GENETIC DIVERSITY OF ORIENTAL BEECH (*FAGUS ORIENTALIS* LIPSKY) FORESTS OVER THE HYRCANIAN ZONE

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Received May 27, 2002; accepted December 30, 2002

ABSTRACT

Genetic variation of *Fagus orientalis* Lipsky was investigated in 14 populations of Hyrcanian forests in the North of Iran. Within populations, average for the proportion of polymorphic loci (95 % criterion), the number of alleles per locus, effective number of alleles, the mean expected and observed heterozygosities were 100, 3.3, 1.341, 0.191, 0.174, respectively. Overall, 30 rare alleles (frequency less than 5 %) were detected. The present study reveals significant allelic frequency differences between populations with a small absolute genetic differentiation with no pattern related to geographic distance. The genetic differentiation between populations measured by Wright's F-statistics does not deviate significantly from zero. A slight deficiency of heterozygotes as compared with Hardy-Weinberg expected proportion was found in the majority of populations.

Key word: isozyme, *Fagus orientalis*, genetic diversity, genetic differentiation

INTRODUCTION

Among the broad-leaved temperate forests on northern hemisphere, Hyrcanian forest types are very specific. These forests, totaling 1.5 million ha, are located on the southern coast of the Caspian Sea and on the northern slopes of the Alborz (also Elborz) mountain range in the northern part of Iran. The Hyrcanian forest ecosystem is considered to be one of the last remnants of natural temperate deciduous forests in the world. In contrast to European broad-leaved forests, the Hyrcanian forests apparently remained from the Tertiary period and are a relic ecosystem[1], although it has been influenced by the Pleistocene glaciations and human activities. Today, these unique forest ecosystems are important not only for conservation purposes such as biodiversity, adaptability to expected climate changes, and for combating desertification, but also for sustainable forest management. This unique area with rich fauna and flora could be used as a gene reserve for restoration of degraded ecosystems (SAGHEB-TALEBI 2000).

The watershed of the Alborz on the Caspian coast is characterized by a mesophilous forest vegetation, originating from the Tertiary, and are therefore very ancient. While not directly affected by glaciations during the Quaternary, beech populations in this area survived intense climate and geological changes resulting from the indirect influence of the ice ages (MOBAYEN & TREGUBOV 1970). The floristic composition of the beech belt vegetation resembles that of European forests, particularly the beechwoods of the Balkans. Particularly this vegetation zone exhibits affinities with the beechwoods of the Balkans. The lower zones, on the contrary, are much more specific and include subtropical elements.

Beech forests cover around 17.6 % of Hyrcanian forest surface and represent approx. 25 % of the standing stock of forest stands in Iran. Pure and mixed Oriental beech (*Fagus orientalis* Lipsky) forests make up the richest and the most productive, and the most important commercial forests in the Caspian zone of Iran.

Information about the genetics of Oriental beech is

[1)] Moreover, Paleobotanical research has proved that many of the species which had occurred in Europe before glaciations but are no longer there, still grow in the Hyrcanian region, such as chestnut-leaved oak (*Quercus castaneifolia*), Caspian elm (*Zelkova carpinifolia*), Caspian alder (*Alnus subcordata*), Persian ironwood (*Parrotia persica*) and Caspian honey locust (*Gleditsia caspica*).

scarce (BUSOV 1993, GÖMÖRY *et al.* 1998, 1999). On the other hand, the closely related European beech, with very similar life-history traits, has been intensively investigated. Both beech species are widespread, monoecious and wind pollinated. Like many other tree species (HAMRICK *et al.* 1993), European beech contains a high level of genetic variation at allozyme gene loci (MÜLLER-STARCK & ZIEHE 1991). The genetic structure of beech stands is influenced by selection and the mating system, in addition to gene flow and the genetic drift. These factors induce an inter- and intra-population genetic differentiation over space and time (MÜLLER-STARCK 1985, GREGORIUS *et el.* 1986, CUGUEN 1986, CUGUEN *et al.* 1988, COMPS *et al.* 1990). The intra-population components of genetic variation in European beech are quite high as compared to inter-population components (PAULE *et al.* 1995, LEONARDI & MENOZZI 1995, TRÖBER 1995, KONNERT 1995; HATTEMER *et al.* 1993, TUROK 1996).

Oriental beech is considered a climax species in most part of the Hyrcanian zone where it grows in many different environments. This environmental hetero-geneity favours genetic differentiation of beech-woods through selection and genetic isolation due to phenological differences (THIÉBAUT *et al.* 1982, FELBER & THIÉBAUT 1982, 1984, THIÉBAUT 1984, N'TSIBA 1984, BARRIÈRE *et al.* 1985, COMPS *et al.* 1987). Genetic variation is considered to be the most important determinant of the ability of forest tree populations to survive in temporally and spatially heterogeneous environmental conditions (MÜLLER-STARCK & ZIEHE 1991).

Despite its importance, genetic characterization of Oriental beech populations has been rarely carried out. Genetic investigation of European beech popula-tions employing isozyme markers started over 20 years ago (KIM 1980); since then, numerous studies have been done (for a review see MÜLLER-STARCK *et al.* 1992, PAULE & GÖMÖRY 1997). Isozyme analysis has also been used to assess the mating system of beech (MERZEAU *et al.* 1989), to prove the correlation between genetic diversity, heterozygosity and adaptability (MÜLLER-STARCK 1985), to study viability selection during development (KIM 1985), to correlate the allelic frequencies with geographical and/or climatic conditions of the population site (GÖMÖRY *et al.* 1992) and to distinguish among closely related species of beech (COMPS *et al.* 1991, GÖMÖRY *et al.* 1993).

