>C</i> <sub>5</sub> | 0.030                | 0.026   | 0.013   | -       | 0.031   | 0.095  | 0.083   | 0.030  |
| <i>Skdh-A</i>   | <i>A</i> <sub>1</sub> | -                    | -       | -       | -       | -       | -      | -       | 0.087  |
|                 | <i>A</i> <sub>3</sub> | 0.860                | 0.875   | 0.880   | 0.973   | 1.000   | 1.000  | 0.990   | 0.896  |
|                 | <i>A</i> <sub>4</sub> | 0.053                | 0.030   | 0.017   | -       | -       | -      | -       | -      |
|                 | <i>A</i> <sub>5</sub> | 0.087                | 0.076   | 0.103   | 0.027   | -       | -      | 0.010   | 0.017  |
|                 | <i>A</i> <sub>6</sub> | -                    | 0.002   | -       | -       | -       | -      | -       | -      |
|                 |                       |                      |         |         |         |         |        |         |        |
| Locus           | Allele                | 9189 SLO             | 9193 GB | 9209 GB | 9228 RO | 9229 RO | 9243 F | 9245 D  | LOH D  |
| <i>6-Pgdh-C</i> | <i>C</i> <sub>1</sub> | 0.720                | 0.840   | 0.830   | 0.947   | 0.926   | 0.815  | 0.743   | 0.824  |
|                 | <i>C</i> <sub>2</sub> | 0.007                | 0.027   | 0.010   | -       | -       | -      | 0.010   | -      |
|                 | <i>C</i> <sub>3</sub> | 0.007                | 0.023   | 0.027   | 0.010   | 0.007   | 0.034  | 0.027   | 0.008  |
|                 | <i>C</i> <sub>4</sub> | 0.130                | 0.083   | 0.100   | 0.023   | 0.034   | 0.067  | 0.150   | 0.143  |
|                 | <i>C</i> <sub>5</sub> | 0.136                | 0.027   | 0.033   | 0.020   | 0.034   | 0.084  | 0.070   | 0.025  |
| <i>Skdh-A</i>   | <i>A</i> <sub>1</sub> | 0.027                | -       | -       | -       | -       | -      | -       | -      |
|                 | <i>A</i> <sub>3</sub> | 0.916                | 0.993   | 1.000   | 0.967   | 0.970   | 1.000  | 1.000   | 0.994  |
|                 | <i>A</i> <sub>4</sub> | 0.057                | -       | -       | -       | -       | -      | -       | -      |
|                 | <i>A</i> <sub>5</sub> | -                    | 0.007   | -       | 0.033   | 0.030   | -      | -       | 0.006  |

9229 – Maramures Romania  
*Pgm-A*<sub>4</sub> only in the provenances:  
 9101 – Maglij Bulgaria  
 9124 – Nave Italy

The Italian provenance is the only provenance without variation at the gene locus *Mdh-C*.

The gene pool distance between pairs of provenances ranges from 4.4 % (provenance 9229 – Maramures to provenance 9245 – Ebrach) to 17.4 % (provenance 9183 – BE (4010) to provenance 9124 – Nave). The English provenance 9183 has very high distance values to all other provenances, all of which are greater than 13 %. Distance values greater than 10 % are considered as being very high. All distance values for the Romanian provenance 9228 – Bihor are also greater than 10 %, which supports the uniqueness of this provenance. With two exceptions this is also the case for the Italian provenance 9124 – Nave.

The uniqueness of the English provenance in respect to its genetic structure is clearly visible in the dendrogram from the cluster analysis (Fig. 2). The same is true for the Romanian provenance 9228 – Bihor, which clearly distinguishes itself from all other provenances. The provenances from southeastern and southern Europe (Greece, Bulgaria and Italy) form their own

distinct group. Within the group, the three stands from the southern Balkan region, which are very similar genetically, cluster together first (Bulgaria, Greece), before the provenance from Italy.