The aim of the present study is to characterize the genetic variation of Oriental beech populations over the Hyrcanian zone by means of isozyme analysis. The results of this analysis should give preliminary information for the evaluation of the genetic resources of Oriental beech in Iran, and contributes to the identification of the genetic resources aimed for *in situ* gene conservation. High levels of genetic diversity and heterozygosity of populations are supposed to be associated with the survival capacity (HERTEL 1992) and adaptability, regardless of the specific allozyme present in the individuals (WILLS 1973).

MATERIAL AND METHODS

Population characteristics and sampling

The Hyrcanian beech forests are located on the northern slopes of Alborz mountains, within an altitudinal range of approx. 600 to 2000 m above sea level. They form a forest strip 600 km in length that is located in 3 provinces of Gilan, Mazandaran and Golestan. Along the northern slope of the Alborz mountains, 5 regions containing 14 beech populations, aged between 80 and 160 years, were investigated. The five regions were selected along the full East to West distribution of beech in the Hyrcanian zone. Within each region, three populations were sampled at different altitudes (the lower limit, the middle, and the upper limit of the beech distribution range) to cover almost the entire geographical range of Oriental Beech in Iran. (Table 1, Fig. 1). In each population, beech twigs with dormant buds were sampled from 50 non-adjacent individuals (to avoid the sampling of related trees) chosen at random over a 3–4 ha area in a homogeneous environment.

Electrophoresis

Enzymes were extracted (using 0.1 M Tris-HCl buffer pH 7) from dormant buds and cortical tissues of each

Figure 1. Distribution of investigated Oriental beech regions (shaded zone in the Caspian region represents approximately the natural range of Oriental beech).

Table 1. Geographical coordinates and characteristics of the investigated *Fagus orientalis* populations.

Region	Altitude (m)	Abbreviation	Latitude N	Longitude E	Slope aspect	Stand composition	Canopy (%)
Gorgan	2000	G-2000	36° 45'	54° 07'	N, NW	Beech 90 %	959090
	1400	G-1400	36° 41'	54° 05'	N, NW	Beech 90 %	
	600	G-600	36° 42'	54° 06'	N, NW	Beech 90 %	
Neka	1400	N-1400	36° 22'	53° 33'	N, NW	Beech 90 %	8090
	900	N-900	36° 29'	53° 27'	N, NW	Beech 90 %	
Sangdeh	1900	S-1900	36° 00'	53° 12'	N, NW	Beech 90 %	957065
	1400	S-1400	36° 03'	53° 14'	SW, W	Beech 70 %	
	900	S-900	36° 06'	53° 16'	N, NW	Beech 90 %	
Kheirud	2000	K-2000	36° 28'	51° 40'	N	Beech 90 %	909090
	1200	K-1200	36° 32'	51° 39'	SE	Beech 90 %	
	600	K-600	36° 35'	51° 33'	SE	Beech 90 %	
Asalem	1900	A-1900	37° 38'	48° 46'	N	Beech 90 %	809070
	1200	A-1200	37° 38'	48° 48'	NW	Beech 90 %	
	600	A-600	37° 41'	48° 48'	N	Beech 90 %	

individual, and were separated by means of starch gel electrophoresis. Protein separation and staining procedures were described by MERZEAU *et al.* (1989) and MÜLLER-STARCK & STARKE (1993). The enzyme systems and gene loci investigated are listed in Table 2.

Data analysis

In order to determine the extent of genetic variation within and between populations, measures of genetic multiplicity, diversity, and differentiation were computed based on genotype and allele frequencies. Differences of allelic frequencies among populations were tested using the probability test (RAYMOND & ROUSSET 1995a). Subsequently, a global test across loci was calculated using Fisher's method (ROUSSET & RAYMOND 1995). Expected Hardy-Wein-berg heterozygosity, effective number of alleles and total number of alleles were used to characterize the allelic diversity. Since the theoretical works of WRIGHT (1965), genotypic structures have often been analysed using F-statistics. F_{IT} is an estimation of total genotypic differentiation, and allelic diversity is partitioned into intra- (F_{IS}) and inter- (F_{ST}) population components. Estimates of the three F-statistics were made according to the method of WEIR & COCKERHAM (1984). Genetic distances among populations were estimated according to NEI (1978). Cluster analysis based on genetic distance matrix was performed using the UPGMA algorithm. To quantify the degree of differentiation among populations, the F-statistics (WEIR & COCKERHAM 1984) was used. BIOSYS-1 (SWOFFORD & SELENDER 1981) and GENEPOP v.3.1b (RAYMOND & ROUSSET 1995b) computer programs were employed for calculations.

RESULTS

Table 3 presents mean allelic frequencies in individual populations. Allelic frequency heterogeneity among populations was revealed in 14 of the surveyed loci. That means the frequencies of most loci are significantly different between the groups of trees sampled at different populations. Because of the modest differentiation and rare polymorphisms, small sizes of the tested classes were not enough to conclude a heterogeneity of allelic frequencies in *Mdh-C* and *Pgm-A*. Five loci out of the 16 found for 10 enzyme systems were monomorphic in 1–8 populations (*Skdh-A* in one population, *Idh-A* in two, *Pgi-B* in three, *Mdh-C* and *Got-B* in seven and *Pgi-A* in 8 populations). Except for loci *Px-A*, *Mdh-A* and *6pgd-A* that showed two frequent alleles in some populations, at each locus, one allele generally appeared more frequently than the others. Six loci (*Got-B, Idh-A, Mdh-C, Pgi-A, -B, Pgm-A*) generally showed a low degree of polymorphism and, although the number of alleles per locus in these systems was three or four, the frequency of one allele was usually high, with all other alleles rare or completely absent from some populations. On the other hand, loci like *Px-A, Px-B, Mdh-A, Mdh-B* and *6Pgd-A* showed quite high polymorphism in almost all populations. The locus *Pgi-B* showed a moderate variation in eastern and central Alborz, but complete fixation in Asalem. On the other hand, one allele was completely fixed at *Got-B* in most

Table 2. List of the enzyme systems and identified loci used.

Enzyme system	EC number	Locus	*N*	Observed alleles in eech locus and their relative mobilities	Quatemary structure
Peroxidase	1.11.1.7	*Px–A*	2344	A: 105, B: 100	Monomer
		Px–B	4433 4323	A'*: 13, A: 52, B: 39, C: 26	Monomer
Leucine aminopeptidase	3.4.11.1	*Lap–A*	5344	A: 106, B: 100, C: 97, D: 94	Monomer
		Lap–B		A: 102, B: 100, C: 98, D: 96	Monomer
Glutamate oxaloacetate transaminace	2.6.1.1	*Got–A*		A: 105, B: 100, C: 95, D:90	Dimer
		Got–B		A': 54, A: 36, B: 18, C: 02	Dimer
Menadion reductase	1.6.99.2	*Mnr–A*		A'*:137, A: 126, B'*: 113 B: 100, C: 74, D*: 63	Tetramer
Isocitrate dehydrogenase	1.1.1.42	*Idh–A*		A'*: 132, A: 116, B: 100, C: 84	Dimer
Malate dehydrogenase	1.1.1.37	*Mdh–A*		B: 130, C: 125, D*: 113, E: 101, F: 88	Dimer
		Mdh–B		A: 118, B*: 109, C: 100, D: 78, E*: 66	Dimer
		Mdh–C		A: 22, B: 18	Monomer
Phosphoglucose isomerase	5.3.1.9	*Pgi–A*		A: 106, B: 100, C: 94	Dimer
		Pgi–B		A': 126, A: 113, B: 100, C: 87, D: 74	Dimer
Phosphoglucomutase	2.7.5.	*Pgm–A*		A: 112, B: 100, C: 94, D*: 88	Monomer
Shikimate dehydrogenase	1.1.1.25	*Skdh–A*		A: 114, B: 100, C: 86, D: 72, E*: 58	Monomer
6-Phosphogluconate dehydrogenase	1.1.1.44	*6Pgdh–A*		A: 110, B: 100, C: 90, D: 80	Dimer

' – alleles; * – alleles were not observed in Iran, but for better comparison with other papers included here..

populations except in the Asalem region.

The values of allelic multiplicity and diversity (Table 4) indicated considerable variation within Iranian beech populations. A total of 55 allelic variants were found at 16 gene loci ranging from 41 in the Sangdeh region to 46 in Kheirood. The mean number of alleles per locus over all population was 3.4. Within populations, mean number of alleles per locus ranged between 2.0–2.7. The proportion of polymorphic loci ranged between 62.5 % in Asalem 600 to 93.75 % in Gorgan 1400, Gorgan 600 and Neka 1400. Genetic multiplicity thus appeared rather heterogenous.

The mean effective number of alleles varied from 1.01 to 1.39 and, except for Sangdeh 1400 (1.01), these values varied within a narrow range from 1.28 to 1.39. No specific longitudinal or altitudinal tendency was found.

Mean Hardy-Weinberg expected heterozygosities (H_e) over all investigated loci ranged from 0.183 (Sangdeh 900) to 0.248 (Neka 900). Significant differences between observed and expected heterozygosity appeared in Neka 900 (H_o–H_e = –0.047), indicating a heterozygosity deficit. However, it is zero in Sangdeh 900 (equilibrium) and +0.005 in Kheirood 2000 (slight heterozygote excess). The highest heterozygosity was observed in Kheirood (Fig. 2).

Among 16 loci in 14 populations, a general tendency was observed, that the expected heterozygosities were slightly higher (mean H_e = 0.191) than the observed heterozygosities (mean H_o = 0.174). In Figure 2, heterozygosities are surveyed as multilocus average for each of 14 populations. The surplus of the $H_e$against H_o is evident in further populations (10 from 14 populations). Mean heterozygosity ranged from 0.168 (Asalem 1900) to 0.226 (Kheirood 1200).

Table 5 shows the comparison of F-statistics (F_{IS}, F_{IT} and F_{ST}) at 16 loci and all regions. All multilocus estimates differ from 0, over the whole area as well as in most regions. Most populations are at equilibrium, or have a slight deficiency of heterozygotes. The generally positive values of F_{IS} and F_{IT} statistics confirm an overall slight deviation from the Hardy-Weinberg

Table 3. Allelic frequencies in individual *Fagus orientalis* populations and probability tests of heterogeneity of allelic freuqencies.