All other provenances form one large group, where in contrast to our expectations, the second Romanian provenance 9229 – Maramures and the Slovenian provenance 9189 – Postojna Javor are found. With its numerous rare alleles we had expected that the Romanian provenance Maramures would cluster with the southern group. Within this large, second group the provenances from the Netherlands, Sweden and the Pyrenees differentiate somewhat from the other provenances.

#### Genetic variation within provenances

Large differences are also found in the genetic variation within provenances. The number of identified alleles vary from 33 (9124 – Nave and 9187 – Gullmarsberg) to 46 (9101 – Maglij). The highest values were found in the southern and southeastern provenances with the exception of the population 9124 – Nave from South Italy.

The genetic diversity  $n_e$  ranges from 1.226 (9124–

Table 4. Genetic distances between pairs for the tested provenances from the provenances trial

|      | 9104  | 9101  | 9189  | 9228  | 9229  | 9124  | 9209  | 9245  | 9182  | LOH   | 9184  | 9170  | 9143  | 9187  | 9183  |
|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 9091 | 0.070 | 0.069 | 0.120 | 0.147 | 0.112 | 0.081 | 0.134 | 0.115 | 0.130 | 0.104 | 0.118 | 0.148 | 0.105 | 0.145 | 0.168 |
| 9104 | -     | 0.068 | 0.110 | 0.118 | 0.075 | 0.096 | 0.115 | 0.093 | 0.116 | 0.091 | 0.120 | 0.145 | 0.101 | 0.137 | 0.168 |
| 9189 |       | -     | 0.091 | 0.144 | 0.085 | 0.109 | 0.112 | 0.092 | 0.105 | 0.080 | 0.095 | 0.127 | 0.084 | 0.132 | 0.164 |
| 9228 |       |       | -     | 0.149 | 0.060 | 0.124 | 0.076 | 0.049 | 0.049 | 0.078 | 0.086 | 0.078 | 0.077 | 0.097 | 0.133 |
| 9229 |       |       |       | -     | 0.116 | 0.150 | 0.123 | 0.118 | 0.145 | 0.119 | 0.135 | 0.155 | 0.129 | 0.116 | 0.168 |
| 9124 |       |       |       |       | -     | 0.102 | 0.053 | 0.044 | 0.060 | 0.060 | 0.083 | 0.108 | 0.075 | 0.091 | 0.138 |
| 9209 |       |       |       |       |       | -     | 0.126 | 0.121 | 0.137 | 0.130 | 0.162 | 0.145 | 0.117 | 0.165 | 0.174 |
| 9245 |       |       |       |       |       |       | -     | 0.054 | 0.060 | 0.084 | 0.093 | 0.099 | 0.093 | 0.075 | 0.147 |
| 9182 |       |       |       |       |       |       |       | -     | 0.055 | 0.053 | 0.074 | 0.082 | 0.067 | 0.089 | 0.138 |
| 9000 |       |       |       |       |       |       |       |       | -     | 0.073 | 0.063 | 0.077 | 0.069 | 0.081 | 0.131 |
| 9184 |       |       |       |       |       |       |       |       |       | -     | 0.054 | 0.105 | 0.082 | 0.103 | 0.165 |
| 9170 |       |       |       |       |       |       |       |       |       |       | -     | 0.109 | 0.085 | 0.087 | 0.162 |
| 9243 |       |       |       |       |       |       |       |       |       |       |       | -     | 0.086 | 0.110 | 0.156 |
| 9187 |       |       |       |       |       |       |       |       |       |       |       |       | -     | 0.106 | 0.141 |
| 9193 |       |       |       |       |       |       |       |       |       |       |       |       |       | -     | 0.131 |