Loci		Population / Altitude [m]														*P*–value
		Gorgan			Neka		Sangdeh			Kheirood			Asalem			
		2000	1400	600	1400	900	1900	1400	900	2000	1200	600	1900	1200	600	
Px–A	*A*	0.125	0.146	0.217	0.217	0.188	0.188	0.149	0.163	0.219	0.319	0.292	0.125	0.133	0.111	
	B	0.875	0.854	0.783	0.783	0.813	0.813	0.851	0.837	0.781	0.681	0.708	0.875	0.867	0.889	0
Px–B	*A*	0.448	0.885	0.840	0.811	0.542	0.826	0.822	0.848	0.844	0.717	0.789	0.813	0.615	0.670	
	B	0.531	0.115	0.160	0.189	0.417	0.174	0.178	0.152	0.156	0.223	0.211	0.187	0.385	0.330	
	C	0.021	0.000	0.000	0.000	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0
Lap–A	*A*	0.000	0.000	0.000	0.042	0.010	0.000	0.000	0.000	0.021	0.000	0.000	0.042	0.031	0.000	
	B	0.969	0.844	0.958	0.854	0.844	0.927	0.948	0.927	0.823	0.915	0.917	0.854	0.875	0.854	
	C	0.031	0.156	0.042	0.104	0.125	0.073	0.052	0.073	0.156	0.085	0.073	0.104	0.083	0.146	
	D	0.000	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.010	0.000	0
Lap–B	*A*	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.010	0.000	0.000	0.021	0.000	0.000	
	B	0.906	0.896	0.896	0.646	0.813	0.913	0.854	0.865	0.792	0.628	0.729	0.771	0.802	0.771	
	C	0.083	0.104	0.104	0.354	0.177	0.087	0.146	0.135	0.198	0.372	0.260	0.198	0.198	0.229	
	D	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0
Got–A	*A*	0.000	0.000	0.000	0.000	0.021	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	B	0.826	0.844	0.906	0.857	0.792	0.813	0.702	0.865	0.936	0.698	0.750	0.938	0.875	0.865	
	C	0.174	0.146	0.094	0.149	0.188	0.188	0.287	0.125	0.064	0.302	0.229	0.063	0.125	0.135	
	D	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.021	0.000	0.000	0.000	0
Got–B	*A'*	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	A	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.000	0.000	0.000	0.010	0.010	0.010	0.021	
	B	1.000	0.979	1.000	0.979	1.000	0.969	1.000	1.000	1.000	1.000	0.979	0.990	0.990	0.979	
	C	0.000	0.000	0.000	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.02
Mnr–A	*A*	0.344	0.167	0.174	0.170	0.208	0.198	0.125	0.208	0.198	0.177	0.229	0.250	0.333	0.293	
	B	0.656	0.833	0.826	0.830	0.781	0.802	0.875	0.792	0.802	0.823	0.771	0.750	0.667	0.707	
	C	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.02
Idh–A	*A*	0.000	0.010	0.010	0.021	0.042	0.052	0.010	0.042	0.010	0.000	0.031	0.000	0.052	0.010	
	B	1.000	0.990	0.990	0.979	0.948	0.938	0.990	0.958	0.990	1.000	0.969	1.000	0.948	0.990	
	C	0.000	0.000	0.000	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.03
Mdh–A	*B*	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	
	C	0.573	0.708	0.596	0.490	0.573	0.521	0.510	0.490	0.424	0.594	0.677	0.594	0.604	0.594	
	E	0.427	0.292	0.404	0.510	0.427	0.469	0.490	0.510	0.576	0.406	0.313	0.406	0.396	0.396	
	F	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0
Mdh–B	*A*	0.052	0.115	0.052	0.104	0.042	0.074	0.042	0.073	0.000	0.021	0.021	0.021	0.010	0.010	
	C	0.844	0.833	0.896	0.813	0.896	0.862	0.865	0.865	0.946	0.927	0.917	0.927	0.938	0.948	
	D	0.104	0.052	0.052	0.083	0.063	0.064	0.094	0.063	0.054	0.052	0.063	0.052	0.062	0.042	0
Mdh–C	*A*	0.010	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.021	0.010	0.010	0.000	
	B	0.990	0.990	0.990	1.000	1.000	1.000	1.000	1.000	1.000	0.990	0.979	0.990	0.990	1.000	0.915

equilibrium towards an over-representation of heterozygotes, although in the region Neka, where beechwoods have been exposed to silvicultural operations, a considerable surplus of homozygotes was observed. At the same time, the Neka 900 population displayed the highest levels of expected heterozygosity and the most significant differences between observed and expected heterozygosity. Only the Kheirood region showed a surplus of heterozygotes. In addition, the results indicated that among the beech populations, except for

Table 3. ***continued***

Loci		Population / Altitude														*P*-value
		Gorgan			Neka		Sangdeh			Kheirood			Asalem			
		2000	1400	600	1400	900	1900	1400	900	2000	1200	600	1900	1200	600	
Pgi–A	*A*	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	
	B	1.000	1.000	0.990	0.990	0.989	1.000	1.000	0.990	1.000	0.927	1.000	1.000	1.000	0.990	
	C	0.000	0.000	0.000	0.010	0.011	0.000	0.000	0.010	0.000	0.073	0.000	0.000	0.000	0.000	0
Pgi–B	*A'*	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.010	0.021	0.000	0.000	0.000	0.000	
	A	0.000	0.021	0.021	0.000	0.010	0.000	0.052	0.000	0.010	0.000	0.010	0.000	0.000	0.000	
	B	0.883	0.927	0.927	0.958	0.948	0.979	0.917	0.990	0.979	0.979	0.969	1.000	1.000	1.000	
	C	0.000	0.000	0.000	0.010	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
	D	0.115	0.052	0.052	0.031	0.021	0.021	0.021	0.010	0.000	0.000	0.021	0.000	0.000	0.000	0
Pgm–A	*A*	0.063	0.073	0.073	0.073	0.073	0.031	0.021	0.031	0.031	0.010	0.010	0.010	0.031	0.010	
	B	0.938	0.917	0.917	0.927	0.927	0.969	0.979	0.969	0.969	0.990	0.990	0.990	0.958	0.990	
	C	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.06
Skdh–A	*A*	0.000	0.000	0.000	0.010	0.011	0.010	0.000	0.000	0.010	0.000	0.000	0.000	0.031	0.000	0
	B	0.979	0.969	0.969	0.885	0.894	0.938	0.948	0.958	0.896	0.948	1.000	0.948	0.906	0.659	
	C	0.021	0.021	0.021	0.042	0.032	0.042	0.000	0.031	0.073	0.031	0.000	0.031	0.052	0.261	
	D	0.000	0.010	0.010	0.063	0.064	0.010	0.052	0.010	0.010	0.021	0.000	0.021	0.010	0.080	
6Pgd–AA		0.074	0.052	0.052	0.000	0.031	0.033	0.010	0.011	0.000	0.021	0.031	0.021	0.043	0.021	
	B	0.511	0.479	0.479	0.500	0.563	0.598	0.552	0.660	0.593	0.564	0.510	0.564	0.424	0.646	
	C	0.415	0.458	0.458	0.500	0.406	0.370	0.438	0.330	0.384	0.415	0.427	0.415	0.489	0.333	
	D	0.000	0.010	0.010	0.000	0.000	0.000	0.000	0.000	0.021	0.000	0.031	0.044	0.000	0.000	0

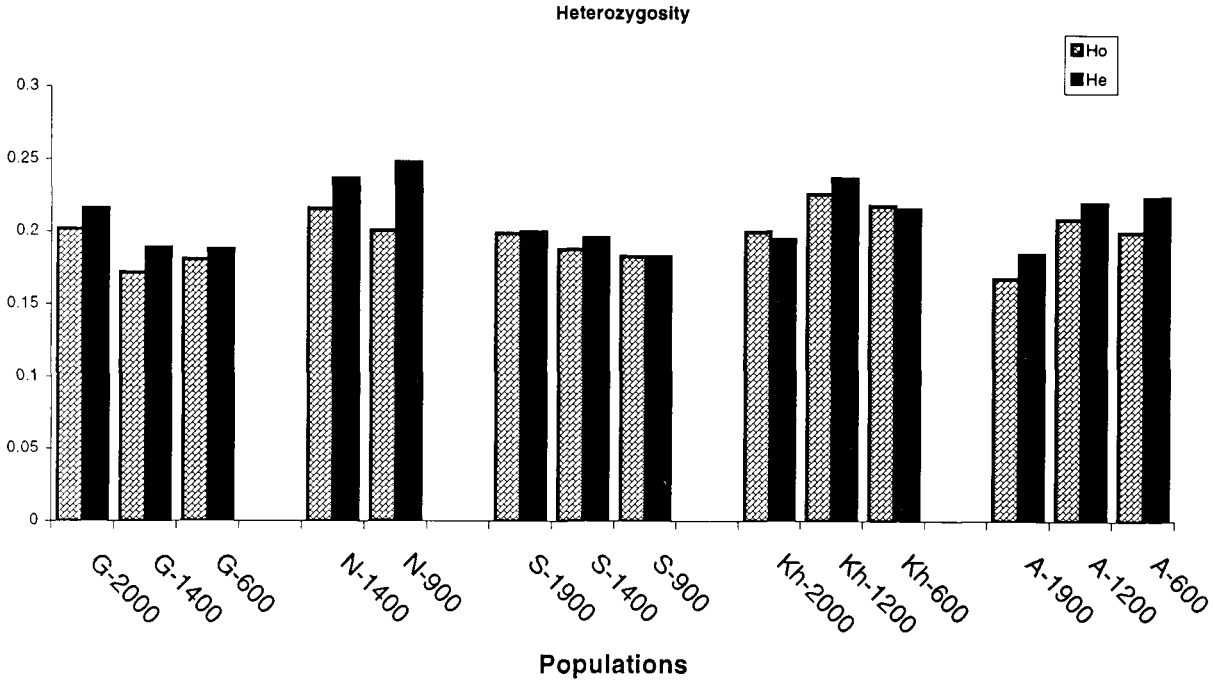

Figure 2. Geographic distribution of mean observed (H_o) and Hardy-Weinberg expected (H_e) heterozygosities according to populations.

Table 4. Characteristics of the genetic variation in the investigated *Fagus orientalis* populations.