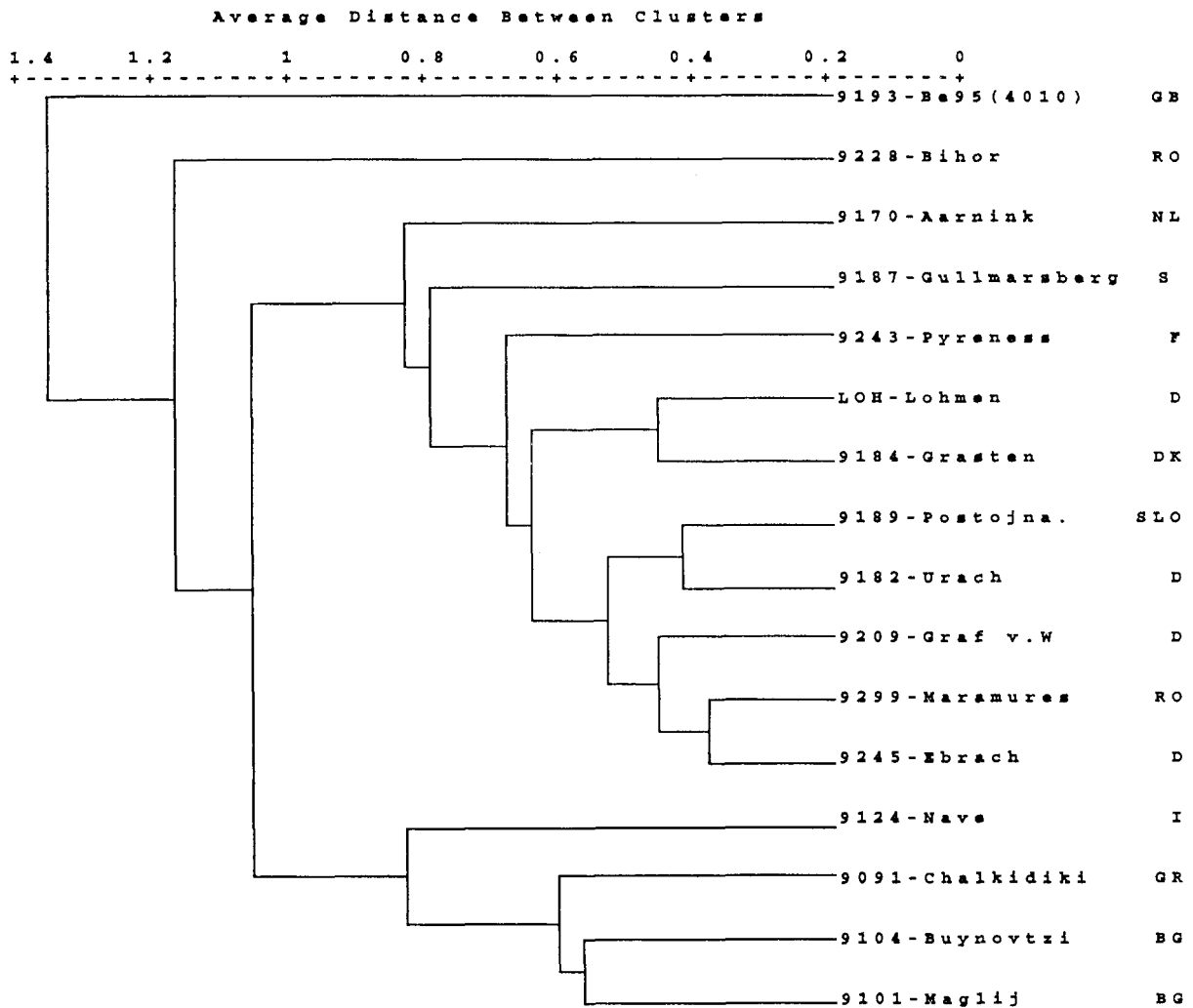


Figure 2. Dendrogram from cluster analysis based on GREGORIUS genetic distance measure between 16 beech provenances included in the International Beech Provenance Trial.