Population	N	n_t	n_a	n_e	n_s	n_r	P^*	P^{**}	P^{***}	H_o	H_e
G-2000	47.8 (0.1)	33	2.1 (0.2)	1.37 (0.4)	3	2	62.5	81.3	81.3	0.202 (0.051)	0.216 (0.050)
G-1400	48.0 (0.0)	39	2.4 (0.2)	1.28 (0.3)	7	4	62.5	93.8	93.8	0.172 (0.034)	0.189 (0.039)
G-600	47.6 (0.2)	37	2.3 (0.2)	1.29 (0.4)	7	4	62.5	93.8	93.8	0.181 (0.042)	0.188 (0.042)
N-1400	47.6 (0.2)	36	2.3 (0.2)	1.37 (0.3)	71	51	68.8	93.8	93.8	0.216 (0.041)	0.237 (0.043)
N-900	47.8 (0.1)	43	2.7 (0.2)	1.39 (0.4)	5	1	81.3	87.5	87.5	0.201 (0.038)	0.248 (0.045)
S-1900	47.2 (0.5)	36	2.3 (0.2)	1.31 (0.3)	8	4	68.8	87.5	87.5	0.199 (0.042)	0.200 (0.041)
S-1400	47.7 (0.2)	34	2.1 (0.2)	1.01 (0.3)	7	3	68.8	81.3	81.3	0.188 (0.045)	0.196 (0.044)
S-900	47.7 (0.2)	34	2.1 (0.2)	1.28 (0.3)	7	2	56.3	87.5	87.5	0.183 (0.041)	0.183 (0.040)
K-200	47.1 (0.4)	36	2.2 (0.2)	1.3 (0.3)	9	6	62.5	81.3	81.3	0.200 (0.051)	0.195 (0.044)
K-1200	47.6 (0.2)	32	2.0 (0.1)	1.39 (0.4)	5	2	62.5	87.5	87.5	0.226 (0.051)	0.237 (0.050)
K-600	47.8 (0.2)	39	2.4 (0.2)	1.36 (0.4)	14	8	56.3	87.5	87.5	0.218 (0.055)	0.216 (0.048)
A-1900	47.9 (0.1)	35	2.2 (0.2)	1.29 (0.3)	10	5	62.5	81.3	81.3	0.168 (0.039)	0.185 (0.045)
A-1200	47.7 (0.2)	37	2.3 (0.2)	1.37 (0.4)	9	4	68.8	87.5	87.5	0.209 (0.048)	0.220 (0.048)
A-600	46.8 (0.8)	34	2.1 (0.2)	1.37 (0.4)	8	3	62.5	87.5	87.5	0.200 (0.048)	0.224 (0.050)

N – mean sample size per locus; n_t – observed number of alleles; n_a – mean number of alleles per locus; n_e– effective number of alleles; n_s – number of area specific alleles; number of rare alleles; H_o – mean observed heterozygosity; H_e – mean expected heterozygosity; P^* – percentage of polymorphic loci (5 % criterion); P^{**} – percentage of polymorphic loci (1 % criterion); P^{***} – percentage of polymorphic loci (no criterion)

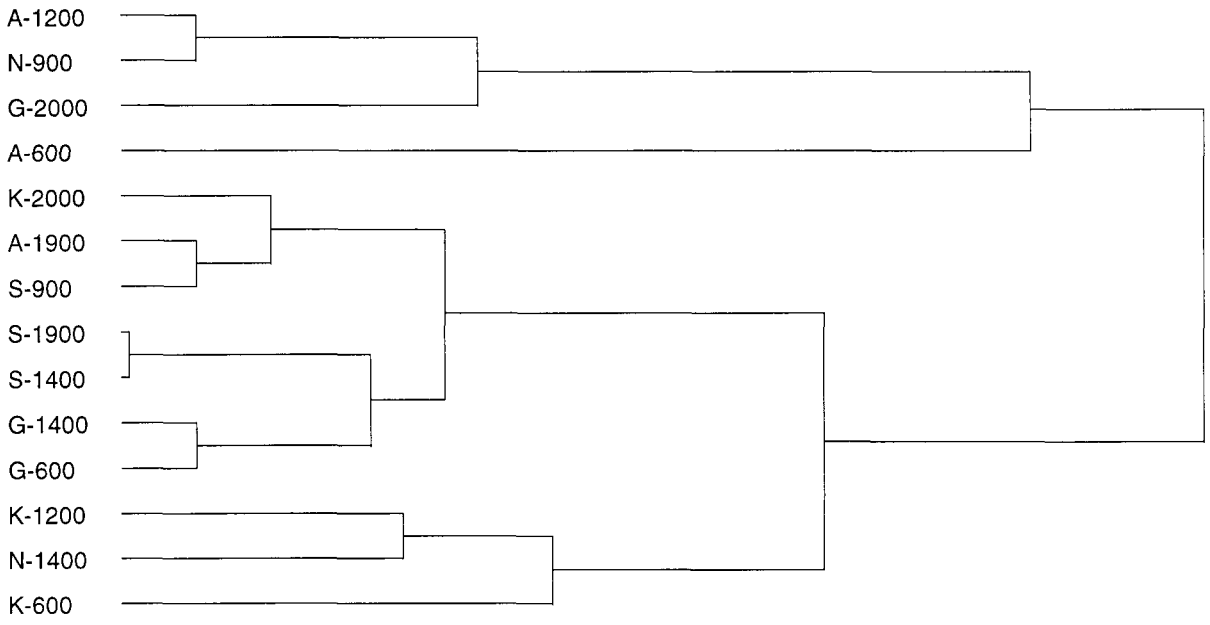

Figure 3. Dendrogram of genetic distances between the 14 populations obtained with UPGMA method.

Neka, the number of loci showing heterozygote excess (with negative values) is equal or greater than the number of loci with a deficit (with positive values), although, F_{IS} values showed a slight heterozygote deficit.