Table 5. Interpopulational variation in 16 beech provenances included in the provenance trial.

| Number of provenance | Country | Provenance       | Number of alleles | Diversity |           | Heterozygosity observed (%) | Differentiation $\delta_i$ (%) |
|----------------------|---------|------------------|-------------------|-----------|-----------|-----------------------------|--------------------------------|
|                      |         |                  |                   | $n_e$     | $v_{gam}$ |                             |                                |
| 9091                 | GR      | Chalkidiki       | 40                | 1.277     | 58.6      | 19.5                        | 21.8                           |
| 9101                 | BG      | Maglij           | 46                | 1.336     | 112.3     | 23.6                        | 25.2                           |
| 9104                 | BG      | Buynovtzi        | 42                | 1.360     | 138.2     | 24.6                        | 26.6                           |
| 9124                 | I       | Nave             | 33                | 1.226     | 38.4      | 16.9                        | 18.5                           |
| 9170                 | NL      | Aarnik           | 37                | 1.334     | 158.6     | 23.5                        | 25.2                           |
| 9182                 | D       | Urach            | 38                | 1.325     | 127.1     | 24.8                        | 24.6                           |
| 9184                 | DK      | Grasten, F.413   | 34                | 1.298     | 80.9      | 20.5                        | 23.1                           |
| 9187                 | S       | Gullmarsberg     | 33                | 1.357     | 172.5     | 26.3                        | 26.4                           |
| 9189                 | SLO     | Postojna Javor   | 41                | 1.363     | 176.3     | 24.8                        | 26.8                           |
| 9193                 | GB      | BE 95 (4010)     | 37                | 1.384     | 233.7     | 28.2                        | 27.9                           |
| 9209                 | D       | Graf von W.      | 37                | 1.382     | 238.3     | 27.2                        | 27.8                           |
| 9228                 | R       | Bihor, Izbuc     | 36                | 1.227     | 29.1      | 19.1                        | 18.5                           |
| 9229                 | RO      | Maramures - Baia | 42                | 1.349     | 154.4     | 25.3                        | 26.0                           |
| 9243                 | F       | 19-Pyreness Or.  | 36                | 1.302     | 94.8      | 23.2                        | 23.4                           |
| 9245                 | D       | Ebrach           | 37                | 1.362     | 179.9     | 26.3                        | 26.6                           |
| LOH                  | D       | Lohmen           | 37                | 1.310     | 95.4      | 23.5                        | 23.7                           |

Nave) to 1.384 (9193 – BE95 (4010) the hypothetical gametic multilocus diversity  $v_{gam}$  from 29.1 (9228 – Bihor) to 238.3 (9209 – Graf v.W.) (Table 5).

The provenances which show the least variation are: 9124 – Nave, Italy and 9228 – Bihor, Romania. Thus the hypothetical gametic multilocus-diversity  $v_{gam}$  for the Romanian provenance is eight times smaller than for the two provenances with the highest diversity: 9209 – Graf v.W. from Northern Germany and 9193 – BE95 (4010) from England. The variation in the provenance 9124 Nave is only slightly higher than in the provenance 9228 – Bihor. Other provenances which show a comparatively low genetic diversity are: 9091 – Chalkidiki, Greece, 9184 – Grasten, Denmark. The genetic variation of the second Romanian provenance 9229 – Maramures, is much higher than the variation in the provenance 9228 – Bihor (e.g.  $v_{gam}$  five times higher) and lies in the middle in comparison with the other provenances.

The differences in observed heterozygosity values ( $H_o$ ) for the investigated provenances are quite large; they vary from 16.9 % to 28.2 %. Low heterozygosity values were found for the provenances 9124 – Nave, 9228 – Bihor and 9091 – Chalkidiki which also had the lowest diversity. The English provenance 9193–BE95 (4010) also has the highest heterozygosity value.

The value for genetic differentiation ( $\delta_i$ ), which due to the method of computation can be expected to be similar to the expected heterozygosity, lies between 18.5 (9124 – Nave and 9228 – Bihor) and 27.9 (9193 – BE95 (4010) and 9290 – Graf v.W.). A comparison between the observed heterozygosity values ( $H_o$ ) with the differentiation values ( $\delta_i$ ) showed no significant or

deficitary number of heterozygotes in the sampled material.

In comparison to the other provenances, the provenance Ebrach has high diversity. However, the diversity found in the provenance trial material is still less than what we found in the mature stand Ebrach and the respective natural regeneration, seed and seedlings. For these populations, under consideration of the same gene loci, we found  $v_{gam}$ -values between 220 and 320 and  $n_e$ -values between 1.41 and 1.44. The observed heterozygosity was between 28 % and 30 % (KONNERT, unpublished).