The single-locus F_{ST} values indicate how individual loci contribute to the genetic differentiation. In general, the most differentiating locus seems to be *Px-B*, followed by *Skdh-A* and *Lap-B*. Generally, low values exhibit the loci with low degrees of polymorphism

Table 5. F-statistics estimated values for individual regions.

Loci	Region								
	Gorgan			Neka			Sangdeh		
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
Px–A	0.056	0.067	0.0115	–0.056	–0.055	0.0014	0.208	0.209	0.0018
Px–B	0.425	0.536	0.1826	0.560	0.497	0.0701	0.269	0.269	0.0009
Lap–A	–0.134	–0.083	0.0455	0.174	0.176	0.0018	–0.072	–0.071	0.0016
Lap–B	0.044	0.045	0.0008	0.184	0.214	0.0372	–0.082	–0.076	0.0060
Got–A	0.179	0.187	0.0095	0.145	0.149	0.0046	–0.110	–0.080	0.0275
Got–B	–0.021	–0.007	0.0140	–0.021	–0.011	0.0105	–0.032	–0.011	0.0211
Mnr–A	–0.015	0.023	0.0380	0.030	0.033	0.0031	–0.082	–0.072	0.0094
Idh–A	–0.011	–0.007	0.0035	0.407	0.410	0.0054	–0.048	–0.036	0.0108
Mdh–A	–0.015	–0.0002	0.0150	0.073	0.080	0.0070	–0.050	–0.049	0.0010
Mdh–B	–0.019	–0.010	0.0087	–0.014	–0.003	0.0109	0.112	0.114	0.0018
Mdh–C	–0.011	–0.011	0.0000	–	–	0.0000	–	–	0.0000
Pgi–A	–0.011	–0.004	0.0070	–0.011	–0.011	0.0000	–0.011	–0.004	0.0070
Pgi–B	0.002	–0.013	0.0106	–0.036	–0.035	0.0012	0.044	0.066	0.0227
Pgm–A	–0.070	–0.051	0.0173	0.075	0.076	0.0000	–0.030	–0.029	0.0009
Skdh–A	–0.029	–0.027	0.0020	0.225	0.225	0.0002	–0.047	–0.039	0.0079
6Pgd–A	0.012	0.015	0.0029	0.017	0.024	0.0067	–0.024	–0.024	0.0082
Mean	0.054	0.01	0.0351	0.123	0.132	0.0156	0.016	0.016	0.007

Loci	Region						Whole area		
	Kheirud			Asalem					
	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}	F_{IS}	F_{IT}	F_{ST}
Px–A	–0.147	–0.137	0.0090	0.163	0.164	0.0008	0.0273	0.0509	0.0243
Px–B	0.302	0.306	0.0055	0.106	0.136	0.0033	0.2992	0.3557	0.0807
Lap–A	0.004	0.017	0.0164	0.148	0.152	0.0045	0.0453	0.0653	0.0209
Lap–B	0.247	0.265	0.0239	0.210	0.218	0.0016	0.1510	0.1931	0.0496
Got–A	–0.061	0.005	0.0623	–0.060	–0.049	0.0108	0.0050	0.0421	0.0372
Got–B	–0.016	–0.005	0.0105	–0.016	–0.014	0.0018	–0.0213	–0.0071	0.0139
Mnr–A	0.091	0.093	0.0028	–0.079	–0.073	0.0056	–0.0165	0.0063	0.0225
Idh–A	–0.027	–0.014	0.0123	–0.047	–0.0213	0.0248	0.0639	0.0808	0.0180
Mdh–A	–0.168	–0.115	0.0451	–0.005	–0.005	0.0001	–0.0365	–0.0172	0.0222
Mdh–B	0.707	0.083	0.0129	0.177	0.178	0.0018	0.0545	0.0735	0.0201
Mdh–C	–0.018	0.011	0.0070	–0.011	–0.007	0.0035	–0.0132	–0.0060	0.0071
Pgi–A	–0.079	–0.025	0.0498	–0.011	–0.004	0.0070	–0.0491	–0.0078	0.0394
Pgi–B	–0.021	–0.018	0.0035	–	–	0.0000	0.0011	0.0319	0.0308
Pgm–A	–0.025	–0.021	0.0035	–0.027	–0.018	0.0082	–0.0114	0.0060	0.0172
Skdh–A	0.144	0.193	0.0580	0.055	0.149	0.0994	0.0870	0.1542	0.0736
6Pgd–A	–0.216	–0.205	0.0087	0.123	0.145	0.0244	–0.0216	–0.0065	0.0148
Mean	–0.007	0.023	0.024	0.072	0.089	0.0185	0.0468	0.079	0.0337

(*Mdh-C*), but there are apparently also polymorphic loci like *6Pgd-A* with almost equal distributions of alleles over the investigated populations. The Gorgan and Sangdeh populations were the most and the least differentiated with F_{ST} values of 0.035 and 0.007, respectively.

A dendrogram (Fig. 3) constructed using the UPGMA clustering technique (SNEATH & SOKAL 1973) showed similar geographic pattern of differentiation. The geographical patterns of genetic differentiation as revealed by genetic distances are not unequivocal, and no grouping of populations due to their geographical origin can be identified. There are four identified clusters in the dendrogram. Apart from some

exceptions, populations from the same regions are not located in a same cluster. The population Asalem 600 showed peculiar characteristics, and proved to be clearly separated from all the other populations. This population is located at the lowest altitude and on the western limit of the distribution range in Alborz, and contains relatively younger trees than the other populations, due to severe exploitation.

DISCUSSION

The genetic variability of Oriental beech in Iran seems to be structured in a pattern comparable with that of other forest tree species with similar life-history traits (widesperad, wind-pollinated, allogamous and autocompatible). Average expected heterozygosity estimates ranged from 18.3 % to 24.8 % with a mean of 19.1 % a value not too far from average heterozygosities reported for other members of the same family (18.7 % for *Quercus macrocarpa* and 20.4 % for *Quercus gabbelii* (SCHNABEL & HAMRICK 1990); 24.0 % for *Castanea sativa* (VILLANI *et al.* 1991) and approximately 21 % for *Quercus* species cited in MÜLLER-STARCK (1991)], or for other European members of the genus *Fagus* (16.4 % to 34.6 % for *Fagus sylvatica* L. (reviewed in PAULE & GÖMÖRY 1997), 22.8 % to 28.2 % for *Fagus moesiaca* (GÖMÖRY *et al.* 1999; HAZLER *et al.* 1997), 25.8 % to 34.7 % for *Fagus taurica* (GÖMÖRY *et al.* 1998)). Comparison with data from literature for the same species is difficult due to differences in the geographical scale considered. GÖMÖRY *et al.* (1998, 1999) reported values between 25.0 % and 30.6 % (for Oriental beech) but in different geographical locations.

GREGORIUS (1978) suggested that the best measure of genetic diversity is the effective number of alleles per locus, n_e, which is the harmonic mean of the values for individual loci (CROW & KIMURA 1970). In our study, n_e values were not significantly different and except for Sangdeh 1400 population, they fluctuated within a very narrow range. It appears that there is not a genetic univocal criterion for the choice of the populations most suitable for production of high quality seeds, and other genetic aspects may play an important role.

The excess of homozygotes found in almost all studied populations (mean F_{IS} = 0.046 (table 5)) is similar to an equivalent estimate for French beech populations (F_{IS} = 0.04 by MERZEAU *et al.* 1994), but is lower than that for the Italian populations (F_{IS} = 0.117 by LEONARDI & MENOZZI 1995). A lack of heterozygotes is often reported among embryos of the more intensely investigated coniferous species (YAZDANI 1985; MUONA *et al.* 1987) but not in later life stages. These differences are usually considered as an effect of selection against selfed individuals (SORENSEN 1969). CUGUEN *et al.* (1988) investigated the lack of heterozygotes in three loci found in 250 European stands. Due to low selfing, they suggest as a complementary explanation the spatial structure of genetic variability, probably generated by reproduction occurring between neighbors. In fact the "isolation by distance" hypothesis has been proposed as the most important cause of heterozygote deficit in beech (COMPS *et al.* 1990). This situation is likely very similar with Oriental beech, which form stands of similar density, and have the same pollen dispersal mechanisms. However, this topic cannot be settled with the information from the present study and deserves further investigation.

We only can speculate about the causes of the excess of observed heterozygosity in Kheirood. Selection against inbred individuals (LEDIG *et al.* 1983) or additional selection against homozygotes as the heterogeneity of the environment increases (MÜLLER-STARCK 1993) may be possible explanations, but experimental evidence supporting these hypotheses is lacking.

Genetic differentiation between Iranian beech populations is low with almost 96 % of the variability found within populations. According to the review by PAULE & GÖMÖRY (1997), the G_{ST} (F_{ST}) estimates for beechwoods (*Fagus sylvatica* L.) in different regions of Europe ranged from 0.006 (in Denmark) to 0.053 (in Croatia). The lack of a clear geographical structure of the genetic variability of beech in Iran is not surprising if we consider the low level of inter-population differentiation (F_{ST} is approximately 4 %). Also, relatively few significant associations between single allele frequencies and altitude were found. Our data indicate that there is an important gene flow among populations, thus the studied beech-woods share almost identical gene pools.

Although the associations between allelic frequencies at some loci and environmental conditions showing possible adaptive role of those alleles were reported in the literature (THIÉBAUT *et al.* 1982; COMPS *et al.* 1990, 1991; GÖMÖRY *et al.* 1992; BELLETTI & LANTERI 1996), no significant correlation was found between allelic frequencies and altitudinal trends in our material.

A lack of differentiation between populations is typical for species like beech and conifers, characterized by large and high-density stands, wide pollen dispersal, and a high outcrossing rate (BELLETTI & LANTERI 1996). Despite the fact that the present range of the beech in the Hyrcanian zone originates during the

Tertiary, suggesting sufficient time to develop differentiation, it does not seem to be the case. On the other hand, the beech population in the Hyrcanian zone was not directly affected by glaciation, so that probably quite large unfragmented populations were preserved during the Pleistocene, so that an important gene flow apparently is not only a recent phenomenon, but also historically it efficiently hampered a differentiation.

Despite a general lack of differentiation, one population appeared quite divergent (Asalem 600). Human impact is suspected to be the cause. The human impacts may result from directly altering the forest through fragmentation, intensive exploitation, or importing trees from other regions, or by changing the direction of selection due to pollution or other environmental changes (SAVOLAINEN & KÄRKKÄINEN 1992).

ACKNOWLEDGMENTS

Thanks are due to Drs. Monika Konnert, Ervin Hussendörfer and Bernard Thiébaut for their comments on the manuscript. Presented paper has been partly done within the PhD thesis of the senior author and within the project 1/7056/20 of the Slovak Grant Agency for Science (VEGA). Thanks are also due to Daren Carlson for correcting English.

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