## DISCUSSION

Due to financial and time limits it was clear that only a selected number of provenances included in the provenance trial could be investigated isoenzymatically. Numerous investigations on the genetic variation of beech (a list of publications on the genetic variation of beech can be obtained from Prof. L. Paule, Technical University, Zvolen, Slovakia) have shown that there are only slight differences between beech populations in Central Europe (see also a summary in MÜLLER-STARCK *et al.* 1992, PAULE 1995 and KONNERT *et al.* 2000). The investigations have also shown however, that the beech populations from the southern regions of its natural distribution range show a high degree of differentiation (eg. COMPS *et al.* 1991a, 1991b, HAZLER *et al.* 1997, GÖMÖRY *et al.* 1999, COMPS *et al.* 2001). Thus it was our goal to look primarily at provenances from the edges of the natural distribution range in addition to a few provenances from Central Europe. We



wanted to see if we could find representative regional-specific information among the material included in the provenance trial.

The results have shown that this is generally the case. The genetic structure of the three investigated German provenances are very similar to other German provenances as reported on by others (e.g. KONNERT 1995, LÖCHELT & FRANKE 1995, TRÖBER 1995, MÜLLER-STARCK, R. 1996, TUROK 1996, KONNERT *et al.* 2000). The same is true for the Danish and Dutch provenances we looked at, at least for those gene loci where a comparison with earlier studies was possible (LARSEN 1996). The Romanian provenance 9229 from the Romanian East Carpathians is very similar to other beech populations from these region (COMPS *et al.* 1990) and to populations from the bordering, Ukrainian Carpathians (VYŠNÝ *et al.* 1995). The genetic structure of the Greek provenance and the two provenances from Bulgaria from the southern Balkan region correspond to the structures found by GÖMÖRY *et al.* (1999) in a investigation of 57 beech provenances in the same region. The Slovenian provenance could only be compared with adjacent provenances from Croatia (HAZLER-PILEPIC *et al.* 1999), however, here we also found comparable results. For all of these provenances one can assume that the material included in the provenance trial is representative of the respective region where the seed was collected.

There are some provenances however, where the material included in the provenance trial does not appear to be representative of the region and one must be careful in interpreting the results of the provenance trial. In such a case provenance trial results can only be interpreted for the stand where the seed was collected from and not refer to the entire provenance region. In our study, this was the case for the English provenance 9193 – BE 95 (4010) where we obtained very unique results. Why we obtained such specific results in the genetic structure of the plants included in the provenance trial needs to be clarified. It would be meaningful to investigate the genetic structure of other beech stands in the region of the above named stand to see if the genetic structure is representative or not. It is known that beech has been widely introduced and naturalized over most of Britain (SAMUEL *et al.* 1993). If the introduced population originated from a sufficient number of parents this provenance should show the same characteristics as other European beech populations. Since this was not the case, the specific structure could possibly be explained by a "founder effect". If the sampled provenance is descendant from only a few parent trees, then this might have led to a bottleneck and consequently a fixation of various alleles in comparison with the other populations.

The specific structure of the Romanian provenance 9228 – Bihor seems to be a result of problems encountered during seed collection or during the nursery phase. The Romanian provenance 9229 – Maramures is completely different from the provenance 9228 – Bihor. The genetic variation within the provenance Maramures is also higher and lies in the middle, in comparison with the other investigated provenances; whereas the provenance 9228 – Bihor shows very low variation. The provenance 9228 – Bihor, does not appear to be representative of other beech provenances from the Carpathians on the basis of its genetic structure and variation.

At the present time it is also not possible to determine the cause of the low variation found in the south Italian provenance 9124 – Nave (Sicily). Possible causes for the low variation might be the result of seed collection (low number of trees harvested), insufficient flowering or pollination or whether the seed stand simply had a low degree of variation to begin with. The population Nave is situated at the southern limit of the natural distribution range of beech. According to COMPS *et al.* (2001) populations from the southeastern part of the distribution range of beech have a high allelic richness and a comparatively low genetic diversity. For both of the Bulgarian, the Greek, Slovenian and one of the Romanian provenances the number of alleles is in fact higher than in other populations. Nave however, not only has low diversity and heterozygosity, but also a very low allelic richness. LEONARDI & MENOZZI (1994) have also found high number of alleles in a Sicilian beech populations in comparison with other Italian populations. This is also an indication that the population 9124–Nave included in the field trial is not characteristic for the provenance region.

On the other side it was already mentioned under „Methods" that the number of sampled trees per provenance was not known, even for the initiators of the provenance trial. This is often the case in provenance studies where neither the number of trees sampled, nor the location within the stand is known. Thus we scored the allelic richness values with caution.

For the Ebrach population the variation in the field trial is lower than in the mature trees and the respective natural regeneration. This can be explained by the fact that seeds for the provenance trial are sampled only from a part of the mature population during one year. The natural regeneration on the other hand, contains the genetic information gathered over many years from many parent trees. It is known that the effective pollen can travel over hundreds of meters and that the number of pollen donors differ from tree to tree and year to year. This clearly shows that the material included in the provenance trial can only represent a very limited amount of the genetic information found in such stands.

In this context more efforts need to be undertaken that such information is not constricted further by incorrect seed collection or unnecessary selection procedures in the nursery phase.

For all provenances with a low degree of variation it is recommended that the original seed collecting stands be investigated by means of gene markers so that false conclusions are not drawn from the results of the field trial. It remains to be seen and it would be very interesting to find out if the differing genetic structure and in some cases the low degree of genetic variation at some gene loci within certain provenances, will be expressed phenotypically in the field trial.

There is no doubt that field provenance trials are of great importance, since only field trials can give information on the phenotypical response of a provenance under differing environmental conditions. In all studies so far, no connection between the phenotypic characteristics of a provenance such as growth, stem quality etc. and the genetic structure at specific gene loci has been established for beech (see: eg. HUSSENDÖRFER *et al.* 1996, TUROK 1996) or other species (eg. v. WÜHLISCH & KRUSCHE 1991). It is undisputed that the genetic variation is the basis for adaptability of a population and that this ability of a population to adapt, needs to be tested in field provenance trials. However, as was shown in our investigations on beech, the material included in our field trials often contains only a limited portion of the „local“ genetic information of a provenance region. Similar results have been found for European silver fir (HUSSENDÖRFER & KONNERT 1997). From the results of such field trials recommendations on specific provenances are sometimes given which are based on material representing only a limited amount of the regional genetic diversity. If the material is not representative, one can obtain contradictory results when the trials are repeated, making it difficult to interpret the results.

Such was the case in an extensive South-German *Abies alba* provenance trial for which the seed was collected in 1982 and 1983 and which was outplanted on 11 test sites between 1986 and 1988 (WOLF *et al.* 1994, RUETZ & STIMM 1995, RUETZ *et al.* 1998). For one provenance (Zwiesel – Bavarian Forest), seed was collected from the same stand in 1982 and 1983. The results of the field trial showed that the same provenance from the earlier seed collection performed poorly whereas the plants from the 1983 collection performed much better. Genetic investigations carried out on the outplanted material showed large differences between the two seed collection years which were from the same seed stand (KONNERT unpublished). The reasons for the genetic difference probably lies in the poor pollination which took place in 1982. The seed collection from

1982, which was a poor seed year, had only 7 % filled seeds in contrast to the 1983 seed collection which had 54 % filled seeds (GAUDLITZ *et al.* 1985). For such provenance trials it is imperative to carry out seed collection only in good seed years and of course from a large number of trees.

In order to avoid such results it is recommended to use biochemical-genetic or molecular genetic methods to evaluate the genetic structure of the material to be tested in conjunction with the field trial to see if it is representative of the population to be investigated. For beech we have detailed knowledge of the genetic variation in the entire distribution range, so that we could carry out such investigations on material included in the provenance trials to see if the sampled material is representative of the respective region. We can furthermore determine the extent of the genetic variation within each provenance included in the trial. This chance should be utilized!

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